

Evolution during Domestication

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During the process of domestication, plants and animals have evolved under conscious and unconscious selection by humans.

Introduction

Domestication is a genetic selection process exerted – consciously or unconsciously – by humans to adapt wild plants and animals to cultivation and herding, respectively. Because of this process, major crops and domesticated breeds arose, which were not only easier to cultivate or herd but also more appealing to consume or process for further uses. During domestication, plants and animals are subjected to natural as well as human selection. Darwin (1868) observed that ‘No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring ... Man therefore may be said to have been trying an experiment on a gigantic scale; and it is an experiment which nature during the long lapse of time has incessantly tried.’

Timeline and Scope

The first attempts at domestication coincided with the origins of agriculture some 10 000 years ago. Around that time, a global warming episode marked the end of the last ice age across the planet. More or less simultaneously in several locations of the world, a change from hunting-gathering to agricultural economies took place, which had profound consequences for humankind, its way of life, and its environment. On the evolutionary time scale leading to *Homo sapiens*, agriculture appeared relatively late. If one were to represent the approximate length of human evolution from the beginning (as identified by bipedalism) to the current time by a 24 h day, agriculture would have started around 23.55.

Prior to domestication, hunter-gatherers had acquired an intimate knowledge of the plants and animals surrounding them. They understood which plants could be harvested with less effort and gave them fruits or seeds that are more palatable or useful products such as fibres to make ropes. They also recognized which animals live in herds and were therefore more likely to tolerate confinement at high densities in a corral. In addition, it appears that some 5000–10 000 years before the initiation of agriculture, hunter-gatherers broadened their resource

basis from large game to include also the hunting or trapping of smaller animals and the gathering of a range of plants. This broadening has been termed the ‘broad-spectrum revolution’ and is thought to have been a stepping-stone to the ‘Neolithic revolution’, as the initiation of agriculture has been called.

The transition from hunting and gathering to agriculture was truly a revolution for humankind. Not only did agriculture arise, but also around the same time, people adopted a sedentary lifestyle and started living in villages. They also developed other technologies such as pottery. The reasons for this momentous change remain in the realm of speculation, however. Various theories have been proposed, the most credible of which revolve around a disequilibrium between the supply and demand of foodstuffs. It is believed that either a population increase or climate change or a combination of the two caused a shortage in the supply of food and that the first attempts at cultivating plants were meant to supplement hunting and gathering before agriculture would eventually become the principal source of food. The fact that agriculture originated in different places of the world at about the same time suggests that major, long-range climate changes may have been an important impetus. There is no doubt, however, that once agriculture became fully established it caused further increases in population in part because of sedentarity and because children became a labour asset in agricultural societies. Although agriculture is now the predominant source of food, feed and clothing materials, hunter-gatherers still exist today although they seem to subsist in apparently inhospitable regions of the world. Among these groups are included the Australian Aborigines and the !Kung of southern Africa. Some agricultural groups still practise hunting and gathering although on a reduced scale.

How quickly did the transition to agriculture take place? There are surprisingly few archaeological data on this question. Nevertheless, available information from archaeobotanical sequences suggests that domestication took approximately a millennium or more. As will be explained later, this rather slow pace for the domestication process probably reflects a low selection pressure because the rather simple genetic control of the domestication

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syndrome should theoretically allow rapid phenotypic modification.

The advent of agriculture was a necessary condition for the development of human civilizations. The surplus of food produced by agriculture allowed labour specialization so that some individuals in early societies could engage in activities other than food procurement, such as commerce, administration and warfare. It is believed that hunter-gatherer societies were relatively egalitarian, but that following the introduction of agriculture, societies became gradually more hierarchical and oligarchic, finally ending up as city-states governed by a ruler, as illustrated by such civilizations as Sumer and Mari (2500–1500 BC) in the Near East.

