Documenting domestication: the intersection of genetics and archaeology

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Domestication, a process of increasing mutual dependence between human societies and the plant and animal populations they target, has long been an area of interest in genetics and archaeology. Geneticists seek out markers of domestication in the genomes of domesticated species, both past and present day. Archaeologists examine the archaeological record for complementary markers – evidence of the human behavior patterns that cause the genetic changes associated with domestication, and the morphological changes in target species that result from them. In this article, we summarize the recent advances in genetics and archaeology in documenting plant and animal domestication, and highlight several promising areas where the complementary perspectives of both disciplines provide reciprocal illumination.

Introduction

The past few decades have witnessed an increase in research on domestication in genetics and archaeology. New techniques for the identification of plant and animal remains, the application of accelerator mass spectrometer (AMS) radiocarbon dating and advances in microscopy have enhanced the ability of archaeologists to detect and date evidence for the initial domestication of plant and animal species. Improvements for extracting, amplifying and sequencing modern and ancient DNA (aDNA), and new methods of phylogenetic analysis have encouraged an expansion in genetic studies of crop and livestock domestication. The growing sophistication of approaches to documenting plant and animal domestication has, in turn, promoted specialization and a narrowing of research focus in both disciplines. This trend towards an increasingly tighter focus, however, has been accompanied by a reduction in productive communication, both between and within the fields of genetics and archaeology. Not only do archaeologists and geneticists tend to share their results and interpretations primarily within their own discipline, but they also, increasingly, limit their interaction to the community of researchers working on either the domestication of plants or the domestication of animals.

In an effort to counter this trend, we have recently compiled an edited volume of selected case studies that focus on central aspects of current research on plant and animal domestication from the perspectives of archaeology and genetics [1]. Here we highlight topical areas where the two disciplines complement each other, providing a more synthetic understanding of domestication as a general process of biological and cultural evolution.

Domestication as a process

Domestication is a unique form of mutualism that develops between a human population and a target plant or animal population, and has strong selective advantages for both partners. What sets it apart from other successful mutualistic relationships is the role of sustained human agency in the propagation and care of plants and animals within the anthropogenic context of domestication. Humans increase the genetic fitness of target populations by intervening in their life cycles and enabling them to increase in numbers and to expand their range and habitat far beyond that of their wild progenitors. Although domesticates might initially have played only a small part in the economies of societies that were still largely based on hunting and gathering, they did provide a buffer against environmental uncertainties and thus a more secure and predictable subsistence base, which, in turn, enabled human societies to grow in size and to expand into new, more-challenging environments.

Domestication is not an instantaneous event in which a wild plant or animal is suddenly transformed into a domesticate. Rather it is a cumulative process marked by changes on both sides of the mutualistic relationship, as both partner populations, over time, become increasingly interdependent. In addition, the domestication process does not invariably follow the same developmental trajectory but is differentially shaped by the particular biological and behavioral profiles of target species and by the cultural context of the human societies involved. To trace this process for different domesticate species and different human societies, it is necessary to determine which behavioral, genetic or morphological markers are appropriate for distinguishing different points along a particular mutualistic relationship as it develops. Recognizing markers that can be used in tracing the process of domestication in different target species and how they relate to the domestication process requires a range of

analytical approaches and diverse disciplinary perspectives in biology and archaeology.

Archaeological markers of domestication in plants and animals

Behavioral and morphological markers in the archaeological record that indicate the existence of a relationship of domestication between human societies and target species take a range of different forms. Behavioral markers of crop plant cultivation, for example, can include preserved field systems; water management projects such as canals or check dams; pollen and phytolith (opal silica bodies) profiles and other indications of forest clearance for field systems; an associated increased presence in human settlements of crop plants and their weedy companions; increased and improved plant food storage facilities; and the appearance or improvement of technology associated with field preparation (e.g. silica sheen on hoes) or plant processing. However, such categories of direct evidence for domestication often do not occur until after reliance on crop plants has been established, limiting their value as markers of either initial domestication or the initial introduction of a domesticate into an economy.

Morphological changes in target plant populations, by contrast, often can be strongly and directly linked to the earliest stages of plant domestication. Several scholars [2–9] identified a range of distinct morphological changes in seed crops that could be expected to result not from deliberate intentional selection for desirable traits by humans, but as the result of unconscious selection: '…selection resulting from human activities not involving a deliberate attempt to change the organism' [9]. These unintentional changes would result from a particular new set of human activities involving target species of plants – specifically, the sustained harvesting and planting of stored seed stock. When humans began to harvest, store and plant seeds over a sustained period, they inadvertently created a new and distinctive selective environment to which the target plant populations under management adapted through genetic and morphological change. Of the adaptive responses by target populations of seed propagated plants to the new human created environment, the most important, and most likely to be visible in the archaeological record are: (i) simultaneous ripening of seeds; (ii) compaction of seeds in highly visible terminal stalk-branch 'packages'; (iii) seed retention (loss of natural seed dispersal mechanisms); (iv) increase in seed size; and (v) simultaneous and rapid seed germination (loss of germination dormancy, reduction in seed coat thickness). Deliberate human selection for specific attributes in seed plants (e.g. larger fruit size, color changes, plant habit) also result in morphological changes that can often be observed in the archaeological record, but these invariably appear after evidence for automatic adaptive responses by the target populations.

By contrast, no clear morphological markers have yet been identified for unintentional selection during the initial stages of human intervention in the life cycle and management of root crops, often propagated by vegetative cloning. Therefore, efforts to document domestication of root crops in the archaeological record have focused on evidence for deliberate human selection, particularly the selection for larger subterranean organs and for starch types that can be more easily processed and prepared. The individual starch grains that form the underground organs produced by extant domesticated crop plants not only differ in terms of morphology, and often in size, from starch grains produced by related wild taxa but also frequently exhibit morphology that is diagnostic at the species level. Given the right archaeological context, careful field recovery and laboratory protocols, starch grains that have been preserved intact on the surface and in the cracks of grinding tools over long periods of time [10] can provide clear documentation of the processing of different wild and domesticated plant foods, including domesticated root crops grown in previously poorly documented low-latitude regions of the world.

Phytoliths can also provide direct micromorphological indications of plant use in low-latitude zones of poor plant preservation. These small pieces of 'glass' formed in the living cells of plants during their life span, for structural support and to deter predation, exhibit considerable morphological variation, are resistant to decay and can be recovered in substantial numbers from a range of archaeological contexts. Distinctive phytolith morphology can enable researchers not only to distinguish between different species [11] but also to differentiate between phytolith forms produced by domesticated crop plants and their wild progenitors, identifying when domesticates first appeared in the archaeological record.

In contrast to crop plants, selection on animals initially brought under human management is most often directed towards modification of behavior in the target species rather than towards morphological change. For example, both inadvertent and deliberate human efforts can select for increased tolerance of penning, sexual precocity and, above all, reduction of wariness and aggression [12,13]. Such selection for reduced aggression might be reflected indirectly by several secondary morphological traits commonly seen in domestic animals and sometimes observable in the archaeological record (e.g. piebald coats and lop ears, smaller brain size, a shortening of facial bones and resultant crowding and size reduction in teeth) [13–15]. Plastic or ecophenotypic (non-genetically driven) responses by animals to the new, sometimes impoverished, conditions associated with initial human management can also be recognized in the archaeological record, and can be used as early markers of herd management (e.g. bone pathologies from penning, dietary changes detectable by isotopic studies of animal bones and evidence of mass 'die-offs' from disease) [16–19]. Archaeologists also look for sudden changes in the abundance of animals or their appearance outside their presumed geographical range [20,21]. They can consider changes in human settlement patterns, the presence of corrals or other traces of animals in settlements (manure or hoof prints) or artifacts related to the exploitation of domestic animals (bits or milk churns) as markers of different stages of the process of animal domestication [22].

Deliberate human selection of breeding partners can also result in morphological changes. The incremental changes in the size and shape of horns in livestock animals

(e.g. sheep and goats) can be directly tied to a relaxation of selection for larger horns, which might represent a liability once they are no longer needed in competition for mates [23]. Other morphological changes can result from range expansion associated with domestication, as managed herds are introduced into new environments (either through a founder effect or through directed adaptation to new habitats). Deliberate human selection for desired traits (size, meat or milk yield and coat quality) can also be recognized in the archaeological record.

One broadly applicable marker of domestication in animals involves sex-specific demographic profiling of prey populations. Faunal assemblages resulting from human hunting differ from those resulting from managed herds. In most managed herds of domesticated livestock, young males are preferentially slaughtered, with only a few allowed to survive and join the breeding population, which comprises adult females of reproductive age. Females are slaughtered when they pass peak reproductive age. The resultant age and sex profile of a managed herd, characterized by an emphasis on young males and older females, is distinctive and different from any produced by human hunting, which reflects a strategy to maximize the return from the hunt (i.e. focusing on older and larger male animals). A new method for constructing sex-specific harvest profiles from animal bone assemblages combines size analysis to determine sex with long bone fusion to determine age [24,25]. When applied to directly-dated archaeological-bone assemblages from Iraq and Iran, this method has succeeded in detecting unmistakable evidence of herd management of goats (*Capra aegagrus*) > 1000 years before the appearance of any morphological markers of domestication for the species [26–28].

