PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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J. R. Harlan

Phil. Trans. R. Soc. Lond. B 1976 **275**, 13-25
doi: 10.1098/rstb.1976.0067

Phil. Trans. R. Soc. Lond. B. **275**, 13–25 (1976) [13]
Printed in Great Britain

Plant and animal distribution in relation to domestication

By J. R. Harlan
Plant Genetics, Department of Agronomy, University of Illinois,
Urbana, Illinois 61801, *U.S.A.*

Distributions of wild progenitors provide useful information concerning regions of domestication and ecological limits of adaptation of domesticated plants and animals. The evidence, however, must be carefully qualified by: (1) possible changes in climate since the initiation of domestication, (2) the effects of human activities which may either decrease or enlarge the ranges of wild progenitors, (3) the possibility that progenitors have evolved as well as the domesticates, and (4) the possibilities of transdomestication.

The distributions of races of domesticated plants and breeds of animals provide useful information on the history and diffusion of domesticates, but patterns of variation differ greatly among species. Variation patterns have been identified that may be termed endemic, semi-endemic, monocentric, oligocentric, or noncentric. Interpretation depends, to a large degree, on an understanding of the processes of domestication.

Introduction

An attempt will be made in this paper to assess rather critically the state of the art with respect to the geography of domestication. It would, of course, be impossible to treat the subject itself exhaustively; that would require a large volume. Instead, I shall present some of the problems to be resolved and illustrate with selected examples. We shall be concerned here with distributions of two general kinds: (*a*) the near relatives and potential progenitors of domesticates, and (*b*) variation patterns of the domesticates themselves.

Useful information can be generated by a study of the nearest relatives of the domesticated plant or animal in question. The information can tell us something about where, or even sometimes when, a species was domesticated. Serious problems of ignorance and interpretation often arise, however. In some cases we have not identified the progenitor with any certainty. More often, the progenitor has been little studied in the field and we are ignorant of its distribution and ecological adaptation. Sometimes we are not sure if the putative progenitor is wild, feral, escaped, naturalized, or a derived weedy race. Indeed, it seems likely that, in some cases, we are no longer able to unravel the evolutionary pathways because of extensive genetic modification of both domesticated and nondomesticated populations.

We have good evidence to believe that climates have changed since initial domestication of some species and that the present distributions of progenitors may not faithfully reflect distributions of the ancient past. Human disturbance over the millennia may have drastically altered original distributions of species. Weedy races may have enlarged their ranges, non-weedy ones may have been seriously reduced and a few have become extinct or nearly so. There are cases of multiple domestication and some domesticates easily revert to a wild or weedy status. In some species the distribution of progenitors is too wide to be very meaningful, and in a few cases domestication may have taken place outside the natural range of the wild races.

It must be admitted that some cases are ambiguous and always will be because the evidence needed to unravel the domestication process has disappeared. More often the ambiguity is due to ignorance and lack of detailed study. Too often we have failed to do our field work. The best approach is to treat each example separately and to depend more on integrated evidence than on the occasional aberrant item that fits with nothing else (Harlan & de Wet 1973).

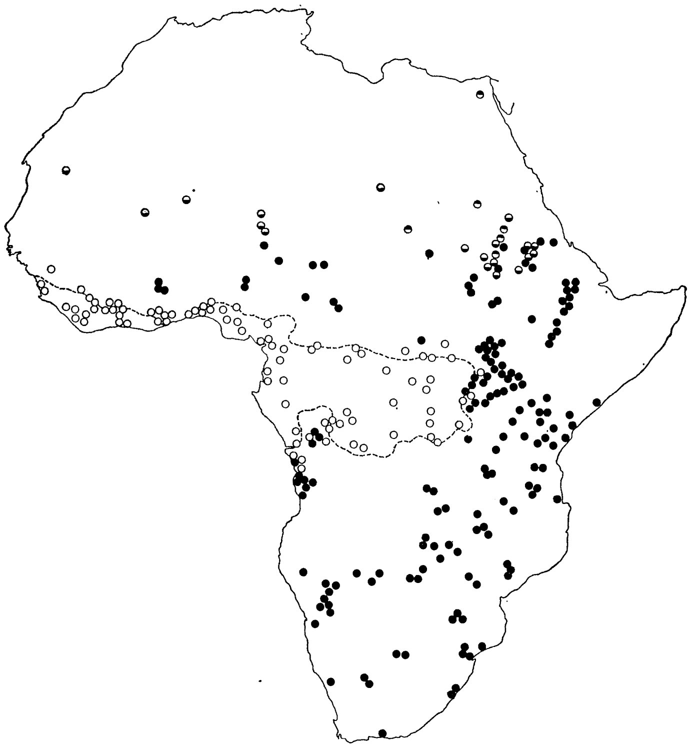


FIGURE 1. Distribution of the wild races of *Sorghum bicolor*. Each circle represents at least one authentic collection either of seed or herbarium specimen. ●, *verticilliflorum* race; ○, *arundinaceum* race; ◒, *aethiopicum* race; ◓, *virgatum* race. Dotted line approximate limit of forest.