Geography of Domestication

Several major and minor centres of domestication (and agricultural origins) have been identified based primarily on the information provided by archaeological and genetic studies (Figure 1). The major centres are usually located in tropical areas between latitudes 35°N and 35°S, in hilly or mountainous areas, and with an alternation of dry and wet seasons. Most of the major crops were domesticated in the Mediterranean and savannah biome, both of which are characterized by an extended dry season (Harlan, 1992). The savannah biome would also include areas with more humid environments such as the dry woodland and tropical deciduous or dry forests. In the northern hemisphere, the dry season occurs in the summer for the

Mediterranean biome and in the winter for the savannah biome.

The existence of a contrast between dry and wet seasons may have provided an impetus towards agriculture as a long dry season would lead to a depletion of foodstuffs, especially towards the end of the season, and a concomitant need to harvest and store enough food to live through this period. It may also explain why many of our major crops are annual species that complete their life cycle in a single wet season. The seeds produced by these plants can be stored during the dry season and planted during the next wet season. In addition, seed dispersal by annual species may be favoured only under the conditions of a dry season, which activates the seed dispersal mechanism.

DNA sequence data, either indirectly through the analysis of molecular markers or directly from the sequences themselves, provides more precise information on the actual area of origin of some crops within a centre of domestication. For example, the origin of maize (Doebley *et al.*, 1984; Wang *et al.*, 1999, 2001) and one of the centres of origin of common bean (Gepts *et al.*, 1986; Gepts, 1988) have been tentatively tracked to the west-central part of Mexico. The origins of einkorn wheat (*Triticum monococcum*; $2n = 2x = 14$) and of bread wheat (*Triticum aestivum*; $2n = 6x = 42$) have been assigned to southern Turkey and Transcaucasia and an area south of the Caspian Sea in Iran, respectively (Heun *et al.*, 1997; Dvorak *et al.*, 1998). Barley, in contrast, may have originated in the mountainous areas of the Levant in the Near East (Badr *et al.*, 2000). The origin of cassava (*Manihot esculentum*) has been located in the western part of Brazil, near the border with Ecuador (Olsen and Schaal, 1999).

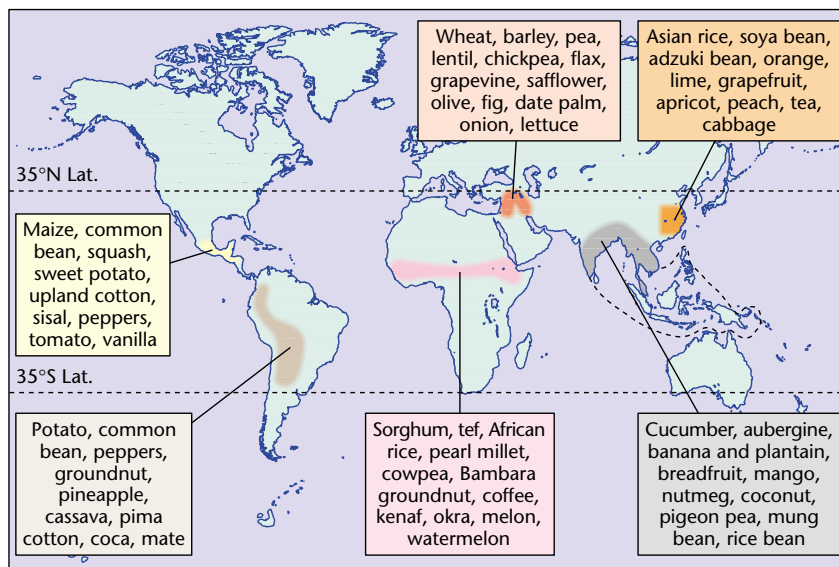


Figure 1 Centres of crop domestication.

Similar studies have been conducted for domesticated animals. Many domesticated animal species were domesticated at least twice in different areas (McHugh and Bradley, 2001). Cattle were domesticated in the Near East (taurine or humpless breed) as well as in India (zebu or humped breed). The pig originated in Europe and in eastern Asia, whereas the sheep came from Europe and central Asia. The water buffalo also was characterized by a double origin, namely in China or Indochina (swamp breed) and in India (river breed). Goats, on the other hand, had possibly three origins. In addition to a major one in the Fertile Crescent, there was a minor one in the Indian subcontinent and a possible third one in central Asia or Europe. No clear centre of domestication could be identified for the horse. Rather, it appears that multiple events in space and time in the Eurasian plains led to the domesticated horse.