Genetic markers of domestication in plants and animals

Geneticists interested in domestication focus on genetic responses to the mutualistic relationship formed between the domestic species and humans. The biological differences between plants and animals have a significant role in the genetic study of domestication. Annual crops or those with short generation times evolve more rapidly, and therefore respond faster to the changing selective pressures under domestication, than do most long-lived animals and perennial or clonally-propagated crops (e.g. fruit trees or tuber crops such as potatoes). Another important difference in the biology of plants and animals with special relevance to the genetic study of domestication is the prevalence of polyploidy in crop plants. Moreover, the possibility of interspecific hybridization is rarely an issue in animals, but represents another complicating factor in the genetic study of plant domesticates.

To trace the evolutionary ancestry of domesticates, geneticists focus on neutrally evolving, noncoding loci and organellar genomes. The rates of evolution among the
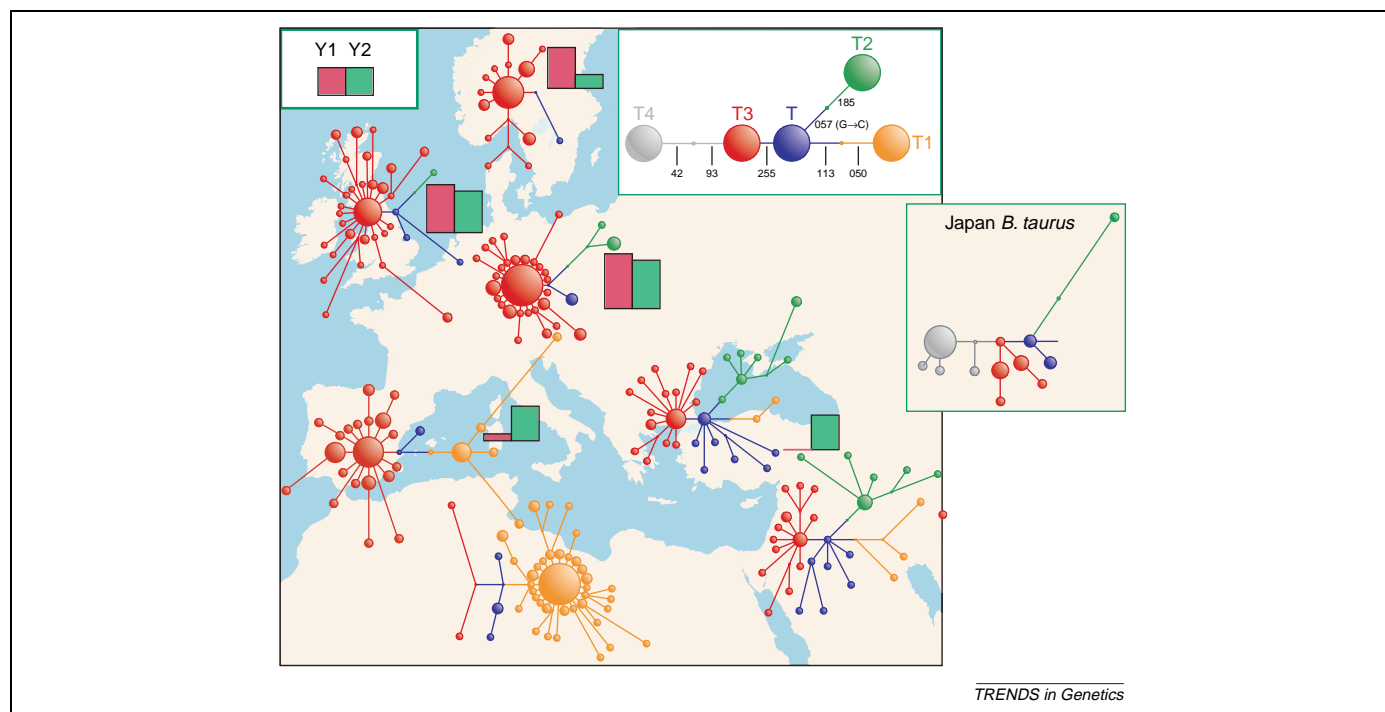

TRENDS in Genetics

Figure 1. The complex ancestry of taurine cattle as shown by mtDNA and Y-chromosome data. Sequencing the most variable region of the mtDNA D-loop shows the regional differences in diversity within domestic cattle (*Bos taurus*), illustrated by reduced median networks superimposed on regions of origin. Sequences fall into five geographically distributed haplogroups distinguished by substitutions at positions (+16 000) given in the skeleton network in the upper inset [29,121,122]. The predominant European cluster, T3 (red), is divergent from sequences derived from European wild ox archaeological samples. It is also found in the Near East, suggesting that European maternal lineages owe their ancestry to primary domestication centres proximal to the Fertile Crescent rather than to local input from the wild. Both African and Far Eastern populations display two additional clusters, T1 (yellow) and T4 (gray), suggesting matrilineal input from local wild oxen. The presence of the African variant in Iberia probably reflects secondary migration across the Mediterranean. Polymorphisms on the Y chromosome delineate two *B. taurus* haplotypes, which are distributed on a north–south axis [102]. The modal southern variant, Y2 (green) is shared between the Near East and much of Europe, the northern haplotype, Y1 (red), seems not to be, suggesting discontinuity. In addition, typing of one of the diagnostic single nucleotide polymorphisms (SNPs) in archaeological samples indicates that Y1 is shared by most European wild oxen. This suggests that insemination of domestic cows of Near Eastern descent by local wild bulls might have been a major contributor to the ancestry of European cattle, but that capture and incorporation of wild cows was not.

nuclear, mitochondrial and chloroplast genomes are not equal, and there are significant differences in the relative rates of evolution in these genomes in plants and animals, which affects their relative usefulness for ancestry studies. In animals, mitochondrial DNA (mtDNA) has a rate of evolution that is five-to-ten times greater than in the nuclear genome, making mtDNA ideal for studying the divergence between wild and domestic populations under the relatively short timescale of domestication (i.e. <10 000 years). Although less variable than mtDNA, nuclear DNA (nDNA) has proven useful in animal domestication research [29]. The Y-chromosome, especially, provides important information on patrilineal inheritance, which can be markedly uncoupled from matrilineal history (Figure 1) [30]. Moreover, noncoding nuclear microsatellite DNA, contributed by both parents, has also proven useful in the detection of shallow time-depth variation seen in the divergence of domestic breeds of animals [31–33].

Mitochondrial genomes in plants have a slower mutation rate than chloroplast genomes (cpDNA) and therefore evolve slowly, limiting their use in domestication studies. Although cpDNA evolves somewhat faster than plant mtDNA, it still lacks sufficient variation to address most questions about variation and change on the 10 000 year span of domestication research. By contrast, nDNA in plants evolves at a rate approximately four times faster than cpDNA and 12 times faster than plant mtDNA [34]. Consequently, genetic studies of plant domestication usually focus on nDNA, using DNA sequences and various highly polymorphic markers that provide sufficient intraspecific variation to document the domestication process [35–39].

The nuclear genome is also key to teasing apart the complicated genetic heritage of polyploid crops, because it can potentially reveal the origins of all their ancestral genomes [40,41]. Nuclear data have been used to investigate the origins of kiwifruit, the tuber oca (Figure 2) and sweet potato, and have been combined with chloroplast genome data to study origins of polyploidy in cotton and tef, an Ethiopian cereal [42–47]. Polyploids with well-established histories, such as cotton, wheat and cole crops, have been used as model systems in recent studies of the complications of genome evolution under polyploidy [48–50].

Plants not only have greater levels of interspecific hybridization but also gene flow between crops and conspecific, wild or weedy populations is frequent. For testing hypotheses of crop–wild–weed gene flow and hybridization, molecular data have the advantages of providing many independent, highly variable markers that are not affected by the environment, and most of which are neutral or nearly neutral [51]. Morphological data in hybrids are not necessarily intermediate between the parental forms [52]. However, hypotheses based on morphological data can be tested using molecular data, and frequently confirm them; for example, most, but not all, of the hypotheses proposed by Heiser of hybridization between wild and domesticated sunflower taxa have been confirmed in this way [53]. Such gene flow can introduce alleles from wild populations into domesticates, as has
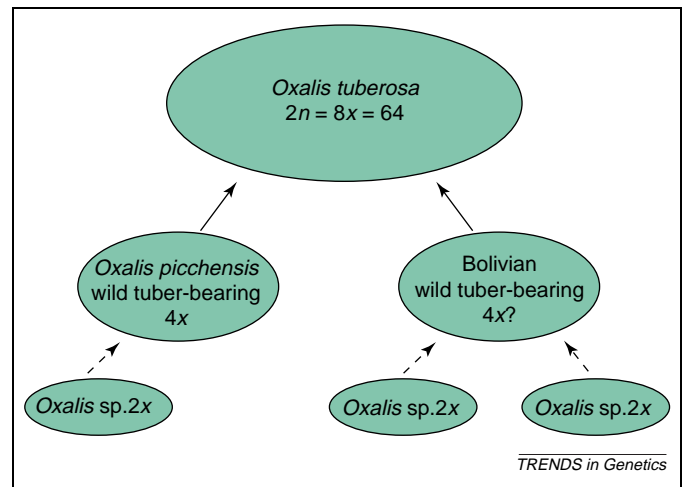