THE SORGHUM MODEL

Sorghum is a useful model because it illustrates several points rather clearly and unambiguously. The distributions of the wild races of *Sorghum bicolor* are shown in figure 1. Each circle represents at least one authentic collection either of seed or herbarium specimen. The distribution is obviously too widespread to indicate the region of domestication. On ecological grounds, however, the *arundinaceum* race (open circles) can be eliminated. That race is adapted to the forest zone (dotted line) and thrives under rainfall much too high for cultivated sorghum to do well. As a crop, sorghum is adapted to the savanna and not the forest. On morphological, genetic and ecological grounds, the *virgatum* and *aethiopicum* races can also be discounted. The widespread and enormously abundant *verticilliflorum* race is by far the most likely progenitor of domesticated sorghum. The range, however, is still too wide to help much in locating the centre of domestication.

Archaeological evidence is rather consistent in showing that agriculture was relatively late in southern Africa and that indigenous African plant domestication, in general, evolved north of the equator and south of the Sahara. If this is true, then sorghum would appear to have been domesticated in the northeast quadrant of Africa, and to the south of wherever the Sahara was at the time.

The *verticilliflorum* race of sorghum is a truly wild grass and frequently a dominant of the tall grass savanna. In Sudan, especially, it may build massive stands over hundreds of thousands of hectares. Two examples of disturbance of the natural stands are worthy of note, at Kassala and Jebel Simsim. With the construction of the Aswan Dam, the waters of Lake Nasser forced the evacuation of some thousands of people from the Wadi Halfa area. An irrigation project was established near Kassala which used water from the Atbara River. Land was levelled, ditched and drained for irrigation. The project was set down in the midst of a vast sea of wild sorghum. The wild grass without any apparent genetic modification has been able to persist along ditches and roadways. It appears to be mildly weedy but is not aggressive in the fields. The people from Wadi Halfa prefer wheat to sorghum so that cultivated forms are not grown on the project and the wild sorghum has had no chance to interact with domestic races.

To the south at Jebel Simsim, the pattern is strikingly different. Here a dryland project was established by ploughing down massive stands of wild sorghum and other tall grasses. Domesticated sorghum was grown as one of the rain-fed crops. Within two years a race of weed sorghum had appeared. The plant type is very much like cultivated sorghum with thick stalks, wide leaves and sometimes even crook-necked peduncles. The spikelets are typical of shattercanes, however, and they shatter by way of abscission layers as do those of wild sorghum. This kind of weed is a serious pest not only in Sudan, but in other African countries where sorghum is grown. It is typically a weed of the field, not along ditches and roadsides. These shattercanes tend to mimic the cultivated races with which they grow. If the crop has loose, open heads, the shattercane will have loose open heads; if the crop has dense heads, the shattercane has dense heads. The weed is obviously derived from genetic interaction between wild and cultivated races.

In the U.S.A. there is another kind of shattercane that has become a serious pest of the fields. This one evolved a secondary seed dispersal mechanism. Instead of forming an abscission layer, the inflorescence branches become thin and fragile a short distance below the basal spikelet of a raceme. Several spikelets may fall together or the rachis may fragment between them, but the abscission layer is suppressed. Genetically, this is accomplished by a single gene (*sh*) in recessive condition. All domesticated sorghums are of the *shsh* genotype while wild type and African shattercanes are *ShSh*. All shattercanes so far observed in the U.S.A. are like cultivated sorghums in this respect and it seems clear that these weeds were derived directly from domesticated sorghum and not by genetic interaction with wild races.

In *S. bicolor*, then, we have four distinct and easily identifiable kinds of races: (*a*) truly wild grasses, (*b*) mimetic weeds, (*c*) U.S. shattercanes with a secondary seed dispersal system, and (*d*) domesticated races. In sorghum there is no ambiguity about which races are wild and which are weeds nor about the origins of the weed races (Harlan & de Wet 1974).

An extensive analysis of variation patterns among the domesticated races revealed some interesting features (figure 2). Of the five basic races of sorghum, the *bicolor* race is the most primitive and has such a widespread and diffuse distribution that it tells us little about the origin of sorghum. The *guinea* race is basically West African, although it is found here and there along the East African highlands and it did find its way to India where it is grown on a small scale.