Compared to the Old World, fewer animals were domesticated in the New World. They also acquired less importance than the Old World animals. The llama, raised primarily as a pack animal and for its wool, is a domesticated form of the guanaco, distributed from the altiplanos of Ecuador and Peru to the lowland plains of Patagonia. The vicuña is a wild species distributed at very high altitudes close to the snow line. It gave rise to the alpaca, which is raised only for its fine wool. An additional New World animal is the guinea-pig, a double misnomer as this animal is actually a rodent distributed solely in South America. It was bred in pre-Hispanic times for feed and religious purposes.

Within a given region, therefore, most major crop plants and animal breeds appear to have resulted from a single domestication. If more than one domestication took place, it was usually at a considerable distance, most likely in isolation and independently (a phenomenon called vicarious domestication). It appears that somehow a domesticated plant or animal 'prevented' the domestication in the same region – for reasons that remain unknown – of additional related species that could fulfil the same role.

Following domestication, crop plants and animal breeds were dispersed over increasingly longer distances, first in the Old or New World and subsequently between the Old and New Worlds. Some examples include the spread of African crops such as sorghum and cowpea along the Arabian and southern Asian coast to India and the spread of maize from its Mexican domestication centre into Central and South America. Crops of the Near Eastern domestication centre (also called the Fertile Crescent because of its shape deriving from the mountains surrounding the Tigris–Euphrates flood plain) were dispersed in four main directions: to the northwest into Europe, the southwest into Africa, to the northeast into central Asia, and the southeast into the Indian subcontinent.

A crucial date with regard to crop plant and animal breed dissemination is 1492, which marks the arrival of

Columbus in the Americas. The increasingly frequent travels between the Americas, on one hand, and Europe, Africa and Asia, on the other, set in motion the so-called 'Colombian exchange', which represented an exchange of crops and domesticated animals between these two worlds. It led to a remarkable broadening of the available agricultural resources not only for farmers but also for consumers who expanded their daily diet in a considerable way.

Evolution of Genetic Diversity

One of the most important determinants in the evolution of crop plants and animal breeds is the level of genetic diversity contained in the domesticated gene pools, especially with reference to the wild ancestral gene pool. Genetic diversity is important as a necessary condition for further evolution in response to selection pressures, not only in the wild but also in breeding programmes. Animal and plant breeders need genetic diversity as a raw material to develop improved breeds or cultivars.

The absence of genetic diversity can have dire consequences as illustrated by epidemics of diseases in excessively uniform crops. The most famous example of this was the potato famine that struck Ireland in the mid-nineteenth century. Excessive reliance on potato as a staple food led to a widespread famine when the crop was devastated by a fungal disease, the potato late blight. Favourable environmental conditions combined with genetic uniformity of the potato crop as a result of its clonal propagation led to a rapid spread of the disease first in 1845 and then in 1846, when it destroyed nine-tenths of the harvest. At least one million people died of starvation and a similar number emigrated to continental Europe and North America. Similar epidemics affecting genetically impoverished crops devastated coffee in southern Asia in the nineteenth century and maize in the USA in the early 1970s.

In general, results of analyses of genetic diversity in a wild progenitor and its domesticated descendant show that the latter have only a fraction of the diversity present in the progenitor (Doebley, 1992; Gepts, 1993). Three major phases in the reduction in genetic diversity can be identified: (1) the domestication process itself; (2) cultivation in the centre of domestication and dispersal in and from the centre of domestication; and (3) modern breeding practices. Firstly, as mentioned earlier, domestication can be traced – at least for those crops or animals where molecular analyses are sufficiently advanced – to a specific location or area within the distribution region of the wild progenitor. The wild populations in that area came to constitute the initial gene pool of the crop or breed and probably represented only a small part of the diversity contained in the entire progenitor species gene pool. Thus,

from the start agriculture has rested on a rather limited genetic foundation. This foundation could be altered at least in the centres of origin through gene flow between wild and domesticated populations. It is possible that in the initial stages of agriculture when fields were still relatively small, gene flow from wild populations would have increased genetic diversity in the domesticated gene pool.

