

Genomics at the Origins of Agriculture, Part One

GEORGE J. ARMELAGOS AND KRISTIN N. HARPER

The causes and consequences of the Neolithic revolution represent a fundamental problem for anthropological inquiry. Traditional archeological evidence, ethnobotanical remains, artifacts, and settlement patterns have been used to infer the transition from foraging to primary food production. Recent advances in genomics (the study of the sequence, structure, and function of the genome) has enhanced our understanding of the process of plant and animal domestication, revealed the impact that adaptation to agriculture has had on human biology, and provided clues to the pathogens and parasites thought to have emerged during the Neolithic. Genomic analysis provides insights into the complexity of the process of domestication that may not be apparent from the physical remains of bones and seeds, and allows us to measure the impact that the shift to primary food production had on the human genome. Questions related to the location and the process of domestication can be answered more fully by analyzing the genomes of the plants and animals brought under human control. The spread of the agriculture package (plants, animals, and technology) by cultural diffusion or demic expansion can also be investigated through this approach. Whether dissemination by farmers or the diffusion of farming knowledge and technology was the source of the Neolithic expansion, this process should be revealed by the pattern of genetic and linguistic diversity and language found from centers of agricultural Neolithic development. In addition, a number of pathogens that were previously thought to have been transmitted from domesticated species to human now appear to have been present in foragers long before the agricultural revolution took place. Furthermore, we now have evidence that humans were the source of the transmission of some parasites to domesticated animals. For all of these reasons, data from genomic studies are providing a more complete understanding of the origins of agriculture, a critical hallmark in human evolution.

Determining the origins of agriculture is archeology's most challenging puzzle. The development and the spread¹ of agriculture represents a major shift in the adaptation of human populations^{2–4} that is the foundation of the world as we know it. The impact of agricultural subsistence on the evolution of culture has been well established.^{4,5} Food surpluses, craft specialization, art, religious hierarchies, writing, social hierarchies, urbanization,

and the origin of the state have all been driven by agricultural development.

There are those who claim that agriculture represents a maladaptation,⁶ metaphorically the human "childhood's end."⁷ Jared Diamond⁸ described it as "the worst mistake in the history of the human race." Criticisms of agriculture also come from some unexpected sources. In the Indian epic *Ramayana*,⁹ agriculture is seen as a curse on mankind¹⁰:

In the Golden Age, agriculture was abomination. In the Silver Age, impiety appeared in the form of the agriculture. In the Golden Age, people lived on fruits and roots that were obtained without any labour. For the existence of sin in the form of cultivation, the lifespan of people became shortened.

Even the Bible (1996 New Living Translation, Tyndale Charitable Trust) (Genesis 3:17–19) despairingly describes agriculture as the penalty for original sin. Humans were driven from the Garden of Eden where all their needs were being met because of that first moral transgression, and were ordained to toil the weed-filled land forever when God decreed:

I have placed a curse on the ground. All your life you will struggle to scratch a living from it. It will grow thorns and thistles for you, though you will eat of its grains. All your life you will sweat to produce food, until your dying day. Then you will return to the ground from which you came. For you were made from dust, and to the dust you will return.

Notwithstanding these criticisms, agriculture provided the lever for the advance that characterizes human civilization.¹¹ While the adverse biological and cultural consequences of agriculture have been documented,^{12,13} we would hardly be engaged in this discussion without it.

While we do not expect that these criticisms will convince many of us to return to a life of hunter-gatherers, it does raise the question as to why *Homo sapiens* adopted agriculture as a means of subsistence in the first place. We have become such "Neolithic chauvinists" that to even raise the question seems misguided. For most students of human evolution, it seems incredible that *Homo sapiens* took so long to "discover" agriculture. As we will show, there were and still are biological and social costs to foragers as they shifted to primary food production. There is also evidence suggesting that many foragers in Europe resisted the spread and use of the Neolithic technology as it moved into the continent.^{14–17}

Delimiting the process of domesti-

George J. Armelagos and Kristin N. Harper are at the Department of Anthropology and the Program in Population Biology, Ecology and Evolution, Emory University, Atlanta, GA 30312. E-mail: antaga@learnlink.emory.edu.