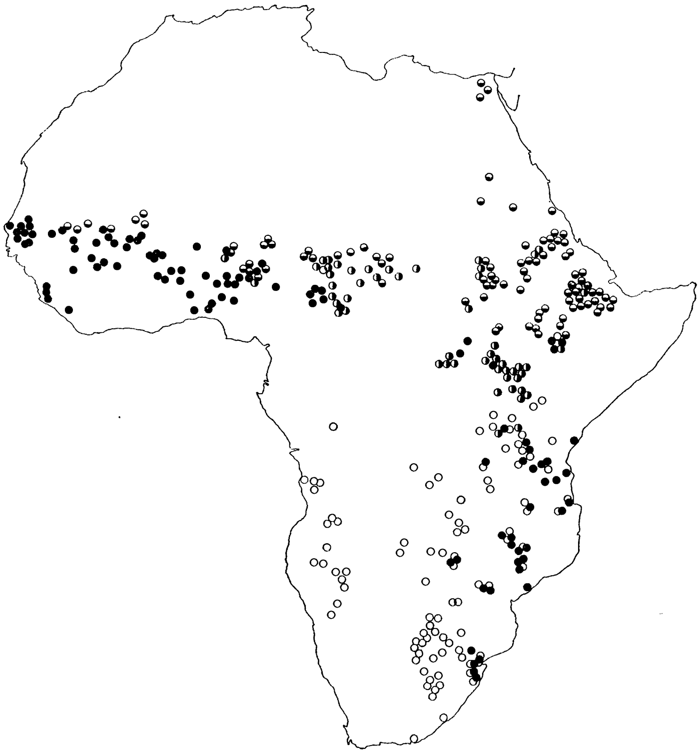


Figure 2. Distribution of cultivated races of sorghum in Africa. ●, *guinea* race and half *guinea* races; ○, *kafir* race and half *kafirs*; ◑, *caudatum* race and half *caudatums*; ◒, *durras* race and half *durras*. The entire collection could not be shown.

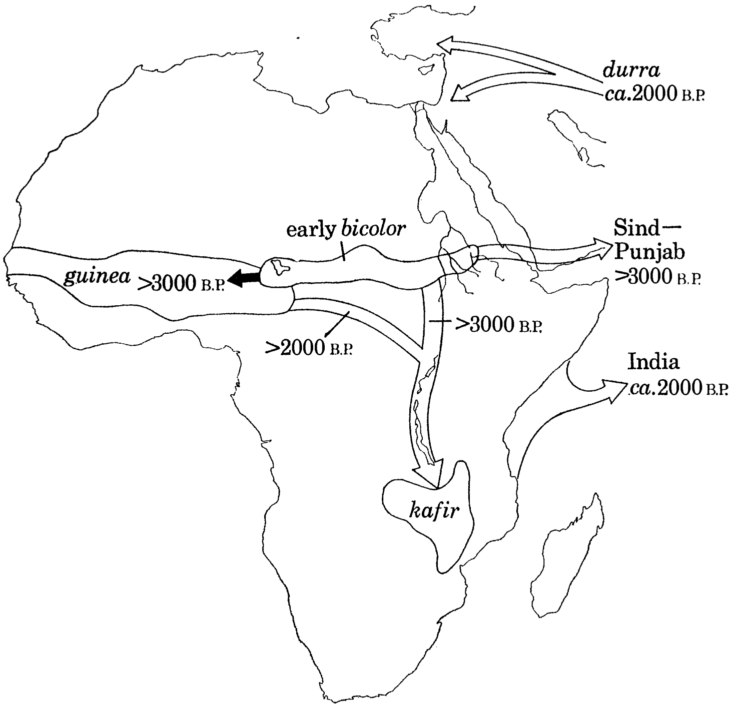


Figure 3. Postulated early history of domesticated sorghum. The most primitive race and the first to be domesticated is race *bicolor*. The specialized races evolved later in different regions.

The *guinea* race is better suited to high rainfall than any other race. The *kafir* race is the common sorghum of southern Africa and was essentially confined to that region until recent times. The *caudatum* race has a clear-cut distribution centred on a Chad–Sudan–Uganda triangle, and has not spread appreciably until recently. (Modern U.S. grain sorghums are basically *kafir–caudatum* intermediates.) The *durra* race is highly specialized, drought tolerant, and is the most common race of India, Pakistan, and the Near East. We have speculated that it may well have evolved in India from an early *bicolor* and is intrusive in Africa (figures 3 and 4) (Harlan & Stemler 1976).