Figure 2. A working hypothesis for the polyploid origins of *Oxalis tuberosa*. The origin of the octoploid tuber crop oca, *Oxalis tuberosa* Molina, was studied using DNA encoding glutamine synthetase (a single-copy nuclear locus that encodes the form expressed in the chloroplast, or ncpGS [44]). As expected for an allopolyploid, multiple copies of ncpGS were found in individual plants of oca, which were separated by molecular cloning. Phylogenetic analysis of these oca cloned sequences and those of wild *Oxalis* species revealed that the three sequence types of oca joined with sequences from two wild tuber-bearing taxa on the ncpGS gene tree. One of the possible scenarios that is congruent with the ncpGS sequencing results is illustrated here. Octoploid oca might have originated by hybridization between *Oxalis picchensis* and an as-yet-unnamed Bolivian wild tuber-bearing taxon. *O. picchensis* of southern Peru is tetraploid [123] and is probably autotetraploid, because it had a single sequence type for ncpGS. The Bolivian taxon is of unknown ploidy level but is probably allopolyploid, because all plants sampled had two sequence types for ncpGS. The lower row shows the unknown diploid progenitors of the wild tuber-bearing taxa. Although this was the simplest explanation of the ncpGS results, other data sources and additional wild tuber-bearing *Oxalis* populations are now being studied and might lead to a modification of this working hypothesis. Reproduced with permission from Ref. [124] ©2006 University of California Press.

been demonstrated in cotton [54] and maize [55,56], and can act over time to diminish the effects of the domestication bottleneck [57]. However, gene flow in the reverse direction, from crops to wild relatives, has been shown in squash [58,59] and beans [60], and some would argue is more frequent than generally thought [61]. Studies of gene flow from domesticates into wild or weedy relatives are important with regard to the escape of genes from genetically-modified organisms [55,61,62]. Continuing crop–wild gene flow subsequent to domestication can make it difficult to interpret patterns in the genetic data, thus obscuring crop origins, and precluding the localization of the area of domestication [35].

A particularly important focus in the genetic analysis of domesticates centers on the study of genes and gene complexes that are specifically selected for (or against) by domestication (Box 1). Because many plant species produce an abundance of seed, they are capable of producing large data sets for mapping qualitative trait loci (QTL) – multiple genes that affect a particular phenotypic feature [63]. Intensive work on corn genetics, for example, has identified several key 'domestication genes' that control features such as branching and glume architecture [64–67] and these loci have been among the first in which the reduction of nucleotide diversity near the site of selection has been studied (Box 2). QTL studies in other crops have identified domestication genes affecting starch composition in rice, fruit size in tomato,

Box 1. Identifying crop domestication genes

Recent studies of the genetic basis for the changes that occurred during crop domestication focused on traits that were the targets of selection and the genes that affect them – 'domestication genes'. One of the methods used in these studies is QTL mapping. This method requires the use of numerous molecular markers scattered throughout the genome and numerous descendents of a controlled cross between parents that differ for the trait of interest. Statistical procedures can identify chromosomal regions that might contain a gene affecting the trait. In well-studied crops there could be a gene that is known to be located in the same chromosomal region (usually because of a mutation in that gene), and that candidate locus can be further tested to determine whether it is the QTL.

One of the first domestication genes to be studied extensively was *teosinte branched1* (*tb1*), which affects apical dominance in maize, such that the maize mutant has teosinte-like branching instead of a single dominant stalk. QTL mapping found a strong effect on plant architecture in the same chromosomal region in which *tb1* was located, and further genetic tests confirmed that *tb1* was the locus that had been identified [131]. Similar methods have been used for one of the most important domestication genes in maize, *teosinte glume architecture1* (*tga1*), which controls the formation of the teosinte cupulate fruitcase that encases the kernel [66,67] and was involved in the crucial step that turned the stone-hard kernels of teosinte into the much more usable kernels of maize. Other loci that have been investigated in maize as possible domestication genes include *terminal ear1* (*te1*) [132], and several loci affecting kernel weight [133]. Mapping and developmental studies found that *suppressor of sessile spikelets1* (*sos1*) was not involved in maize domestication, although its mutant phenotype of single rather than paired spikelets appears similar to teosinte [65].

Domestication often affects gene regulation. Selection can affect the regulatory (promoter) regions of genes, for example, *tb1* and *tga1* (Box 2), or can target regulatory loci rather than protein-coding genes. In an important domestication gene that affects fruit weight in tomato, *fw2.2*, human selection seems to have targeted mutations in the promoter region of the gene that cause it to activate earlier in fruit development [69,134]. The tight edible inflorescence of cauliflower and broccoli is affected by a regulatory gene, *cauliflower* (*BoCAL*) [70]. An exception is the mutation in the *waxy* gene of rice that affects the gene splicing and hence starch composition, leading to the glutinous rice favored in East and Southeast Asia [68].

The idea that domestication traits are controlled by few genes with large effects has been confirmed in some cases [71,135,136], but it is not universal. The classical domestication trait of the shattering rachis is controlled by one locus in sorghum and three loci in rice but is affected by ten loci in maize [137]. Sunflowers seems to differ from most other crops studied to date, in that its domestication traits are influenced by numerous loci of moderate or slight effect [138].

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the modified inflorescence of cauliflower and broccoli, and multiple traits in common bean [68–71].

Research focused on the identification of 'domestication genes' in animals, despite some successes, lags significantly behind that in plants. Causative mutations for several monogenic traits, such as those for coat color in several species, have been identified. Intensive research on polygenic traits related to production has resulted in the identification of loci such as insulin-like growth factor 2 (*IGF2*) in pigs, which is associated with differences in muscularity, back fat and heart size in a wild boar–domestic hybrid [72]. The completion of genome projects in several species will greatly facilitate the search for the genes that were the drivers in the journey from the wild to domesticity.

Areas of cross-illumination in the archaeological and genetic documentation of domestication

Archaeologists and geneticists use different tools to illuminate different aspects of the process of domestication in plant and animal species. Therefore, it is particularly important for archaeologists and geneticists to combine their disciplinary expertise to unravel the course of this important process. There are several areas where the possibility for cross-illumination between archaeology and genetics are particularly promising.

Identification of wild progenitors of plant and animal domesticates

Identifying the wild progenitors of domesticates is important to understand domestication. The application

Box 2. Domestication bottlenecks and footprints of selection

Reduced diversity of DNA polymorphisms in domesticates compared with those in wild progenitors can take two forms. There is often a genome-wide reduction in diversity – the 'bottleneck' of domestication – in which a subset of the genetic diversity found in the wild progenitor is retained in the domesticate, owing to the relatively small population that was initially domesticated. The extent of the bottleneck depends on both the number of individuals in the founding population and the duration of the bottleneck. However, an even greater reduction of diversity can occur in specific regions of the genome that are tightly linked to the sites that were the targets of selection. When a strongly selected allele is quickly brought to fixation in the population, other tightly linked loci can also be brought to fixation, reducing diversity in a 'selective sweep' that is known as the 'signature' or 'footprint' of selection on domestication genes.

Domestication bottlenecks have been demonstrated in several crops, including pearl millet [139], cotton [140], potato [141] common bean and lima bean [60,92]. The extent of the domestication bottleneck of maize in two neutral loci *adh1* [142] and *glb1* [143] was found to be 83% and 60%, respectively, of the diversity in teosinte; other neutral loci in maize show similar proportions [131,144,145]. A secondary bottleneck associated with the dispersal of the crop from its homeland can be narrower than the domestication bottleneck itself if only a few individuals and their descendents were disseminated around the world, for example, potato and coffee [141,146].

A reduction in diversity of domestication genes has been studied in several maize loci and in the *BoCAL* regulatory gene affecting the inflorescence development of broccoli and cauliflower [70]. In maize, studies of variation in domestication genes *tb1* and *tga1* have uncovered strong evidence of the effects of selection, but the greatest reduction in diversity was not in the protein-coding part of the gene, but rather in the upstream regulatory region [66,147,148]. In contrast to the evidence of selection found in *tb1* and *tga1*, other loci, such as *adh1*, *glb1* and *te1*, seem to have evolved in a neutral fashion [131,145].

Elevated diversity might also point to domestic selection of a different nature. Beja-Pereira *et al.* [149], for example, found that Northern European cattle breeds showed significantly more alleles than expected at several milk protein loci. This was in contrast to the pattern in southern Europe and the Near East – prompting a suggestion that local selection pressures might have left a detectable footprint. Interestingly, the north central European region also shows a maximum for a human genetic trait that is unambiguously post-domestic: the ability to drink raw milk into adulthood, lactose tolerance. This leads to a tempting conclusion that parallel selection processes have been at work in these two mammals brought about by the development of intensive dairy economy.

Box 3. Identifying the progenitor of maize

Maize (*Zea mays* ssp. *mays*) looks so unlike any wild grass that identifying its wild ancestor has been challenging. In the 1930s, Mangelsdorf and Beadle proposed different alternative hypotheses regarding the origin of maize, and it was not until the advent of biochemical and molecular genetic techniques in the 1980s that a 40-year-old debate was resolved, and Beadle was proven correct. Mangelsdorf had suggested that maize was domesticated from a wild maize (that is now extinct), and that the diversity in the extant species is the result of substantial introgression with closely related *Tripsacum* grasses. Beadle, by contrast, proposed a much more straightforward origin: that maize had been domesticated from a still extant annual grass – teosinte.

In the 1980s, the first molecular studies targeting the wild ancestor of maize involved isozyme variation and mapped restriction sites of the chloroplast genome [150]. Phenetic analyses of isozyme data of maize and several teosintes showed that the domesticate was most similar to the teosinte populations of the subspecies *Z. mays* ssp. *parviglumis* found in the central Balsas river valley of southwestern Mexico. By identifying these extant central Balsas populations of *Z. mays* ssp. *parviglumis* as the probable modern descendants of ancient progenitor populations, these initial studies not only tentatively identified the wild ancestor of maize, but also suggested the region where maize probably had been initially been domesticated.