cation has traditionally relied on the recovery of artifacts associated with food processing.^{18,19} These have included the remains of plants, such as seeds, charred fragments, undifferentiated tissue,²⁰ pollen,²¹ phytoliths,^{22,23} and lipids found in pottery shards.²⁴ In addition, animal bones showing morphological changes related to domestication,²⁵ demographic patterns of culling of animals,²⁶ stable isotopes reflecting dietary transitions,²⁷ and changes in settlement patterns²⁸ have all been used to infer the shift to primary food production. Now, recent technological breakthroughs in plant and animal genetics have led to what Bruce Smith²⁹ described as the “consilience of biological and archaeological approaches,” in which the genetic fingerprints and geographic distribution of domesticates and their progenitors have been integrated more fully into traditional archeological analysis. Improved radiocarbon age determination using the accelerator mass spectrometer (AMS), which directly measures ¹⁴C isotopes, has made dating the domestication of plants and animal more precise. Since only minuscule amounts (as small as 100 micrograms) are required for analysis, even a single seed can be dated.

In this review, we will examine the role that advances in genomics have played in improving our understanding of the basis for the Neolithic revolution. More specifically, we will examine how *Homo sapiens* transformed the genetic makeup of plants and animals, and the subsequent feedback that these economic changes had on our species' genome. Renfrew^{30,31} is so positive about the profound advances made in genomics that he has proposed a new discipline called archaeogenetics. Archaeogenetics uses molecular genetics to examine issues related to population prehistory, and has been applied to questions of agricultural origin and expansion.³²

BACKGROUND: THE ORIGINS OF AGRICULTURE

For thousands of millennia, hominids existed as foragers who, it has been suggested, struggled to eke out an existence by gathering and hunting in marginal environments. Why hominids remained in a state of existence that Thomas Hobbes³³ in *Leviathan*

described as “solitary, poor, nasty, brutish and short” remains a matter of debate. Some early archeologists took an almost Hobbesian view, asserting that the Paleolithic struggle for existence was so difficult that foragers had little time to amass the necessary knowledge for domesticating plants and animals. However, Braidwood³⁴ argued that the accumulation of biological and cultural knowledge would have reached a level at which agriculture would have become inevitable. In another scenario, the “discovery” of agriculture was a purposeful action that would have been made by any

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sensible human once the connection between the seed and plant was made. We now know that foragers had an acute awareness of plants in their ecosystems,³⁵ and that knowledge was not the limiting factor.

The explanations for the origin of agriculture traditionally rely on describing ecological factors that drove the change in subsistence strategy. However, some archeologists have argued that social factors were the key to the shift to primary food production.^{36,37} For example, Brian Hayden³⁶ has suggested that the origin of domestication was triggered by social factors center-

ing around competitive feasting. All of the domesticated animals and most of the domesticated plants were originally prestigious markers of wealth, and were used primarily in the context of competitive feasting. Eventually, the intensified production of luxury food would have led to their use as staples in everyday life.

It has been suggested that grains would have been initially collected for fermentation. This idea was pursued in an “in-print” symposium³⁸ organized by Braidwood, in which participants discussed the possibility that the earliest collection of grain was for making fermented drinks.

Explanations that focus on environmental changes occurring at the end of the Pleistocene as the impetus for the origin of agriculture remain the most vigorously debated. V. Gordon Childe³⁹ was one of the first to suggest that desiccation at the end of the Pleistocene was the driving force for the Neolithic revolution. As a consequence of this desiccation, during the Holocene plants, animals, and humans were forced into areas where permanent sources of water remained; these “oases” became refuges for them. Childe^{40,41} argued that the “propinquity” of plants, animals, and humans in these “oases” made domestication inevitable, since the human proximity to the plants and animals would have resulted in more intensive interaction and a greater understanding of the potential of plants and animals as food sources.

Braidwood tested and rejected Childe's hypothesis because he did not find the dramatic environmental changes that would have forced people into refuge areas.⁴² Instead, he found that the “hilly flanks of the fertile crescent” located in the Zagros Mountains were an ideal location for the earliest plant domestication. The presence of many potential domesticates, Braidwood believed, would have made it an ideal location for agriculture's beginnings.

The study of the location of regions where domesticated plants were found with their wild relatives has a long history. In 1927, N. I. Vavilov, a Russian botanist and plant geographer, began an intensive research program to survey and collect the plants found in areas that represented foci of plant domestication. He suggested that domesticated plants would be

found in areas that show the greatest plant diversity.⁴³ The concept of domestication centers was later replaced with more complex models.^{44,45} Harlan⁴⁴ argued that each of these areas, centers and noncenters, had to be dealt with as unique situation that had its own process for domestication. Vavilov's and Harlan's research has borne fruit with genetic fingerprinting of domesticates and their progenitors. In fact, genomic analyses have provided evidence that forces us to consider a much more complex pattern of domestication in the proposed agricultural centers and to consider domestication in areas that were thought to be devoid of cultigens.