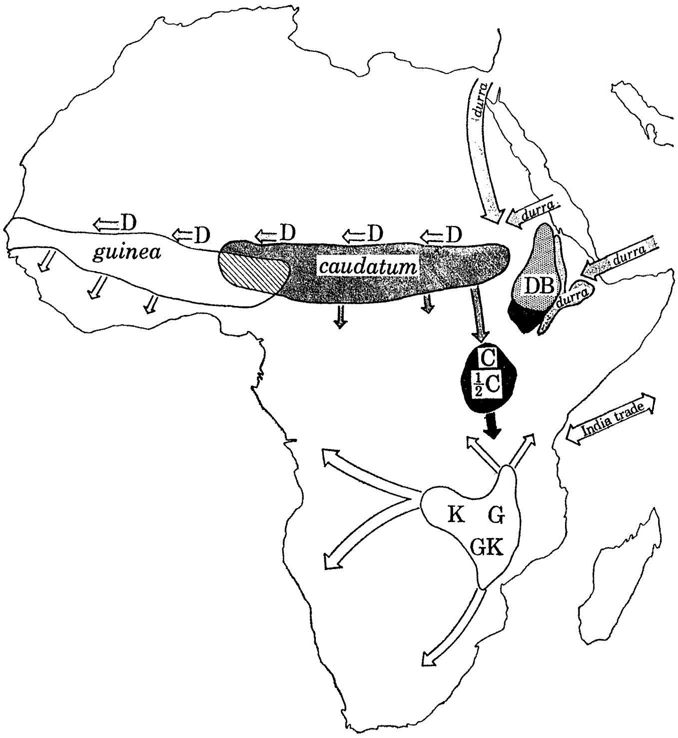


Figure 4. Postulated later events in the evolution of domesticated sorghum. C, *caudatum*; D, *durra*; G, *guinea*; K, *kafir*; DB, *durra–bicolor*; GK, *guinea–kafir*. Dark shaded area in southern Ethiopia has an unusual assemblage of races, but has not been adequately studied for interpretation.

The evolution of the basic races of sorghum in different geographic regions is clear and unambiguous, but a satisfactory interpretation is not so clear. Did the four specialized races each evolve from a primitive *bicolor* as postulated in the figures, or were there two to several independent domestications? The variation pattern is too neat and consistent not to mean something but there are alternative interpretations. Where is the centre of origin or a centre of diversity? We have postulated an origin based on distribution of wild races and integrated anthropological evidence. The origin is not discernible from an analysis of variation within the crop. There is no centre of diversity for sorghum although each of the four specialized races has a centre. As far as domesticated sorghum is concerned, the pattern is noncentric; the crop does not have a centre.

The pattern may not be uncommon. A similar situation might be argued for American beans (Brücher 1968; Gentry 1969), radish (Sinskaya 1931), *Brassica campestris* (Sinskaya 1928), possibly cattle, pigs, and dogs (Isaac 1970). Noncentric variation patterns appear to be characteristic of domesticates with wide distributions that were derived from progenitors that also had extensive geographic distributions.

OTHER EXAMPLES

We have recently analysed another African cereal (*Pennisetum americanum*) in some detail. It is also morphologically, ecologically and genetically clear and unambiguous in that there are three kinds of races easily distinguishable: (*a*) truly wild grasses, (*b*) mimetic weeds of the fields, and (*c*) domesticated forms. Pearl millet (also called bullrush millet) is the most drought resistant of tropical cereals and is grown in the driest zones in which farming can be practised both in Africa and India. The wild races are found in the Sahara and along its southern fringes (figure 5).

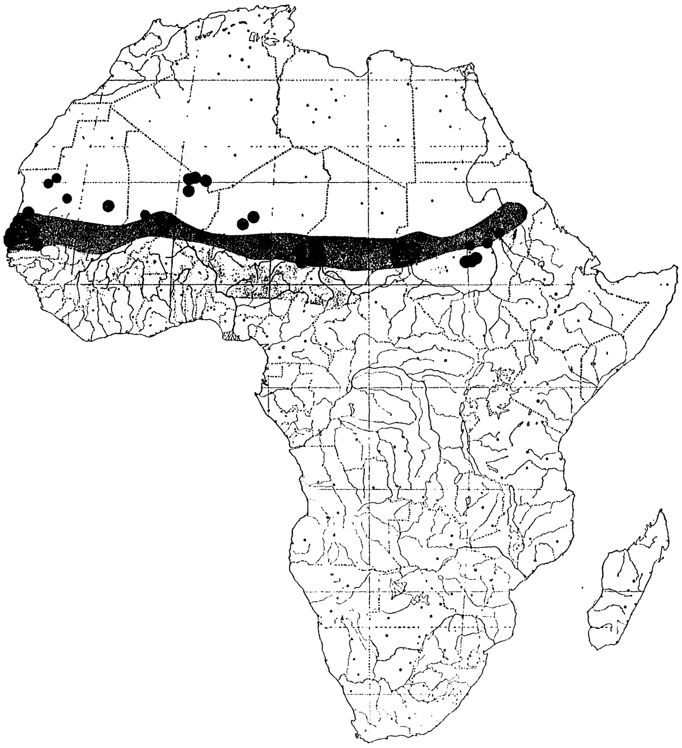


FIGURE 5. Distribution of wild races of pearl millet (●) and the northern pearl millet belt of Africa. Dark shading, millet the dominant crop; light shading, millet grown but less important than sorghum. The crop is also grown in eastern and southern Africa in areas not relevant to its origin.

Domesticated pearl millet shows a variation pattern somewhat analogous to that of sorghum. The *typhoides* race is widespread, found in every area where pearl millet is grown and the only one to escape the continent of Africa until the distribution of recent collections. Three other races have limited distributions along the pearl millet belt: *nigritarum* in Chad, Niger, eastern Nigeria, *globosum* in western Niger, Mali, Upper Volta, and *leonis* in Sierra Leone and Senegal. Any sort of a centric pattern is rather obscure other than a long belt in the Sahel from Sudan to Senegal.