Secondly, cultivation also reduced genetic diversity through selection pressures induced by the agro-ecosystem and directly (consciously or unconsciously) by humans. Furthermore, the occasional crop failure could have also reduced genetic diversity. Although the devastated crops would have been replaced with seed stocks or breeds from adjacent areas, any replacement could lead to a loss of existing diversity. Furthermore, dispersal within the region or centre of origin or from this centre to other regions or continents of the world also caused a further reduction in genetic diversity. This dispersal entails selection in new environments as well as genetic drift effects resulting from the small sample size actually disseminated. Some crops or animals have actually been dispersed multiple times. For example, some of the crops domesticated in Mesoamerica or South America were first transported to Europe, from where they were further dispersed to other continents such as North America. Every leg of this voyage represented an additional episode of selection and genetic drift, which further reduced the level of genetic diversity of the crop in the newly cultivated areas compared with the diversity in the centre of domestication.

Thirdly, modern plant and animal breeding has further reduced genetic diversity of domesticated gene pools. In part, this is due to the focus on a limited number of commercial classes or breeds favoured by the agricultural industry or the public. Concurrently, breeders focus primarily on elite \times elite crosses to allow them to sustain the progress they have made in previous years. The cost associated with this approach is that the genetic diversity is gradually decreased to that contained in the elite germplasm, unless a conscious effort is made to introduce additional genetic diversity. In crops, several sources exist to markedly increase genetic diversity, depending on the crop involved. They include wild relatives, landrace or heirloom cultivars, and obsolete cultivars and advanced breeding lines.

These sources of genetic diversity are conserved for posterity either *ex situ* (off site) or *in situ* (on site). In *ex situ* conservation, samples of genetic diversity are conserved in gene banks (Frankel *et al.*, 1995). For seed-propagated crops, seed samples are conserved at low humidity (6–7%) and cold temperature (–20°C). For vegetatively propagated crops and for plants with recalcitrant seeds (e.g. tropical fruit trees), living collections of plants are maintained. There are international and national networks of gene banks. *In situ* conservation relies on the activities of farmers in the centres of domestication (see **Figure 1**), who have been maintaining the diversity of crops for thousands

of years and continue to do so, at least in those areas where agriculture is maintained as an economically viable activity (Maxted *et al.*, 1997).

The Role of Hybridization, Escape from Cultivation, and Polyploidy

In most cases, domesticated plants and animals belong to the same biological species as their wild progenitor. They can therefore hybridize with ease and their progeny is viable and fertile. These hybridizations are the first step in the formation of hybrid swarms, feral or weedy populations that combine traits of domesticated and wild types and live near existing or abandoned fields. Such hybridizations and the occurrence of these hybrid swarms have been documented in the major crops (Ellstrand *et al.*, 1999). Their role in the maintenance or loss of genetic diversity in crop or animal populations and that of their wild relatives remains to be fully studied.

One of the consequences of hybridization is the development of allopolyploid crops. Some of our major crops result from ancient or more recent polyploidization events. Maize and soya bean are thought to result from ancient events whereas wheat and cotton have arisen more recently. Polyploidy provides several opportunities for organisms. It can broaden their adaptation by combining the adaptation of the constitutive genomes. It can also provide opportunities for new gene interactions. In cotton, for example, some of the genes promoting fibre production originated in the fibreless parent. By combining genes from the fibre-producing parent with those of the fibreless parent, new epistatic gene interactions may have been created, some of which increased the expression of genes increasing the quantity, size and strength of the fibre (Jiang *et al.*, 1998).