It is now clear that the process of domestication began earlier than we had previously thought. This evidence lends support to the ecological equilibrium models proposed by Lewis R. Binford⁴⁶ and Kent Flannery^{47,48} to explain the shift from foraging to primary food production. In this sense, the Neolithic transformation was an extended process that took place over tens of thousands of years, belying the notion of rapid change that usually characterizes a revolution.

What were the forces that initiated the change to agriculture? Lewis R. Binford⁴⁶ provided the seminal model for agricultural development that has influenced a generation of archeologists. Binford proposed an equilibrium model in which changes in population density or the environment would result in systemic reequilibrating of the cultural system. Changes in climate and other factors such as increased proficiency in hunting led to a decline in the availability of large mammals. Populations were thus forced to rely on less desirable resources such as fish and fowl, which were exploited more intensely than they had been before.

The increase in population that resulted from this semi-sedentary existence and the extensive exploitation of resources resulted in these populations overreaching the environment's carrying capacity. If suitable habitats were available, the population overflow would "bud off" and expand into a new location. However, as the desirable habitats become occupied, budding populations would be forced to move into increasingly less desirable hinterlands. To survive in these less desirable habitats, populations would have had to rely

on intensive exploitation of less desirable plants and animals.

Binford found archeological evidence of more diversified and intense hunting, food processing, and food storage in these areas. Artifacts such as grinding stones and tools for harvesting plants were used as evidence of the increased exploitation of these resources. Recently, sophisticated microscopic analysis of stone wear and the recovery of identifiable food residues has supported Binford's assessment, suggesting that plant collecting and processing began at least 40,000 ago.¹⁹ These analyses indicate that the

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Paleolithic populations were exploiting woody and starchy plants, as well as birds and mammals. A variety of flint hafted tools were used to harvest wild plants. The recovery of projectile or thrusting spears for hunting animals¹⁹ points to the more intensive use of small animals. Bar-Yosef⁷ points out that earlier interpretation of these tools, that they were used for cutting reeds to be used to construct wall thatch and roofing is a hypothesis that remains to be tested. Given the new technology for analyzing plant residues on artifacts, this controversy can be resolved.

Flannery⁴⁷ expanded Binford's model with a more formal theoretical approach. He argued that Paleolithic gatherer-hunters in southwest Asia were primarily interested in small-to-medium-sized ungulates, and initially ignored the small mammals, bird, fish, tortoises and crabs.⁴⁹ However, these foragers were eventually forced to make an economic decision to broaden their dietary niche to include plants and animals that they had pre-

viously ignored. Flannery described this profound shift in adaptation as the "broad spectrum revolution" (BSR), and suggested that this shift became the stimulus for the eventual transformation to primary food production. Evidence of milling tools, an increase in the number of animal species recovered, and preserved plant remains were the benchmarks used to assess the impact of the BSR. Unfortunately, the archeological evidence derived from artifacts and animal remains was often ambiguous, and the BSR is thought by many to be an excellent theoretical model that we have no means of testing.

Recent research on late Paleolithic adaptation has demonstrated increasing support for the BSR,^{49,50} Stiner,⁵¹ Stiner and colleagues,^{52,53} and Munro⁵⁴ have provided strong archeological evidence of a dietary shift that is predicted by the BSR. Their work has revealed small and highly dispersed population pulses (increases) in the early Middle Paleolithic, and evidence of a major population spurt in the eastern Mediterranean before the end of the Middle Paleolithic.⁵² More significantly, later Upper and Epi-Paleolithic population pulses were also associated with a major shift in human subsistence strategy.

Tests of the BSR model that measured the species or genera found at a site failed to find evidence of a broadened dietary niche. Stiner⁵⁰ and Stiner, Munro, and Surovell⁵² moved beyond this taxonomic listing of animal species and, instead, used predator-prey models in their analysis. These models incorporated optimal foraging theory, life-history measures of the prey, and population ecology instead of taxonomic "signatures" of the recovered resources.⁵⁵ By grouping prey into slow-moving and easily collected (tortoise and shellfish) and fast-moving (rabbits and birds), they discovered a pattern of exploitation. Foragers hunting the faster-moving prey (the "original fast food," as one author commented) was a significant shift in subsistence strategy, and one that set the stage for agricultural development.