On the other hand, the distribution (figure 5) looks rather truncated, and the question must be raised: was pearl millet domesticated in the Sahara before the present desiccation? Wild races still occur in the desert. We know that the whole of the Sahara was inhabited by neolithic peoples through the fifth and sixth millennia B.C., and that a fair number of villages persisted as late as the first millennium B.C. Perhaps the centre of origin and/or centres of diversity were wiped out by desiccation (Clark 1970).

The effects of a change in climate are suggested by distributions of spontaneous barley (figure 6), einkorn (figure 7), and emmer (figure 8). Disjunct distributions occur in each case

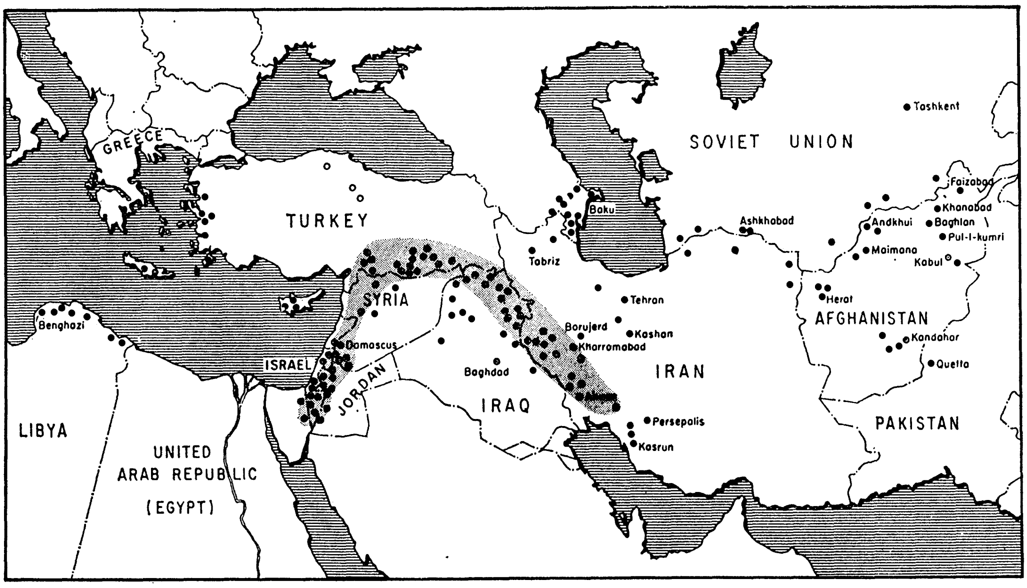


FIGURE 6. Distribution of spontaneous barley. In the shaded area, wild barley may occur in fairly primary habitats; elsewhere it grows more often in segetal habitats (from Harlan & Zohary 1966).

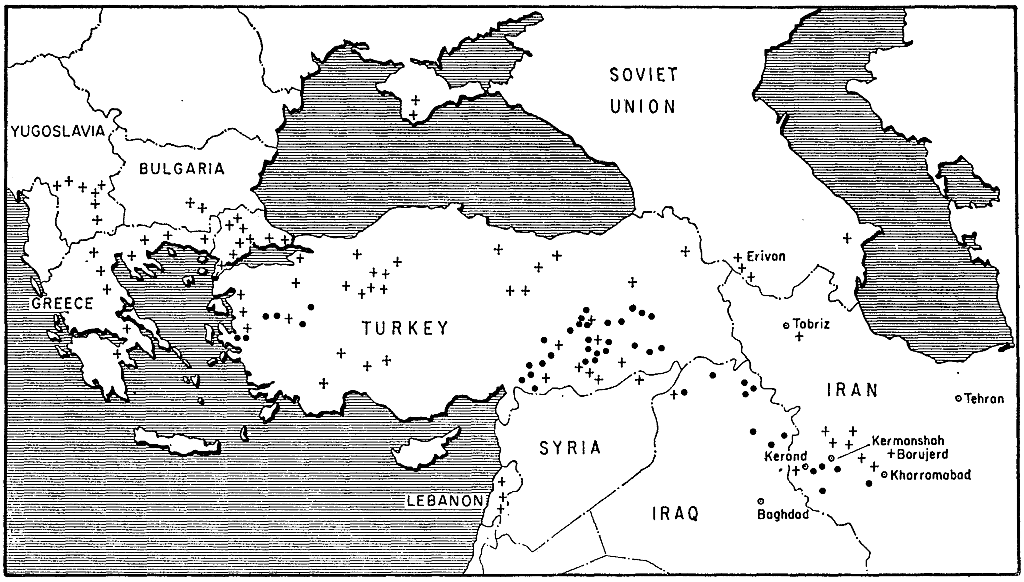


FIGURE 7. Distribution of wild and weedy einkorn. ●, fairly primary habitats; +, populations in segetal habitats (from Harlan & Zohary 1966).

with the implication that distributions were once continuous and became disjunct through a shift in climatic zones. A shift to the southward would close the gaps in each case. There is considerable evidence to indicate that the Mediterranean winter rainfall climate had shifted substantially southward during the period of higher rainfall in the Sahara just mentioned. Wendorf & Schild (1976) reported barley-like pollen from Nile Terraces of Upper Egypt dated to about 12000 B.C. The present distribution of spontaneous barley may great underestimate the region available for wild grain harvests and domestication of the Near Eastern cereals.