The Domestication Syndrome

Because of the selection process operating during domestication, crop plants acquired a set of new characters that assured their adaptation to cultivated environments and increased their usefulness to farmers and consumers. An examination of a wide diversity of crops shows a recurring pattern involving a set of concurrent traits – the domestication syndrome – that distinguish them from their wild progenitors.

Among crops harvested for their seeds, the best-studied group so far, two of the main domestication traits concern seed dispersal and dormancy. Wild plants disperse their seeds at maturity. This is achieved by distinct mechanisms depending on the type of plant. For example, among wild grasses, the axis of the inflorescence becomes brittle at

maturity of the plant. This brittleness, in turn, releases the seeds, which are then dispersed on the soil around the plant. In the legume family (bean, soya bean, pea, etc.) and the cabbage family, the fruit (a pod and a silique, respectively) opens at maturity and releases the seed. This opening can sometimes be explosive and propel the seeds for a few metres around the plant. Domesticated plants have lost the ability to disperse their seeds for obvious reasons. The axis of the inflorescence in cereals remains whole and the pods and siliques of legumes and cabbage-like plant remain closed at maturity, thus facilitating the harvest of the grain.

Once dispersed, the seeds become part of the soil seed bank. Wild seeds can remain for several years. Every year only a fraction of the seeds germinate, whereas the others remain dormant. The spread of germinating seeds across several years provides a mechanism for plants to minimize the negative effects of unfavourable years. In domesticated plants, dormancy has been eliminated and seeds germinate readily after they are produced. The absence of dormancy provides the farmer with dependable germination and a predictable stand of plants in the field.

An additional trait distinguishing domesticated plants from their wild ancestors is a more compact growth habit. Cereals have fewer branches ('tillers') than their wild counterparts do; the extreme case is maize, which has only one main stem whereas its wild progenitor, called teosinte, has 10–20 branches. Among legumes, some wild relatives are viny, high branched plants; their domesticated descendants are short (< 50 cm), bushy plants with few branches. The expansive growth habit of wild plants helps them compete with other plants for sunlight and other resources. Domesticated plants, in contrast, show reduced competitive ability, because it would only reduce the productivity of other plants of the same crop.

In wild plants, the scheduling of fruit and seed maturation at the beginning of the unfavourable season (cold season in temperate regions and dry season in tropical and subtropical regions) is of paramount importance to ensure high seed production and dispersal. For example, in tropical regions, maturation in the dry season is a necessary condition for the opening of fruits in legumes, which depends on the dryness-induced shortening of fibres along the openings of the fruit. In turn, this shortening causes the fruit to open and disperse the seeds it contains. Scheduling of maturity takes place indirectly via scheduling of flowering. Flowering in many plants depends on the length of the night. Temperate plants generally flower under long days (short nights) whereas tropical plants flower under short days (long nights). When tropical plants such as many of our crops are dispersed to temperate regions, many of them will experience a delay in flowering because they will be grown in the summer under long days. This delay will prevent them from flowering in time to produce grains before the first frosts. Other dispersals, for example within the centre of origin, also involve changes in

day length as well as temperature, which often interacts with the day-length-sensing mechanism. Under these circumstances, crops have been selected for their insensitivity to day length, which broadened their geographic adaptation considerably.

Reproduction is changed in other ways. Domesticated plants sometimes show an increase in self-pollination or vegetative reproduction. These two reproductive modes allow plants to remain true-to-type more easily than with cross-pollination. In fruit crops, vegetative reproduction is sometimes associated with sterility (i.e. the lack of development of seeds), as is the case with banana and the navel orange.

Other traits are related more closely to consumer acceptance. Many of the harvested parts in domesticated plants are much larger than in their wild progenitors. Domesticated seeds in some crops can be from 5 to 15 times larger than seeds of their wild progenitors. As was observed by Darwin, the harvested parts also display a broader range of colours and shapes. Examples of this characteristic are the many colours of bean and maize seeds, the different types of tomato (size, shape and colour of the fruit), and the various types of lettuce leaves, selected largely for aesthetic reasons. The presence of toxic compounds has not prevented the domestication of plants. However, there has often been selection leading to a reduction or loss of these compounds. An example is provided by cassava, where sweet cultivars have a reduced content of a cyanogenic glucoside that releases the highly toxic cyanic acid. Nevertheless, bitter cultivars of this crop still contain high levels of this compound, which may offer protection against insect pests. Farmers have then developed ways to detoxify these bitter varieties, for example by extensive washing or boiling of the grated root pulp.