The phylogenetic tree based on cpDNA was consistent with the idea that the cultigen, *Z. mays* ssp. *mays*, belongs to the same species as three wild teosinte subspecies (i.e. *Z. mays* sspp. *parviglumis*, *mexicana* and *huehuetenangensis*) because their chloroplast haplotypes were intermingled together in the same clade [150]. Although it confirmed the close relationship of these taxa, this mixing of haplotypes meant that the cpDNA data did not enable determination of which subspecies was the progenitor of maize.

A more recent distance analysis by Matsuoka *et al.* [56] of data from 99 microsatellite loci comparing maize with the three teosinte subspecies, however, confirmed earlier results, which indicated that ssp. *parviglumis* accessions from the central Balsas river valley were the teosinte populations closest to domesticated maize. The study also provided additional support for a single domestication event. Matsuoka *et al.* found that all the 193 domesticated maize plants sampled from the pre-Colombian range in North and South America clustered together and were separate from 71 teosinte plants of three *Z. mays* subspecies. This single cluster is consistent with a single origin of domestication and with earlier results based on isozymes and chloroplast DNA, neither of which supported multiple domestications of maize [150]. However, identifying the Balsas watershed as the place where maize was probably initially domesticated should be tempered with the realization that undiscovered or extinct populations might be yet closer to maize, and species distributions might have changed since the time of the domestication.

Similarly, although future excavation of sites in other areas of southern Mexico could perhaps change the picture somewhat, the earliest available archaeological evidence for domesticated maize provides a separate line of evidence indicating that maize was derived from teosinte within, or close to, the Balsas watershed, while also providing a conservative, time-certain temporal framework for when this major crop plant was domesticated. Direct accelerator mass spectrometer radiocarbon dates obtained on two maize cob fragments recovered from Guila Naquitz in Oaxaca, ~100 km northeast of the Balsas watershed, have been dated to 6300 years before present (Bp) [151–153], providing the earliest evidence for domesticated maize in the archaeological record. Matsuoka *et al.* estimate maize was domesticated as early as 8000 years Bp.

of molecular information to the reconstruction of plant and animal phylogenies has been key to charting the ancestry of domesticates. Genetic studies have frequently confirmed the earlier identifications of wild progenitor species, such as sheep [73,74] and goats [75], based on morphology, geography or cytology. Genetic studies have also resolved long-standing controversies about the ancestry of domesticates. For example, Doebley's definitive identification of the subspecies of wild teosinte grass that gave rise to corn ruled out alternative phylogenies that included complicated hybridizations between wild grasses and mythical ancestral species (Box 3) [55,76]. Similarly, Olsen and Schaal's research on cassava succeeded in identifying the wild progenitor of this major tropical crop plant [38,39]. Sometimes long-accepted progenitor species are shown to be closely related sister species. For example, recent genetic analysis has shown that the condiment species Chinese chive (*Allium tuberosum*), originally thought to be descended from the wild onion species *Allium ramosum*, is now thought to have developed through multiple domestications of a possibly extinct sister species [36]. The list of potential progenitors can be narrowed down in the complicated lineages of polyploid crops, as Emshwiller and Doyle have done for the South American tuber oca (*Oxalis tuberosa*) (Figure 2) [43,44]. In some examples, where the wild progenitor is either largely or entirely extinct, aDNA has yielded crucial clues about the ancestry of important domesticates (e.g. cattle [77] and horses [78]).

The correct identification of wild progenitor species, in turn, contributes to the development of archaeological markers capable of distinguishing between the archaeological remains of wild and domestic individuals. Bruno's matrix of morphological traits capable of distinguishing domestic quinoa in the archaeological record, for example, is based on early allozyme research that identified the wild progenitor species of this important Andean crop plant [79]. Wheeler and colleagues' genetic analysis sorted out the complicated parentage of domestic camelids in South America [32], and has been crucial to the development of osteometric criteria for distinguishing between domestic llamas and alpacas and their progenitors, guanaco and vicuña [80].

Documenting the number and location of domestication events and the dispersal of domesticates

Another area of intersection between genetics and archaeology is documenting the location(s) of initial domestication and the trajectory of subsequent dispersal of domesticates. Genetic analysis has supported a single origin for certain domestic crops and livestock species. Not only did Doebley and colleagues identify the progenitor species of corn, for example, they also located the probable geographic center of corn domestication in south central Mexico [56] (Box 3). This research has, in turn, helped guide archaeological efforts at documenting initial domestication and diffusion of maize. For example, Piperno and Ranere are seeking evidence of early landscape modification, and macro- and micro-fossil evidence of

Box 4. Ancient DNA documents the development of key domestication genes in prehistoric maize

Archaeologists have long studied morphological changes in ancient maize cobs, whereas geneticists studied domestication genes in extant maize and teosinte. Jaenicke-Després and colleagues [84] demonstrated the strength of combining parallel research pathways. Their analysis of archaeological maize cobs from Mexico (Figure Ia) and the southwestern USA (Figure Ib) showed that aDNA can reveal the effects of human selection on other traits that occurred in concert with the selection on the morphological traits directly observable from the cobs themselves. Direct AMS dating of archaeological cobs provide a precise time table for the selection of these traits. Building on previous studies of maize domestication genes, they show that the DNA from ancient cobs can reveal information about the human selection influencing parts of the plant that were not preserved in the archaeological record, such as the stem and kernels. Mexican cobs from the Ocampo Caves in Tamilaulipas that date from 4000 years ago,

just before maize entered the southwestern United States, already show the effects of human selection on three genes (*tb1*, *pbf* and *su1*) that affect plant architecture and the protein and starch composition of the kernels (Figure Ic). Whereas selection appears to be complete on the alleles for an unbranched stem and protein composition (within the limitations of a small sample size), the locus affecting starch composition showed interesting differences in allelic frequency between ancient cobs from Mexico and later cobs from Tularosa Cave in southwestern USA, dating to 1000–2000 years Bp. All Mexican cobs had the form of starch that now predominates in that region, producing the softer kernels preferred for tortillas. Although still retaining some starch diversity, more recent cobs from New Mexico showed selection for the form of starch eventually found in hard-kernelled North American cultivars, such as Northern Flint and its modern hybrid derivatives.
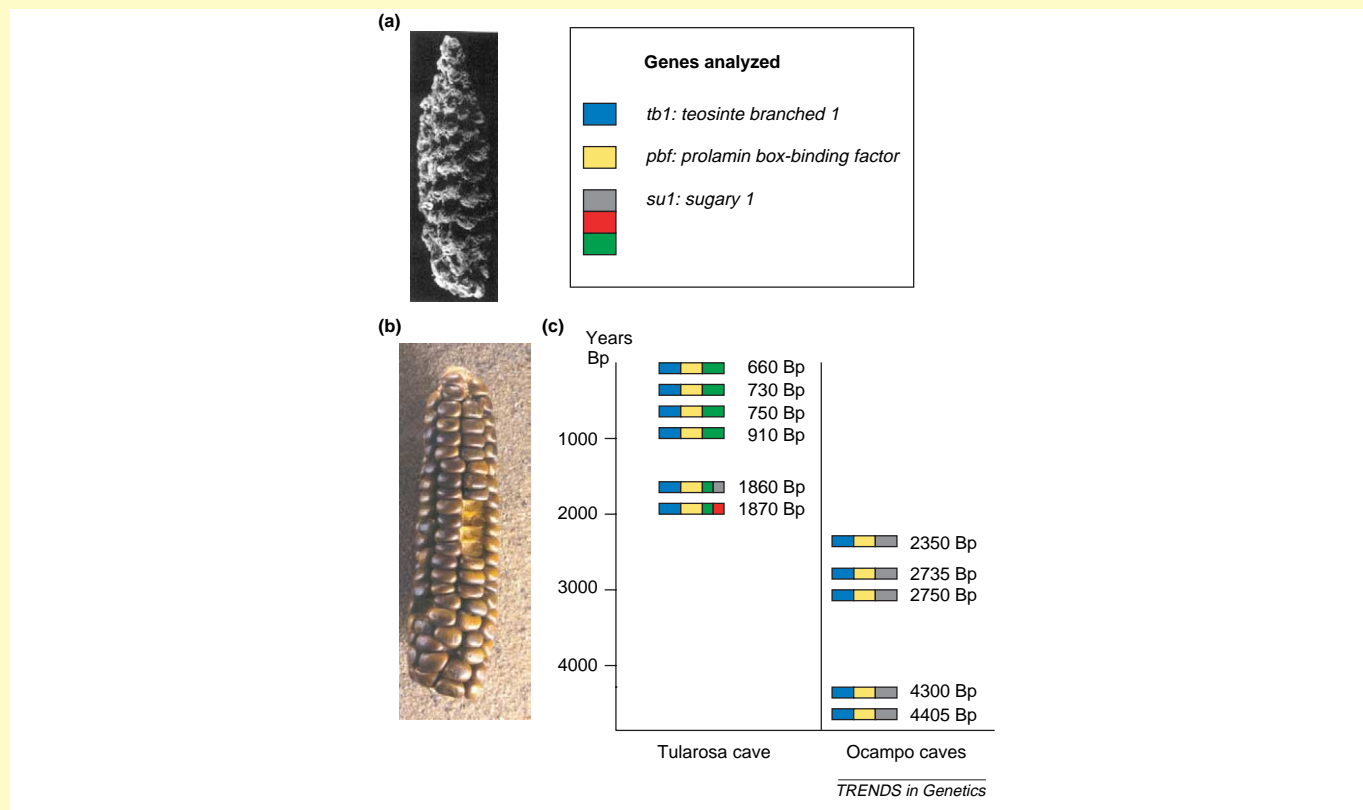