Small animals were an important dietary source throughout the Middle, Upper, and Epi-Paleolithic periods,⁵⁶ but the type of small prey changed dramatically during the last 200,000

years. Initially, in the Middle Paleolithic, “slow-growing,” “slow-moving” tortoises and marine mollusks were the dominant resources while, in the early Upper Paleolithic, agile and fast-maturing animals such as birds, hares, and rabbits became important dietary items. Hunting fast-moving prey would have required more intensive efforts, but the faster prey was a resource that could sustain intensive and long-term harvesting before undergoing extinction. Harvesting fast-moving prey gives a ten-fold greater exploitation before they are exhausted as a resource. Hockett and Haws^{57,58} and Haws and Hockett⁵⁹ object to the reliance on optimal foraging theory that is the foundation of the models proposed by Stiner and others. They suggest that the reliance of optimal foraging theory on energy capture provides a limited perspective and propose an alternative approach, which they describe as nutritional ecology. Nutritional ecology argues that a balanced diet, which results, by chance or choice, is essential for survival, and it trumps models that consider just energy capture. The implication of Haws and Hockett’s⁵⁹ model of nutritional ecology is that demographic pressures do not determine changes in diet; rather, changes in human population densities are dependent on diet. The Upper Paleolithic foragers consuming small nonterrestrial animals and increasing plant resources had a “selective advantage” over groups that were “optimally foraging” at a higher trophic level.⁵⁹ This interpretation provides an interesting alternative. However, models that deal with dietary breadth remain the predominant theoretical approach.

Munro⁵⁴ has tested this approach with an analysis of the Natufian during the Younger Dryas (13,000 to 11,600 cal bp) and its implication for the origin of agriculture. The unique Natufian adaptation is characterized by intensive exploitation of gazelle, which involves the extraction of edible products (meat, marrow, and grease).⁶⁰ Munro argues that the intensive foraging provided the agricultural know-how. The Late Natufians developed a more “cost-effective” demographic solution to the environmental stress brought on by the climatic changes of the Younger Dryas. She claims that there was a reduction in site occupa-

tion and an increase in population mobility.

The expansion of dietary breadth has also been observed in the use of plant remains. For example, Weiss and coworkers⁴⁹ excavation of the Paleolithic site (Ohalo II) in Israel dated to 23,000 ybp provided extensive ethnobotanical evidence of a major subsistence change, one that further supports the BSR. Wild wheat, wild barley, and small-grained grasses comprised a major portion of the diet, pushing the reliance on grains back at least 10,000 years earlier than previ-

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ously had been thought. Wild barley and wheat were ground into a starch and baked on oven-like hearths that were found at the site.⁶¹ In a span of 15,000 years, a preference for cereal grains became increasingly important for foragers. Seed exploitation eventually disappeared.

Harlan⁶² demonstrated that in three weeks a family could hand strip enough wild einkorn grain to last them a year. Hand stripping would have been limited to a short period in the annual cycle before the rachis shattered and dropped its seeds to the ground. Kislev, Weiss, and Hartmann⁶³ found that even if the wild grains ripened, shattered, and dropped to the ground, they still could be collected. From May to October, one person could collect an average of 0.337 kg of wild barley and wild wheat in an hour. This is enough grain to feed one person for half a day to a full day. Alternatively, the grains could be used for sowing seeds, which would facilitate the process of domestication. Regional analysis of an area that experienced the shift to primary food

production highlights the complexity of agricultural origins.⁶⁰

The models of Binford and Flannery consider population pressure as a key trigger for the shift in subsistence strategies. Following Ester Boserup,⁶⁴ a number of influential publications expanded on the role of population growth as the basis for subsistence change. Mark N. Cohen⁶⁵ argued that at the end of the Pleistocene human populations had expanded into all the habitable areas of the globe, forcing them to become more sedentary. Population pressure created a food crisis, as foraging has reached its carrying capacity and could not provide adequate subsistence. These findings echo those of Stiner and coworkers,⁵³ who demonstrated that specific population pulses were associated with expanding environmental exploitation.