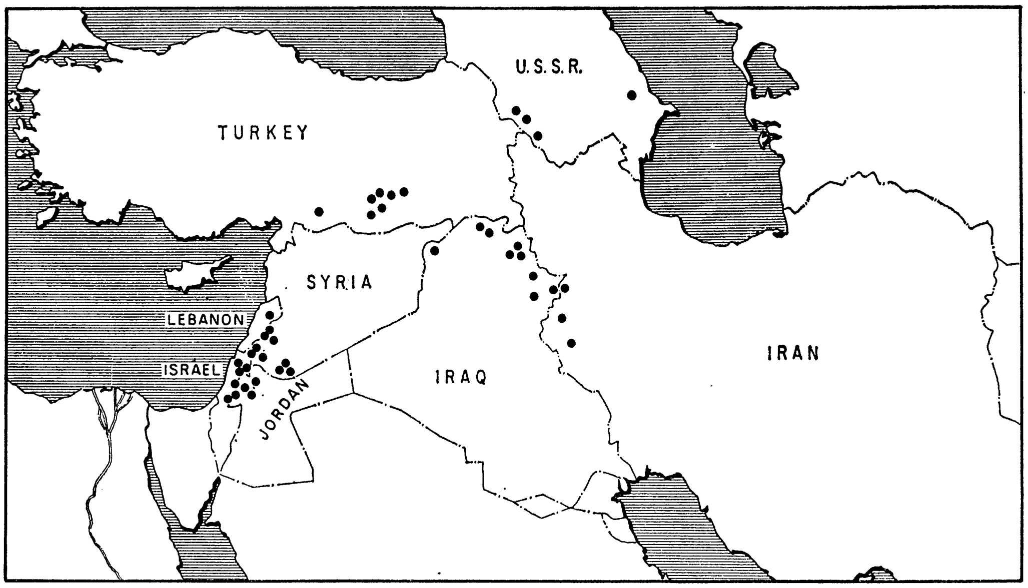


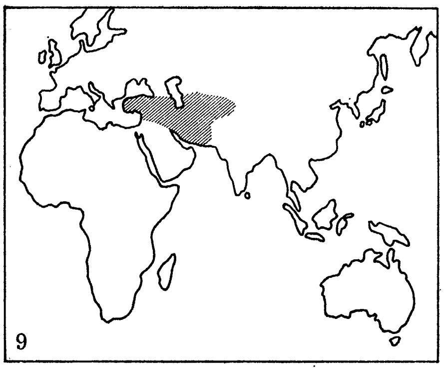
FIGURE 8. Distribution of wild emmer (from Harlan & Zohary 1966).

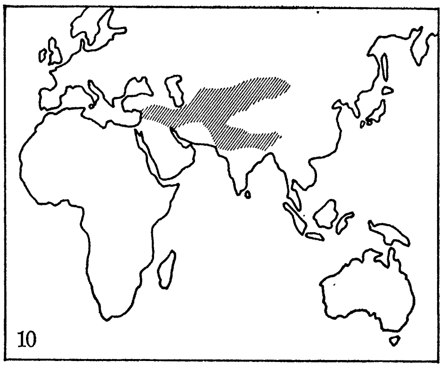
At the time these maps were prepared (Harlan & Zohary 1966) we attempted to distinguish wild races from those that might be derived weeds. The attempt was only partially successful and I do not believe we have learned enough in the meantime to alter our views. There is a race of wild barley that grows along wadi bottoms far removed from farming areas. It is easily recognized and distinct morphologically from the other spontaneous races which may grow in fairly undisturbed sites or may be enormously abundant along roadsides, the edges of fields, in abandoned gardens or even on top of mud walls. Einkorn can also be weedy or not weedy with no obvious difference in morphology, while emmer does not seem to have evolved weedy races and is almost always found in relatively primary habitats.

If these interpretations are approximately correct, it might be reasonable to assume that the ranges of spontaneous barley and einkorn have enlarged somewhat with the spread of agriculture while the range of wild emmer may have contracted. At any rate, it must always be borne in mind that geographic distributions may be drastically altered by human activities as well as by changes in climate.

As for animals, the problems are basically the same. Reported distributions of wild goat (figure 9), sheep (figure 10), and cattle (figure 11) are presented (Isaac 1970). While their ranges overlap to some degree, these animals did not necessarily occupy the same ecological niches. The wild goat is fairly well restricted to rough and precipitous topography while wild sheep prefer more open country and gentler slopes. The range of wild cattle was so great that a distribution map tells us very little about the region(s) of initial domestication.