Genes analyzed

- *tb1: teosinte branched 1*
- *pbf: prolamin box-binding factor*
- *su1: sugary 1*

Years Bp	Tularosa cave	Ocampo caves
660 Bp	■	
730 Bp	■	
750 Bp	■	
910 Bp	■	
1860 Bp	■	
1870 Bp	■	
2350 Bp		■
2735 Bp		■
2750 Bp		■
4300 Bp		■
4405 Bp		■

TRENDS in Genetics

Figure I. The analysis of archaeological maize cobs.

early maize in the Balsas River Valley of south central Mexico[*] – the genetic 'ground zero' for initial maize domestication identified in Doebley's work. Other archaeological efforts are using a variety of markers and techniques to track and date the diffusion of corn out of the centre of initial domestication southward through Central and South America [81,82] and north into the southwest USA and the rest of North America [83]. Combined analysis of morphology and aDNA of directly dated archaeological corn cobs from sites in Mexico and the southwestern USA by Jaenicke-Després *et al.* [84] has tracked the timing of selection of three maize domestication genes at various points of its dispersal from

the initial center of maize domestication (Box 4). Genetic studies focusing on the geographical center for the domestication of various wheat species in the Old World [37,85], also thought to have arisen from a single center of origin [86], are consistent with archaeological evidence for initial wheat domestication [87].

Recent archaeological and genetic research, however, suggests that multiple domestication events are more common in plants than originally thought. Rejecting earlier 'out of Mexico' models for the diffusion of domesticates into the eastern region of North America, for example, Smith and colleagues proposed that squash (*Cucurbita pepo*) was domesticated independently in the USA, based on combined archaeobotanical and modern biogeographic data [87] – an argument consistent with genetic evidence that indicates two independent

domestication events for *C. pepo* [58,59]. New genetic evidence for eastern and western Mediterranean centers of olive domestication [88,89] supports a similar multi-origins model, based on the morphological analysis of modern and archaeological olive pits [90]. Genetic analyses also identified two centers of domestication of the common bean (*Phaseolus*) – one in South America and another in Mesoamerica [91,92]. Although a comprehensive AMS radiocarbon analysis of pre-Columbian beans determined when domesticated beans appeared initially in South America and Mesoamerica [93], there are no morphological markers (macro or micro) that can be used to differentiate the beans domesticated in these two areas.

Multiple domestication events are even more common in animals. Most domestic animals that have been

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Box 5. Genetics and archaeology detect the first global economy

A vibrant ancient Indian Ocean trading network linking Africa, Arabia, South Asi, and points east can be traced through the genetic and archaeological study of traded plants and animals. Freeman *et al.* [154] have reconstructed, from multiple microsatellite data sets, a gradient of the genetic influence of zebu cattle (*Bos indicus*) extending from India through the Horn of Africa into the interior of that continent (Figure I), suggesting that zebu were introduced into Africa through an Indian Ocean corridor rather than overland through Suez [155]. Pictorial representations of humped cattle in Egyptian tomb paintings [156] indicate that zebu entered the African continent >4000 years ago.

The banana (*Musa* sp.) is another crop that moved across the 'great lost corridor of mankind' [157] that linked the east coast of Africa, the eastern coast of Arabia and the southern coast of Asia. Based on present day geographical distribution of various banana complexes in Africa, the banana, a Southeast Asian domesticate, is estimated to have been introduced into East Africa by at least 3000 years Bp [158]. Direct evidence for the introduction and subsequent diffusion of bananas in Africa is provided by opal phytoliths recovered from archaeological sites. Phytoliths of Southeast Asian origin *Musa* have been shown to be morphologically distinguishable from *Ensete* phytoliths, a member of the Musaceae family indigenous to Africa [159]. *Musa* phytoliths have been recovered from archaeological contexts in Central Africa that are securely dated to ~2500 years Bp. The banana (along with other tropical Southeast Asian root crops such as yams (*Dioscorea* sp.) and taro (*Colocasia* sp.) seems to have formed an important crop complex that might be linked to major population increase in humid regions of Central Africa [158].

Crops such as sorghum (*Sorghum bicolor*), finger millet (*Eleusine coracana*) and pearl millet (*Pennisetum glaucum*), which were probably domesticated on the southern margin of the Sahara ~5000–3000 years ago [87], moved out of Africa in the opposite direction. Imprints of these grains are found in mud-brick impressions from sites on the Oman peninsula [160] dating to ~4500 years Bp and in carbonized plant remains at various sites on the Indian subcontinent [157,161] beginning at ~4600 years Bp. Unlike winter-growing wheat and barley, introduced into the Indian sub-continent from the Near East sometime earlier, these African crops were pre-adapted to the Indian summer monsoon growing season and might have helped fuel a rapid growth of Harappan village communities that supported the first Indus civilization [161].

Another domesticate involved in this far-flung trading network was the donkey (*Equus asinus asinus*). A phylogenetic tree based on mtDNA control region sequences from donkeys and their relatives (Figure II) [129,162] confirms an African origin for the domestic donkey. The use of these animals in overland trade is attested by the discovery of donkey remains at Tel Brak in northeastern Syria, which is ~4300 years old [163] and at Tal-e Malyan in highland Iran [164], which is ~4800 years old.

Other domesticates engaged in overland trade during this time included the horse (*Equus caballus*) – which combined genetic and archaeological evidence suggests was domesticated (probably multiple times) and quickly spread across the Central Asian steppe ~5000–4000 years ago [78,162]. The recovery of bones, dung and woven fiber from the Bactrian camel (*Camelus bactrianus*) at Shar-i Sokhta in Iran suggests that this well-known caravan animal was domesticated ~4500 years ago [165]. Together these studies bear witness to thriving sea-borne and overland global trading networks spanning much of the ancient world, which had profound implications for the course of human history across this broad region.
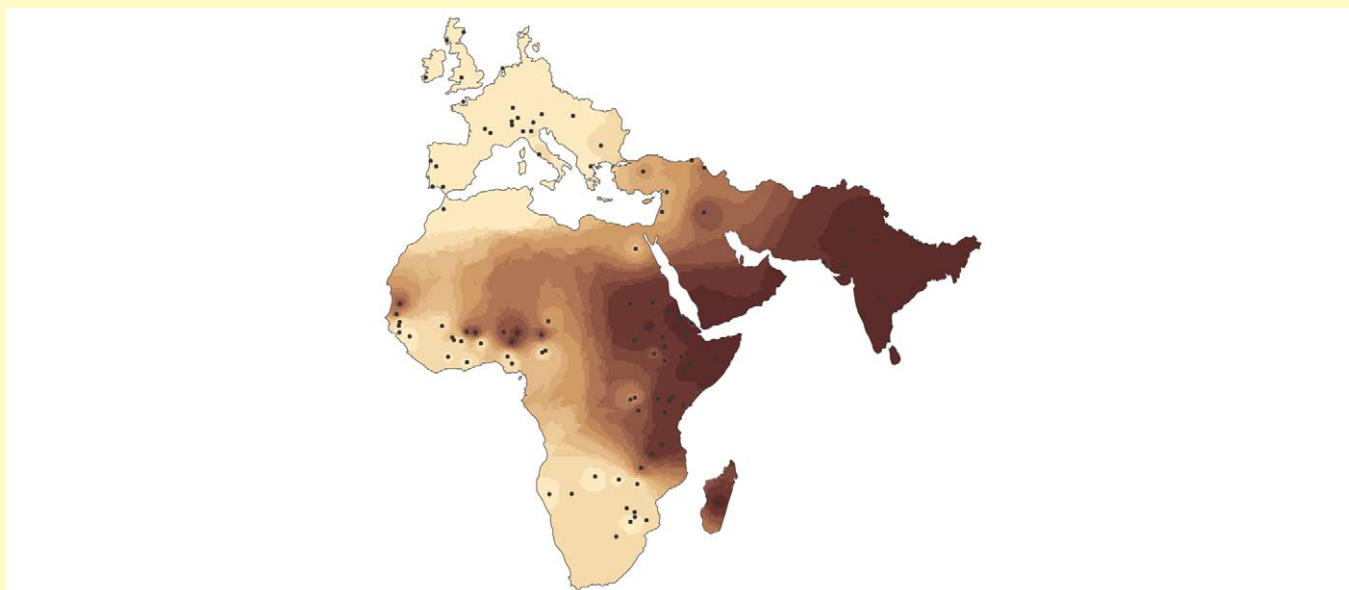