In animals, selection during domestication has affected primarily size, appearance and behaviour. In contrast to plants, there has been a selection in the initial stages of domestication for smaller size. This is quite a general trait and is actually the main criterion to distinguish domestic from wild animal remains. Subsequently breeds with both larger and smaller body sizes than that of the wild progenitor were selected. For example, domestic horses vary from the small ponies of the Shetland Islands and Iceland to the large Belgian draft horses of western Europe. Additional traits include external characteristics that would allow humans to distinguish different breeds, such as ear size and droopiness and tail length and curliness. Colour of the coats of domestic breeds changed from that found in wild animals, which often had camouflage characteristics. Some domestic coats became piebald with areas entirely devoid of pigment. Length of coats would reflect adaptation to the local environment, with longer and thicker coats found in breeds from colder areas. Shedding of the coat in sheep, for example, was selected against to increase the production of wool.

Many characteristics in domestic animals arise from the retention of juvenile traits into the adult phase. These include the deposition of fat under the skin and in muscles. In addition, there is often a shortening of the jaws, without a reduction in size of the teeth at least in the first stages of domestication, especially in the dog. The horns of cattle, goats and sheep acquire very different sizes and shapes under domestication. In some cases, increases in horn size were selected for religious, status or aesthetic reasons.

One of the juvenile traits extended into adulthood is the submissiveness of younger animals. This would have greatly facilitated human control over domestic animals, in addition to the innate temperament of some animals to stay closer to humans and display a less aggressive or tamer behaviour. An additional trait reinforced by human selection was the tolerance of being corralled and living in a captive environment. Many of the animals that were domesticated already displayed social characteristics in the wild (the cat is an exception). In addition, they showed promiscuous sexual behaviour rather than lifetime pairing. This would allow humans to choose individuals for mating. Another major evolutionary consequence of domestication was the loss of the seasonal rhythm of reproduction so that animals could bear young more than once a year and in any season.

In some seed-propagated crops, the inheritance of the domestication syndrome has been investigated using genome-mapping approaches. The crops studied include maize (Doebley *et al.*, 1990; Doebley and Stec, 1991), beans (Koinange *et al.*, 1996), tomato (Grandillo and Tanksley, 1996), rice (Xiong *et al.*, 1999), and pearl millet (Poncet *et al.*, 1998, 2000). The outcome of these studies was similar. Although there are generally marked phenotypic differences between wild progenitors and domesticated descendants, the overall inheritance of the syndrome is quite simple. It involves recessive genes with major effects (in addition to genes with minor effect). The joint effect of these genes accounts for most of the phenotypic variation observed in segregations, i.e. many domestication traits are highly heritable. Many of these genes are linked in a limited number of regions of the genome. Some of these domestication genes have actually been cloned and analysed. These include the *tb-1* gene for growth habit in maize (Wang *et al.*, 1999, 2001), the *fw2.2* for fruit weight in tomato (Frary *et al.*, 2000), the *Hd-1* for flowering time in rice (Yano *et al.*, 2000), and the SHATTERPROOF gene for fruit opening in *Arabidopsis* (Liljegen *et al.*, 2000).

An important consequence of both plant and animal domestication is that fully domesticated crops and animal breeds have become dependent on humans for their survival and, conversely, the human species would not be able to survive at current population levels without domesticated plants and animals as a source of food. There is, thus, a mutually beneficial relationship between domesticated plants and animals, on one hand, and humankind, on the other. Partially domesticated crops

and breeds only show a few domestication traits or these traits are only partially expressed. Furthermore, many plants and animals are used by humankind, yet they have not been domesticated.

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