Recently, Richerson, Boyd, and Bettinger⁶⁶ reviewed the environmental evidence and provocatively argue that agriculture was impossible during the Paleolithic but mandatory in the Neolithic. They claim that in the Pleistocene and even the late Pleistocene, when foragers had developed sophisticated knowledge of the environment, the glacial climate was too dry and the atmospheric CO₂ was too low and too variable to sustain agriculture. In the Western Mediterranean basin from 80,000 to 20,000 years ago, climatic changes were frequent and rapid, often in just a 1,000-year period.⁶⁷ Later, when climatological changes in the Holocene led to progressive subsistence intensification, agriculture became “mandatory.” This interpretation is supported by the independent development of agriculture in various areas of the globe.

ISSUE ONE: THE DOMESTICATES

Vavilov⁴³ proposed that the agricultural centers of origin and dispersal included Southeast Asia (coconut, rice, and sugar cane), China (Chinese cabbage, and soybeans), India (cucumber, eggplant, and pigeon peas), the Fertile Crescent (wheat, barley, oats, and figs), the Mediterranean (almonds, cabbage, and olives), Mexico and Central America (maize, tomato, squash, and pumpkin), and the Andes (peppers, potato, and rubber). The concept of agricultural centers was

based on the premise that each crop was only domesticated once in certain areas predisposed to domestication. Such centers have been explained as the byproduct of the rare confluence of various environmental factors favorable to agriculture, including climatic, geologic, biological, and cultural factors.⁶⁸ Over time, the theory of agricultural centers has been modified by Harlan,⁴⁴ but expounded by Diamond in *Science*,^{69,70} *Nature*,⁷¹ and the popular literature.⁷² However, it is clear that this theory will have to be modified under the weight of new genomic analyses.

Another question concerns the processes and tempo governing domestication. David Rindos^{73,74} proposed a version of Braidwood's propinquity theory and argued that the co-evolution of plants, animals, and humans would naturally have led to domestication. In the course of evolution, this long interrelationship would naturally have led to the domestication of plants, and those that were not domesticated would have been preyed upon or parasitized. Some plants responded to human harvesting by inducing humans to increase their production in competition with other plants.⁶⁶ Humans modified the environment to such an extent that the precursors of domesticated plants flourished in the disturbed environment.

Zohary^{45,75} suggested that some plants are intentionally domesticated and others unconsciously domesticated. He argued that unconscious selection played a major role in the domestication of cereal crops. Wild plants were transported to a very different human-modified environment in which new traits were automatically selected for, leading to a "domestication syndrome." The wild plants lost their wild-type seed dispersal devices (shattering spikes), resulting in more even and rapid seed germination, more erect plants, and an increase in seed numbers and size.

Plants

Vavilov⁴³ pinpointed domestication centers as regions that showed the greatest biological diversity. Today, some continue to use diversity, in particular genetic diversity, to identify the origin of a crop in such a man-

ner,⁷⁶ although this hypothesis has been criticized^{44,77,78} on the grounds that geographic gaps between crop progenitors and the first crops are common.⁷⁹ For example, wild sorghum shows the most diversity in Africa, but appears to have been domesticated in India, outside of its natural growing range. Likewise, rice has been domesticated along the Yangtze river, far north of the area in which the highest diversity of wild rice is found.⁸⁰ This pattern suggests that the lack of a wild plant in a particular area leads to its domestication since this is

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the only way that people would be able to exploit the species for food. Similarly, the first evidence of domesticated maize occurs in the Mexican highlands, while the progenitor of the crop resides in the lowlands.⁸¹

The study of maize employed a method of genetic analysis that is considered more reliable and is more widely used than the one described earlier, in which genetic markers in numerous samples of crops and possible wild progenitors are examined to determine where the wild plants most similar to the crop occur naturally. The number of domestication events that occurred can be determined by building phylogenetic trees, and examining the dates at which the different lineages of plants diverged from a common ancestor. A date far preceding the possibility of agriculture implies that multiple domestication events must have occurred. Support-

ing evidence for one or many domestication events may be drawn from the type of traits that enabled domestication,⁸² such as the number of genetic changes that are necessary to create a domesticated form and the likelihood that these changes would occur multiple times. Finally, models of domestication must be tested against the backdrop of archeological data.