Again, it is necessary to assess the effects of changes in climate and vegetation and the influence of human activities. In general, the archaeological record for animals is better than for plants because bones are better preserved, often more diagnostic, and are more easily recovered. Ancient distributions of animals are usually better known than those of plants. This is a help, but there are problems in distinguishing wild from domesticated forms, especially early in the process of domestication, and there are problems in identification of progenitor races. Wild cattle and horses have become essentially extinct because of hunting and the present ranges of some other animal species are much reduced.





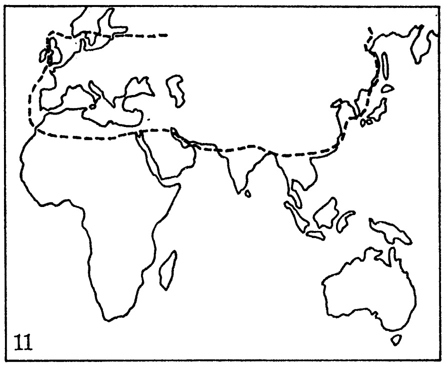
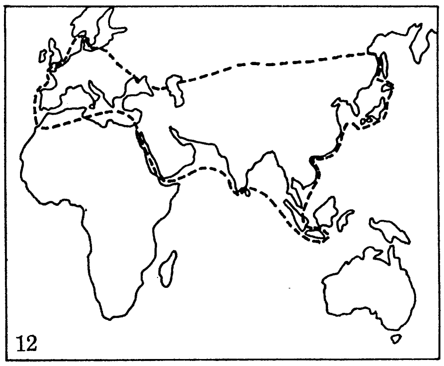
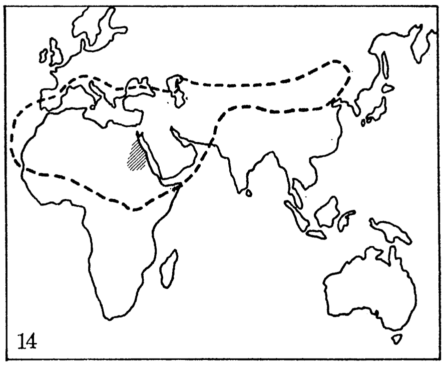


Figure 9. Distribution of wild goat (after Isaac 1970).
Figure 10. Distribution of wild sheep (after Isaac 1970).
Figure 11. Distribution of wild cattle (after Isaac 1970).

On the whole, the case for domestication of the goat within the area of its recent range is reasonably good. The sheep is more complicated for want of consensus as to which wild race was actually domesticated. The vast range of wild cattle leaves open the possibility of multiple domestications. Distributions of pig (figure 12) and species of *Canis* (figure 13) invite similar conclusions. The ass also had a wide distribution (figure 14) but the area of domestication is thought to be Egypt and Nubia.

Species with very wide natural distributions are very likely to have been domesticated more than once. Cattle, dog, pig, sorghum, rice in Asia (figure 15), foxtail millet (*Setaria italica* from *S. virdis*) panic millet (*Panicum miliaceum*), and bottle gourd (*Lagenaria siceraria*) are examples. Useful information may be developed by a detailed study of both wild and domesticated races





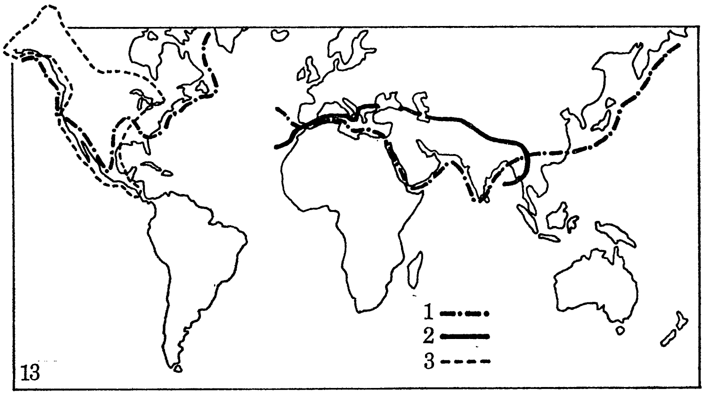


Figure 12. Distribution of wild pig (after Isaac 1970).

Figure 13. Distribution of *Canis* spp. (1) southern limit of the wolf; (2) northern limit of the jack (3) coyote (after Isaac 1970).

Figure 14. Distribution of the wild ass. Shaded area thought to be centre of domestication (after Isaac 1970).

Figure 15. Distribution of wild rice in Asia.

as outlined for sorghum above, but such analyses may not resolve the problem of multiple domestications. It is extremely difficult, if not impossible, to sort out variation patterns derived from long and complex histories from those generated by repeated domestications.