Figure I. The origin of *Bos indicus*. The genetic influence of *B. indicus* is indicated by degrees of shading. Zebu admixture in modern African cattle is particularly strong in the Horn of Africa and in Madagascar, whereas a much less marked introgression is clear in the Near East. Reproduced, with permission, from Ref. [154].
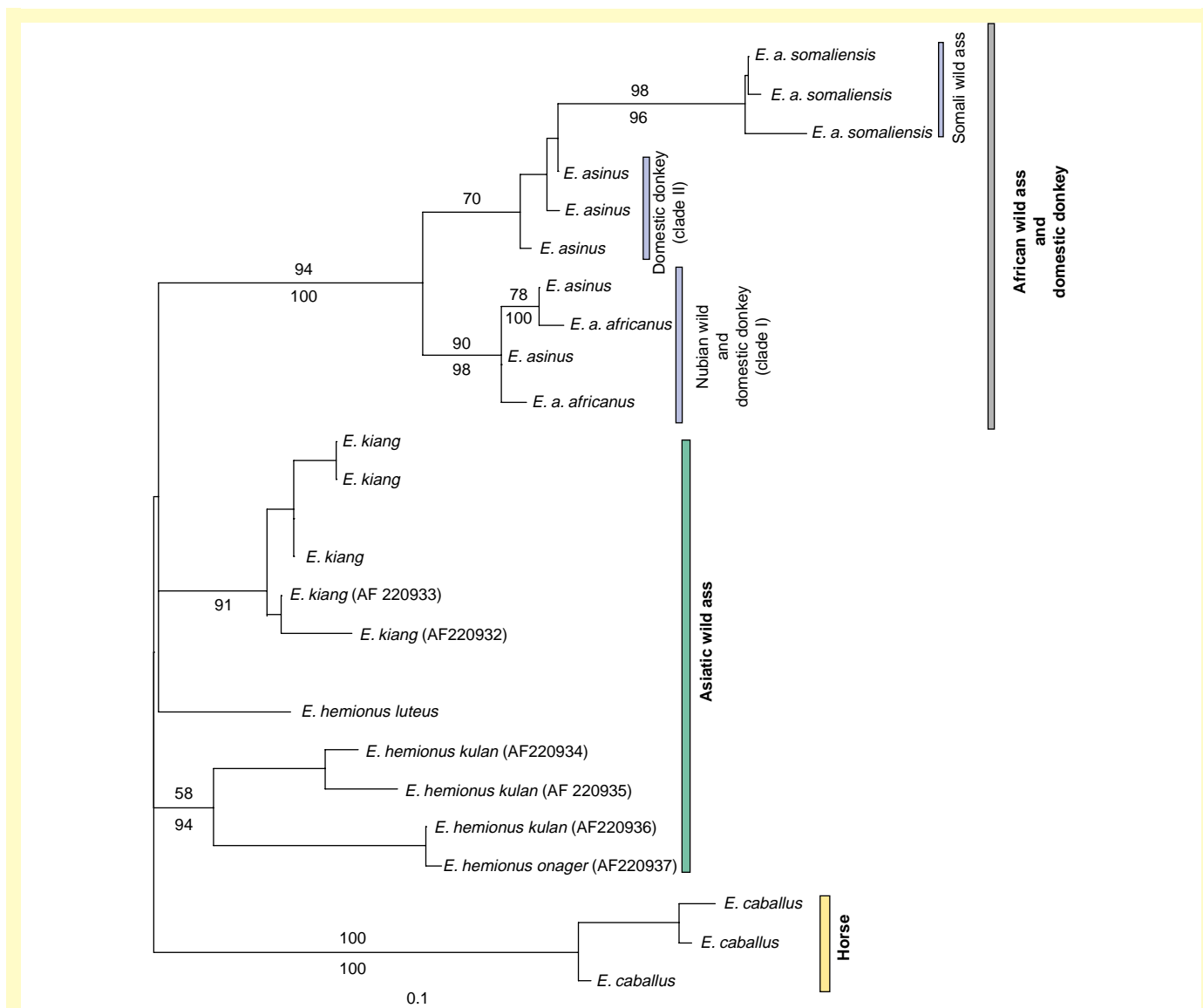
Figure II. A phylogenetic tree based on mtDNA control regions sequences from donkeys and their relatives. Two clades (I and II) of haplotypes are indicated, suggesting two distinct domestication events. The average sequence divergence between these two clades was 15.73±0.61 substitutions (3.29±0.01%) with a maximum divergence of 27 substitutions (5.64±0.01%). One clade is most closely linked to the Nubian wild ass (*E. asinus africanus*), currently found in northeastern Sudan. The other clade shows affinities to the Somali wild ass (*E. asinus somaliensis*), currently found near the Red Sea or the Gulf of Aden. Reproduced, with permission, from Ref. [164] ©2006 University of California Press.

subjected to genetic analysis seem to have been domesticated several times. Genetic data have supported archaeological arguments for multiple independent domestication events in some studies but not in others. Archaeological analysis promises to provide important resolution on the timing and geographic location of domesticated events. Analysis of bovine mtDNA [77], for example, has provided evidence to help bolster archaeological arguments for an independent center of cattle domestication in North Africa [94], while questioning archaeological arguments for an independent center of cattle domestication in Europe (Figure 1) [95]. Recently, a study of modern wild and domestic pig mtDNA by Larsen *et al.* [96] found evidence for at least six different domestication events across the wide geographic distribution of wild boar.

Parallel archaeological analyses by the same team have used several different markers to trace at least four examples of pig domestication in Europe, the Near East and the Far East [97]. Phylogenetic analyses of goat and sheep have identified three distinct domestic lineages in each, suggesting that these species were domesticated at least three different times [75,98]. Moreover, in sheep and goats there is one major geographically widespread lineage that probably represents the initial domestication event and two-to-three smaller, more restricted lineages that probably represent later events. Ancient DNA extracted from goat remains from Iran [99] place these specimens within this larger lineage of domestic goats, implying a Fertile Crescent origin for this main lineage, consistent with long-standing archaeological evidence [100]. There is

also some archaeological evidence for an independent domestication of goats in eastern Pakistan [101] that might correspond to one of the smaller goat lineages identified by genetic analysis. New demographic profiling techniques for identifying initial attempts at human management of sheep and goats are promising for locating and dating the initial domestication of these species, both within the Fertile Crescent and elsewhere [26,27].

However, genetically independent domestication events are not necessarily culturally, or even biologically, independent. Perhaps many of the proposed genetically recognized 'independent' domestication events in animals represent the movement of a few domestic individuals into an area, with the genetic signature of the introduced founders subsequently submerged in the recruitment of local wild animals. Transport of domestic males into new regions would not be visible in the mtDNA of their descendents, for example, nor would insemination from the wild. As exemplified by the studies of Götherström *et al.* [102], Y-chromosome data are crucial to resolving these issues (Figure 1).

The application of molecular data to the study of domesticates has also been helpful in distinguishing primary domestication events from later or more-restricted events, and in tracing the diffusion of domesticates (Box 5). This is especially true for animal domesticates, which vary in their degree of phylogenetic discontinuity and phylogeographical patterning, which, in turn, has bearing on the speed, direction and herding strategies used in the diffusion of these domesticates (Figure 3). Integrating and correlating genetically derived scenarios with the archaeological record is essential. Genetic data tracking the movement of domestic dogs across Asia into the New World [103] and of pigs [96] and rats [104] in Oceania, for example, offer insights into the direction and pace of human migration into these regions. But such genetic scenarios need to be reconciled with the archaeological records of human dispersal into these areas [105,106].

Documenting the temporal sequence of domestication

Defining the temporal framework of domestication is an obvious area of mutual interest, and also an occasional source of disagreement, between archaeologists and geneticists. An initial estimate for the origin of domestic dogs based on molecular data, for example, placed their divergence from wolves at ∼135 000 years ago [107], > 100 000 years earlier than the first morphological evidence for dog domestication based on fossil bones from Europe and Asia, which were dated to ∼13 000–17 000 years ago [108]. Although Wayne and colleagues have recently qualified this early estimate, they defended the molecular evidence for an early wolf–dog divergence by arguing that genetic change, morphological change and speciation in animals undergoing domestication will occur at different points in the domestication process [109]. This is an important point, particularly in animals where domestication is likely to operate first on behavioral attributes rather than on morphology. However, it is difficult to reconcile the substantial gap that exists
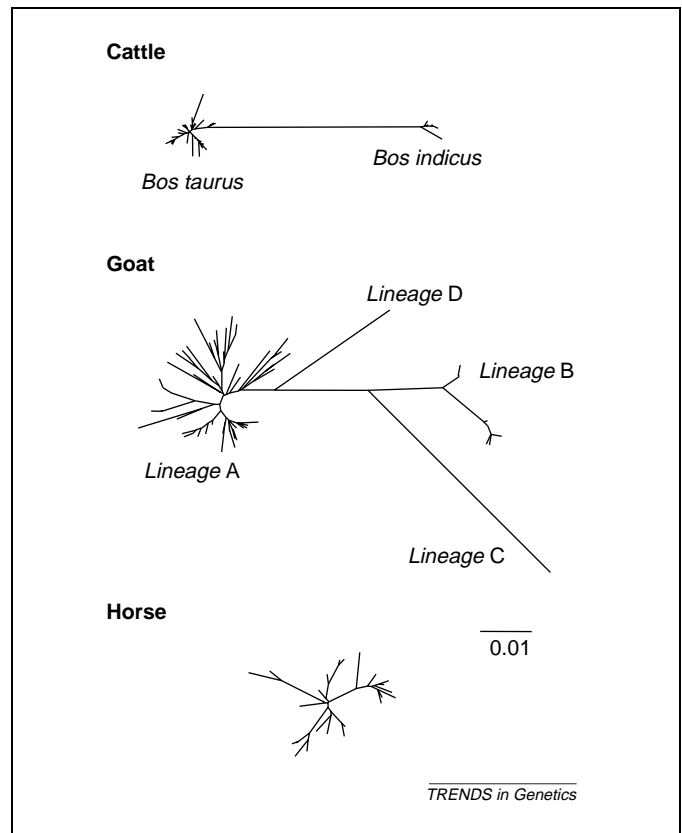