Despite a bevy of genetic studies on the domestication of virtually every major extant crop species, little consensus exists regarding the identification of centers of domestication. Some consider that existing genetic studies⁸⁵ support the idea that the Fertile Crescent was the single center of many of our most important crops. These studies indicate that emmer wheat,⁸³ einkorn wheat,^{84,85} peas, and lentils^{45,82} have been taken into domestication only once or a very few times. Many believe that genetic and morphological evidence makes a strong case for barley having been domesticated multiple times,⁸⁶ with a hotly contested possible second origin in Morocco.^{87,88} Others contend that genetic evidence indicates the crop was only domesticated once,^{89,90} although that domestication has been placed in the Jordan Valley rather than southeastern Turkey.⁹¹ In addition, it has been proposed that single domestication events occurred outside the Fertile Crescent, with one example being domestication of the bunching onion in Northern China.⁹²

There is much evidence for multiple domestication events outside the Fertile Crescent. Grapevines appear to have been domesticated at least twice in the Mediterranean,⁹³ as do olives.⁹⁴ Based on genetic analysis, independent domestications of millet are proposed to have occurred in up to three different regions: China, Europe, and the Afghanistan-Lebanon area.^{95,96} However, an exception to this multiple-domestication rule may be maize, which has been reported to have been domesticated only once, in southern Mexico.⁸¹ Yet, upon examination of ancient maize DNA, researchers have observed a surprising amount of variation. This finding indicates that one domestication event encompassed a founder population with high variability, that the crop was domesticated once but continued to receive genes from wild plants, or that, in

fact, maize was domesticated multiple times.⁹⁷

In addition, it appears that at least a few locales need to be added to and subtracted from the list of putative agricultural centers. The analysis of banana samples collected throughout the world suggests that the fruit was first domesticated in the New Guinea-Philippines area.⁹⁸ There is increasing evidence that the New Guinea-Malaysia area is a significant source of domestication for many plant species.⁹⁹ In particular, breadfruit, sugar cane, taro, and the greater yam appear to have begun their trajectory as crops in this area.

Similarly, the lowlands of South America are emerging as an important center of crop domestication. Genetic analysis of cassava, or manioc, indicates that the crop emerged from wild progenitors in the southern Amazonian basin.^{100,101} Archeological¹⁰² and phytolith evidence¹⁰³ has also revealed the cultivation of crops such as the peanut, two species of chili pepper, and the jack bean. Such complexity has led some to propose that the concept of agricultural centers does not apply to this region.¹⁰³ This suggestion receives support from genetic analysis of the family including squash, pumpkins, and gourds, which indicates six independent domestication events in America,¹⁰⁴ and from evidence that the common bean may also have multiple origins in South America.¹⁰⁵

In contrast, some now believe that the crops of the Eastern United States were actually domesticated in Meso-America before making their way across the country. If so, then one center of domestication could be subtracted from Vasilov's list. However, genetic analyses of the crops in question do not seem to support this view. For example, although the oldest remains of fully domesticated sunflowers have been found in Mexico,¹⁰⁶ Mexican plants did not make a significant genetic contribution to the present crop.¹⁰⁷

In the final analysis, it seems that an overarching idea of centers of agriculture in which a number of crops were domesticated in a short time in a small place may have to be abandoned in favor of an understanding of crop domestication that treats each region differently. Some regions, such as North America, appear to have expe-

rienced numerous crop domestications in a short time within a small area. In the Near East, the area of domestication seems to have been larger, while in Mexico the span, in terms of both space and time, was much larger.²⁹ The idea that many crops may have undergone multiple domestications has also been supported by genetic analyses of crop samples, as well as studies of the traits linked to domestication. Many of those traits seem to be under the control of single genes that can change at a rapid tempo.¹⁰⁸

The exact number of independent plant domestications may actually be underestimated because of the types

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of analyses presently being performed. This has been suggested by studies using mathematical models of genetic variation stemming from multiple domestication events.¹⁰⁹ Although current studies suffer from limitations such as this, and the problems associated with sampling crop and wild plants, they are revolutionizing our understanding of the tempo and process of plant domestication.

Animals

The questions surrounding the domestication of animals parallel those addressed by genetic studies of plants. In short, we want to know whether animal domestication was a compli-

cated, multi-step process that rarely occurred or if, instead, it occurred in many places as humans felt similar needs. For a long time, it was believed that most, if not all, important domestic animals emerged from the Fertile Crescent, the same area that witnessed the domestication of so many important crops. Genetic analyses have been especially valuable in the study of animal domestication, as the use of morphological traits in determining whether archeological remains represent domestic or wild lines has been criticized.²⁶ Genetic studies have allowed us to delve into the origins of the domestic animals that accompanied agriculture, prompting a reexamination of the role of the Fertile Crescent as an unparalleled center of domestication and providing a better understanding of the process of domestication itself.

In studies of animal genetic diversity, multiple domestication events are proving to be the rule. Because of the ease with which goats are cared for, they have been considered good candidates as a species that has experienced multiple domestications.¹¹⁰ In fact, analysis of the mtDNAs of modern lines suggests that they arose from three separate domestication events.¹¹¹ One line is found all over the world, consistent with the domestication in the Fertile Crescent indicated by archeological remains.²⁵ Another line is limited to western Pakistan, consistent with a hypothesized origin of the cashmere lines,¹¹² while a final and very rare line has uncertain origins. A regional study examining goat lineages in India finds it difficult to reconcile even this three-domestication scenario with the data.¹¹³ In all cases, a single domestication event 10,000 years ago is unlikely to account for the high level of variation found in goat populations.

Similarly, analysis of mitochondrial and nuclear DNAs places the common ancestor of European and Asian pigs at 500,000 years ago. This estimated date is well before any reasonable date for domestication, and suggests that more than one event must have occurred.¹¹⁴ A previous study¹¹⁵ dated the divergence of the two types of pig at 2,000 years before present, a date that is consistent with one domestication event. However, this study has been criticized on the grounds that it



Figure 1. Molecular data suggest that domesticated cattle may have three separate origins.

did not consider interbreeding between the two types in modern times, a practice that would make the two groups more genetically similar than their original separation would imply. Sheep were also domesticated at least twice, with European and Asian lineages resulting from domestication of separate populations.¹¹⁶

In addition to demonstrating the commonness of multiple domestication events, genetic studies have revealed that areas outside of the Fertile Crescent played important roles in animal domestication. For example, it was believed that the humped cattle of India arose from selective breeding of humpless cattle, the hypothesized original type, which, based on archeological finds, was believed to have been domesticated in the Near East during the Neolithic.^{117–119} Studies of mtDNA¹²⁰ and microsatellite variation¹²¹ now indicate that cattle were domesticated at least twice, with Indian cattle arising separately from African and European cattle, which are more closely related (Fig. 1). Further studies of mtDNA suggest that African and European cattle may also have separate roots,¹²² with African lines emerging from indigenous cattle domesticated in a single region,¹²³ most likely the eastern Sahara,¹²³ and European lines hailing from the Near East.¹²⁴ It is further thought that Japanese Black cattle represent a third domestication of wild aurochs,¹²⁵ one

that involved local populations of this species (aurochs; *Bos primigenius*). Similarly, donkeys appear to have been domesticated at least twice, with these events occurring solely in Africa.¹²⁶

Genetic analyses are also providing insight into the processes at work in domestication. Archeological evidence suggests that horses may have first been domesticated on the Eurasian steppes, where they were an important food source. Surprisingly, the analysis of mtDNA in horses hints at a large number of domestications from wild populations over a wide, even unconstrained, geographical area.¹²⁷ However, an alternative interpretation of the data is that horses were domesticated only in one or a few areas from a highly diverse source population.¹²⁸ On the other hand, it has been discovered that the variation in mtDNA is not matched by that in the horse's Y-chromosome: astoundingly, a large-scale study of horses found that stallions from across the world share the same haplotypes.¹²⁹ The ability to trace female and male inheritance separately through analysis of mtDNA and the Y-chromosome, respectively, illustrates the important role that selective breeding has played since the origin of domestication. While mares were domesticated from a wide variety of populations, stallions must have been few in number and

taken from a very limited breeding stock.

Genetic studies also cast light on the relationship between morphological characteristics and the domestication of animal species. Domestication is often associated with selection for traits that render an animal productive, docile, and easy to care for. In the archeological record, such traits are used to determine when domesticated animals first appeared. However, the correlation between domestication and these morphological traits has been questioned since the recent discovery that archeological goat remains, which, based on morphological traits, appeared to have come from wild populations must actually have come from domesticated groups, based on the culling patterns present.²⁶