Figure 3. Three paradigms of domestic animal mtDNA diversity: phylogeographic discontinuity, distribution and dispersal. Neighbor-joining networks of mtDNA control region sequences from cattle, goat and horse are shown. Cattle haplotypes fall into two clusters separated by a long internal branch. These clades correspond alternatively to *Bos taurus* and *Bos indicus* origins, are the products of separate domestications and show strong phylogeographical discontinuity when sampled appropriately to avoid hybrids. Other large domesticates, such as water buffalo (*Bubalus bubalus*) and pig (*Sus scrofa*), also show multiple origins and strong geographical structure – as with cattle primarily on an east–west axis. Goat (*Capra hircus*) lineages also partition phylogenetically, into at least four clusters that show phylogeographical distribution [125] – with a geographic structure that is less distinct than that of cattle. One of these goat clusters, *lineage A* is predominant numerically, ubiquitous and undoubtedly reflects the primary caprine domestication process [75]. The other three lineages show some restriction in geographical distribution, suggesting additional domestications. This pattern of multiple clades with moderate geographical partitioning, which could alternatively reflect substantial secondary mixing owing to the portability and tradeablity of small livestock, is also exhibited in sheep (*Ovis aries*), dog (*Canis familiaris*) and chicken (*Gallus gallus*) [126,107,127]. Llama (*Lama glama*), alpaca (*Vicugna vicugna*) and asses (*Equus asinus*) also possess moderately distributed mtDNA clades [128,129]. By contrast, the phylogeography of the horse (*Equus caballus*) mtDNA is weak [78], a pattern of dispersal that probably reflects a domestication process that was not limited in time and space to the same extent as the other species discussed. This pattern probably reflects the effects of extensive migration on the genetic structure of this most mobile of animals [130].

between the molecular clock estimate of wolf–dog divergence and the first appearance of morphological change in the form of tooth crowding in early dogs, which is felt to be directly linked to selection for less aggressive behavior in initial domesticates.

Molecular clocks are better scaled for species divergences that occurred millions or tens of millions of years ago, not for populations (e.g. domesticates) that diverged <10 000 years ago. Evidence of unequal mutation rates among different taxa and different genomes also challenge the basic assumption of a molecular clock that has a regular mutation rate [110–114]. Therefore, many geneticists, particularly those focusing on plant domestication,

Box 6. The origin and diffusion of cassava

Cassava (*Manihot esculenta* Crantz subsp. *esculenta*) also known as manioc, tapioca, mandioca and yuca, is a primary calorie source in the tropics and the sixth most important crop plant worldwide [166]. Recent genetic and archaeological research combined to locate the origin of this important root crop and trace the direction and pace of its diffusion out of its center of origin. Olsen and Shaal's analysis of three low-copy nuclear genes of populations of cultivated cassava and possible progenitor species (*M. esculenta* ssp. *flabellifolia* (Pohl) Ciferri and *M. pruinosa* Pohl) identified the former wild taxon as the sole progenitor of cassava, which probably developed in a single domestication event [38,39]. This result was supported by data from microsatellites from the same populations (Figure I).

Analysis of starch grains from modern cassava and its wild progenitor by Piperno show clear morphological differences that can identify fossilized starch granules extracted from stone tools recovered from archaeological sites [167]. Archaeological evidence for the use of cassava from the poorly studied Amazon Basin is currently lacking. Cassava starches, however, have recently been extracted from grinding stones recovered from sites in the Porce and Cauca Valleys of North Central Columbia that are ~7500 years old and from Aguadulce Shelter in Panama, which is ~6900 years old [168]. In addition, pollen grains likely to be from cultivated cassava have been found in archaeological contexts on the Gulf Coast of Mexico and Belize dating to ~5800 years Bp and 4500 years Bp, respectively [169,170]. Cassava starch granules have also recently been recovered from processing tools in Puerto Rico dating from 3300–2900 years ago [171]. Together these suggest an early origin for cassava and its rapid diffusion out of the Amazon Basin throughout the Neotropics and the Caribbean.
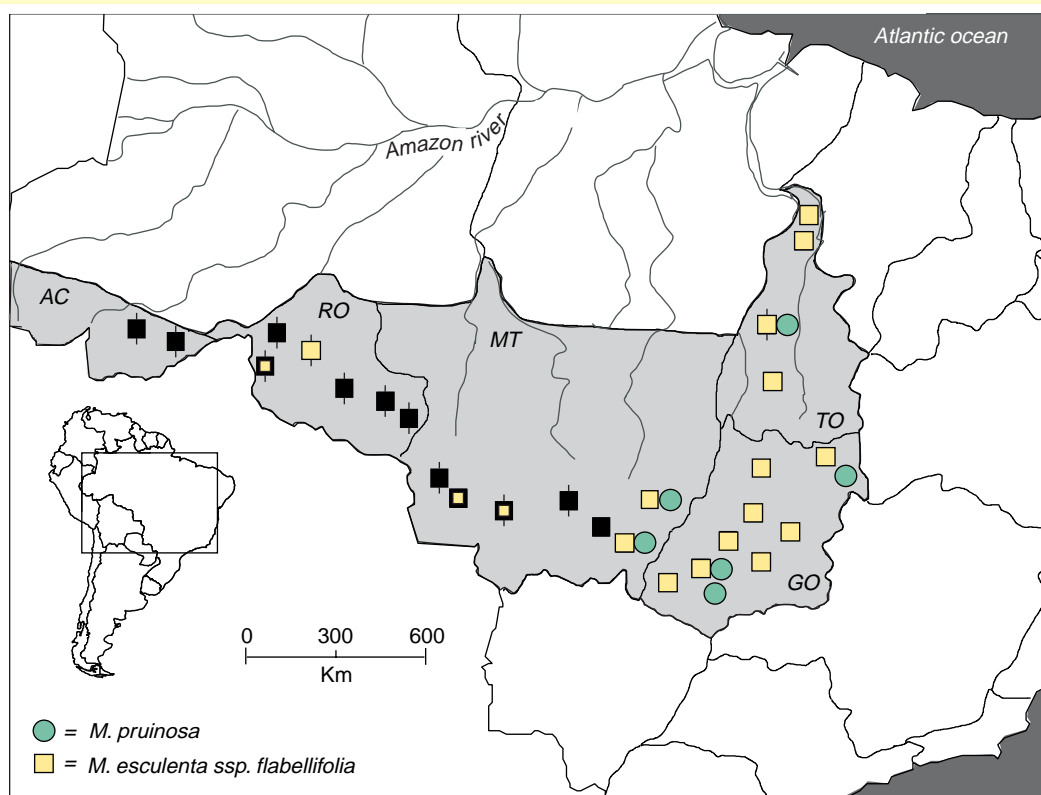

Figure I. The origin of cassava. Populations of *Manihot esculenta* ssp. *flabellifolia* that contain either cassava G3pdh haplotypes (yellow with black outline), or cassava haplotypes for G3pdh and at least one other of the three nuclear genes examined (black), and populations that group with cassava in the microsatellite analysis (those with vertical bars) [172]. These populations cluster along the southern border of the Amazon Basin, strongly suggesting that this region is likely to be the center for the origin of cassava. Reproduced with permission from Ref. [172] ©2006 University of California Press.

recommend against using the molecular clock to measure the short timescales involved in domestication. Instead they advocate using directly dated archaeological evidence for domestication to anchor and ground-truth genetic evidence for the origin and dispersal of domesticates with the archaeological record (Box 6) [115,116]. Nonetheless, genetic data can resolve questions of relative timing, for example, by rejecting the idea that tetraploid cotton only formed after humans brought A-genome cotton to the Americas [46].

The promise of ancient DNA

The utility of genetic studies of modern domesticates in tracing initial domestication and dispersal can be confounded by thousands of years of selective breeding, hybridization and introgression that separate modern domesticates from their progenitors. However, aDNA holds promise for opening a direct window on these past events. Because DNA encased in animal bone is likely to be preserved and high-copy mtDNA in animals is suitable for tracking divergence over shallow timescales, aDNA has been more widely used in the study of animal domestication than in plants. It has been useful in tracing the dispersal of primary domestic species such as cattle [77], horses [78], dogs [103], goats [99] and pigs [117] out of the areas of their initial domestication. But it has proven difficult to extract and replicate aDNA from the bones of animals that date to the initial phases of domestication,

particularly those from early archaeological contexts in the arid Near East, which served as a hearth of domestication for most of the major livestock species.

The application of aDNA to the study of archaeological plant remains is more challenging, owing to preservation issues and because low-copy nuclear DNA is more useful in the study of plant domestication. Despite this, aDNA has been recovered from dried plant remains from favorable archaeological contexts and has been used to track genetic responses of plants at various points along the pathway to domestication [118,119]. The research of Jaenicke-Després et al. [84] on aDNA in maize is a model for the integration of genetic and archaeological research in tracking the direction and timing of the dispersal and evolution of a major crop plant (Box 4). Another study of ancient chloroplast DNA extracted from New World plant remains, dating from >9000 years ago, has documented the dispersal of morphologically domesticated bottle gourd into the New World from Asia (Box 7) [120]. Such studies will be required to track the timing and function of genetic change in plants and animals undergoing domestication and to correlate these changes with the appearance of associated behavioral and morphological markers in the archaeological record.