Genetic studies of dogs appear to suggest a similar discordance between domestication and the classic suite of "domesticated" traits. The unearthing of small canine remains in Israeli sites dating to 12,000 years ago¹³⁰ has led many to speculate that dogs were domesticated in the Near East around the time of agriculture's beginnings. However, two analyses of mtDNA variation in dogs have produced results indicating that modern canines are the result of multiple domestication events, although these analyses differ in the details of when and how these domestications took place. The first study suggests that the dog lineage originated 100,000 years ago, well before the anticipated date for such a domestication, based on other evidence for different animal and plant species.¹³¹ The authors pointed out that canine and hominid bones have been found in close proximity dating back to 400,000 years ago, and that dogs may have been domesticated at an early date wherever wolves and humans came together.¹³² If this is true, then dogs must not have acquired their present characteristics, the morphological traits visible to archeologists, until the onset of agriculture, when present-day selection pressures would have been instituted for the first time.

A second examination of mtDNA confirmed the occurrence of multiple domestication events, but suggested a more recent origin for the domestic dog (15,000 to 40,000 years ago).¹³³ This range of dates was more consistent with archeological evidence of

dog remains exhibiting domestic traits.^{134,135} In addition, the authors asserted that the domestication events were limited to East Asia, a view that would explain the morphological similarities between modern dogs and Chinese wolves.^{136,137} Ancient DNA studies tip the scales in favor of an origin significantly predating the first appearance of “domesticated” dog remains, indicating that Native American dogs originated from multiple lineages of Old World dogs.¹³⁸ This finding requires that domestication events were limited to Eurasian wolves and that dogs accompanied humans as they crossed the Bering Strait. It echoes the earlier caution concerning morphology and domestication status emerging from the study of goat domestication.

The timing of the domestication of the house cat (*Felis silvestris catus*) is not entirely resolved. There is clear archeological evidence that the cat was domesticated in Egypt by 2,000 years BCE. However, the purposeful burial of a cat with a human in Cyprus was recently uncovered at a 9,500-year-old site.¹³⁹ In addition, the genomic analysis of felid species has suggested a domestication date of about 7,000 years ago.¹⁴⁰ Regardless of the its exact timing, the domestication of cats was likely the result of encouraging them to share human settlement in villages to protect granaries from rodents.^{141,142} The changes in the domesticated cat made it easier to live with by making the animal smaller, with less complicated brains (decreased by 70%) and smaller adrenal glands that removed much of the alertness for which it had been selected by nature.^{143,144} The cat’s affiliative behavior toward people (rubbing and licking) has been suggested to be a preadaptation for domestication. However, Cameron-Beaumont, Lowe, and Bradshaw¹⁴⁵ found that affiliative behavior is patchily distributed among the smaller Felidae and is not associated with species closely related to *Felis silvestris catus*. Instead, they claim that the domestication of the cat was the “result of a specific set of human cultural events . . . rather than a unique tendency to tameness. . . .”¹⁴⁵

Genomic analysis demonstrates that multiple origins, or at least multiple domestication events, are the rule when considering the emergence of domestic animals. This high num-

ber of domestication events complicates our understanding of the spread of pastoralism. Consideration of the various lineages of the domesticates present today suggests that a single wave of farmer-pastoralists from the Fertile Crescent may have replaced European indigenous peoples. However, Africa and Asia seem to have possessed their own domestic centers, with domesticates that have endured until the present day. Therefore, replacement of these peoples does not seem likely.

Surprisingly, the analysis of mtDNA in horses hints at a large number of domestications from wild populations over a wide, even unconstrained, geographical area. However, an alternative interpretation of the data is that horses were domesticated only in one or a few areas from a highly diverse source population.

Implications of Plant and Animal Domestication for the Spread of Agriculture

It has been proposed that the presence of a large number of domestications indicates the spread of technology necessary for domestication, rather than the spread of domesticates themselves.¹²⁷ Other studies cite east-west gradients of cultivar genes in Europe as support for demic diffusion models of the spread of agriculture.¹⁴⁶ Still other studies suggest that the spread of a domesticated sheds little light on the movement of humans, citing the example of the potato, a crop that spread in the opposite direction from its cultivators. However, the trajectory of a domesticated does shed light on human trade.

The importance of location for predicting the genetic characteristics of cattle, in which it accounts for 85% of variation, and its relative insignificance in goats, in which it accounts for a mere 10% of variation, implies that goats have experienced a much greater amount of intercontinental trafficking, consistent with their smaller size and ease of transport.¹¹¹

Part Two will appear in the next issue.

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Forthcoming Articles

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