Concluding remarks – the promise of increasing collaboration

It is becoming increasingly clear that collaborative research efforts that integrate genetics and archaeology hold promise for advancing our understanding of both the domestication of individual species and the origins of agriculture. The need for collaboration between geneticists and archaeologists reflects a shared recognition that the process of domestication is complex and multifaceted. It involves a long sequence of mutualistic interactions between human societies and various target species and, as a result, relevant information takes a variety of different forms at different points along the trajectory of domestication.

An initial hurdle for archaeologists and geneticists is to recognize and acknowledge that not all data pertaining to the domestication process resides within the boundaries of their own discipline. Once they begin to consider the complete spectrum of information that exists, the true cross-illumination potential of genetic and archaeological data will be clear and will result in more-comprehensive and accurate characterizations of domestication. We have discussed several recent and ongoing collaborative projects involving archaeologists and geneticists that address multiple data sets in an effort to understand domestication. Such integrated efforts represent the leading edge

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Box 7. Gourds and dogs enter the New World

The recent integration of archaeological and genetic research on both the bottle gourd (Lagenaria siceraria) and the dog (Canis familiaris) has substantially clarified our basic understanding of the initial domestication of these two early domesticates, their late Pleistocene radiation from Asia across Beringia into the New World and their subsequent diffusion throughout the Americas.

The bottle gourd has long represented an African enigma for researchers interested in the domestication of New World plants. Indigenous to Africa and long valued as a container crop rather than as a food source, the bottle gourd has consistently been recovered in archaeological association with the earliest evidence of New World domesticated plants in many regions of the Americas. Given the genetic similarity between modern African and New World land races of domesticated bottle gourd and the absence, until recently, of any well-documented wild bottle gourd populations that could be employed to establish the wild versus domesticated status of archaeologically recovered rind and seed specimens, the prevalent default consensus has been that L. siceraria was carried by ocean currents as a wild plant from Africa to South America.

A recent study combining genetic and archaeological lines of evidence, however, has overturned this wild from Africa consensus. Erickson et al. [120] analyzed modern Asian and African land races of bottle gourd, along with 12 directly dated rind fragments recovered from archaeological sites in northeast America, Mexico and South America (Figure Ia). Comparative morphological analysis showed that the archaeological rinds represented domesticated plants (the rinds were significantly thicker than those of recently described wild L. siceraria fruits from Zimbabwe), and direct AMS radiocarbon dates indicated that bottle gourd was present as a domesticated plant in the Americas by 10 000 years ago.

Ancient DNA analysis of the archaeological rind fragments yielded even more surprising results. Three DNA sequence polymorphisms that consistently distinguished between modern African and Asian landraces of bottle gourd were identified within the chloroplast genome: two separate 5-bp insertion deletions (InDel) and a G→A transition SNP [120]. The nine archaeological rind fragments predating the arrival of Europeans from which DNA could be amplified

were identical to the modern Asian reference group, indicating that domesticated bottle gourds were carried to the New World during the late Pleistocene from Asia, not from Africa. Although it is possible that the bottle gourd could have been carried from Asia to the Americas by the north Pacific current, it is more probable that, along with the dog, this early domesticate accompanied Paleoindian colonists as they crossed Beringia into the New World.

In a parallel genetic study, Leonard et al. [103,109] resolved the long-standing question of whether the dog was independently domesticated from the gray wolf (Canis lupus) in both Eurasia and the Americas. Analysis of a 425-bp portion of the mtDNA control region obtained from a total of 24 pre-European contact dog skeletal elements recovered from archaeological sites in Alaska, Mexico, Peru and Bolivia, when compared with sequences from 259 modern wolves (30 localities worldwide) and 140 modern dogs (67 diverse breeds), indicated that all ancient and modern domesticated dogs worldwide share a common origin from Old World gray wolves. Further analysis (Figure Ib) shows that ancient dogs from the New World are derived from four distinct haplotypes of modern dogs from throughout the world, suggesting that at least five founding dog lineages invaded North America with humans as they colonized the New World.

This, in turn, suggests there was a substantial amount of divergence in ancient Eurasian domestic dog lineages before this migration. The earliest archaeological evidence for domesticated dogs in the Old World, dating to 13 000–17 000 years Bp comes from several widely dispersed sites extending from the Near East across eastern Europe, and raises questions as to exactly when and in what location(s) the gray wolf was first domesticated. Although the earliest domesticated bottle gourd in the Old World dates to 8000–9000 years Bp in China and Japan, it is reasonable to estimate that it was initially domesticated in the same timeframe as the dog (~13 000 years Bp or earlier), given its arrival in central Mexico by 10 000 years Bp.

Interestingly, both the dog and the bottle gourd, which stand out as the earliest species to have been brought under domestication, are similar in that they are both utilitarian in nature, valued mostly for uses other than as a source of food.
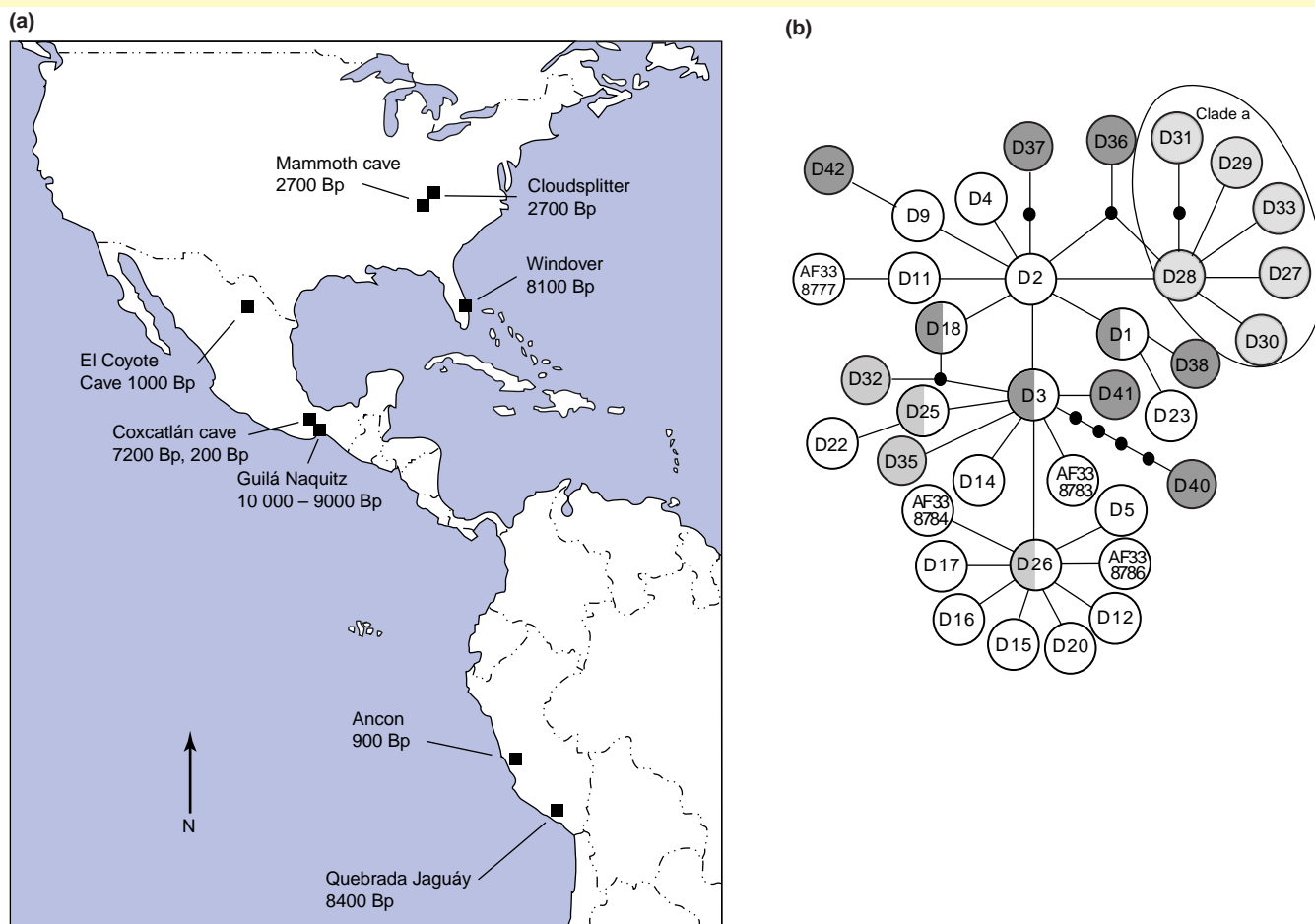
Figure I. The domestication of gourds and dogs in the New World. **(a)** Archaeological sites and the age of bottle gourd specimens analyzed by Erickson *et al*. [120]. **(b)** A minimum spanning network in which haplotypes occupy nodes, and each branch represents a single nucleotide substitution shows that ancient dogs from the New World (dark gray from Alaska, light gray from Latin America) are derived from four distinct haplotypes of modern dogs from throughout the world (shown in white) (D2, D3, D9, D26), with an additional lineage (not shown) derived from haplotype D6. Reproduced, with permission, from Ref. [109] ©2006 University of California Press.

of research in this rapidly expanding area of scientific inquiry.

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