It is clear that man tends to be attracted by the same kinds of plants and animals everywhere. Camelids were domesticated in Asia and South America, ducks in both the Old and New Worlds. Different species of *Amaranthus*, *Solanum*, *Dioscorea*, *Lepidium*, *Lupinus*, *Gossypium*, *Canavalia*, *Ipomoea*, and *Prunus* were domesticated in the Eastern and Western hemispheres. *Oryza glaberrima* was domesticated in Africa and *O. sativa* in Asia. In the Americas, five species of *Cucurbita*, five of *Capsicum*, seven of *Annona*, and four of *Phaseolus* entered the domestic fold. In the Old World, we may count six species each of *Brassica* and *Vigna*, at least five of *Prunus* and *Allium*, several of *Dioscorea*. I have recently compiled a list of crops (Harlan 1975) that includes no less than forty genera with two or more domesticated species. If this is a general pattern, as it appears to be, it would be surprising if widespread species were not domesticated several times in different parts of their geographic ranges.

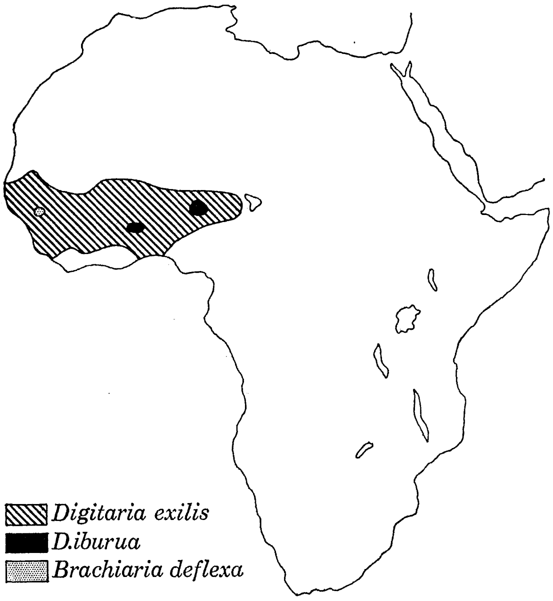


Figure 16. Distribution of three African millets. *Brachiaria deflexa* and *Digitaria iburua* are endemic crops, *D. exilis* semi-endemic.

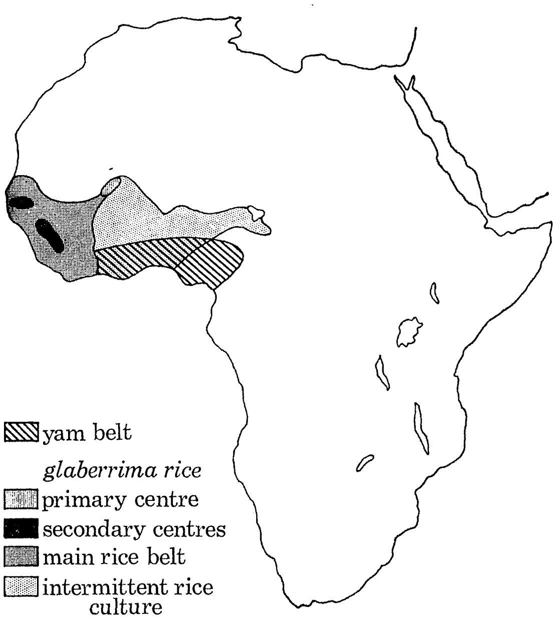


Figure 17. Distribution of semi-endemic African rice and the African yam belt.

Classification of distribution patterns

The interactions of time, space, and biological evolution are revealed by the distributions of domesticated plants and animals. I have classified distribution patterns into the following kinds (Harlan 1972, 1975).

Endemic. A domesticate occupying a well-defined small geographic region. The progenitor may be widespread or restricted. The centre of origin and the centre of whatever variation there is must coincide. Examples are guinea millet (figure 16), black fonio (figure 16), *Paspalum scrobiculatum*, *Panicum miliare*, *P. sonorum*. Among animals the Mithan of Burma-Assam might be mentioned.

Semi-endemic. Domesticates with a somewhat wider range. A centre of diversity may be discernible with some diffusion out of it, or as in the case of African rice, there may be several nodes of variability (figure 17). Other examples include *Eragrostis tef*, *Guizotia abyssinica*, *Digitaria exilis* (figure 16), reindeer, Bactrian camel, yak, the South American animal domesticates, llama, alpaca, guinea pig, Muscovy duck, etc.

Monocentric. Domesticates with wide distribution and a discernible centre of origin, which is also likely to be a centre of diversity. These tend to be rather recent plantation crops such as coffee, rubber, cacao, oil palm. Perhaps the ass (figure 14) might fit the pattern, but in general widespread ancient domesticates are likely to have more than one node or centre of diversity.

Oligocentric. Domesticates with wide distribution and two or more discernible centres of diversity. Familiar examples are wheat, barley, pea, lentil, chickpea, flax, maize, lima bean, water buffalo, sheep, goat, horse, chickens, ducks, etc.

Noncentric. Domesticates with ample distribution but no clear centre of origin or centre of diversity as shown for sorghum earlier. Other examples are American beans, radish, colza (*Brassica campestris*), and bottle gourd. It may be that the pig, cattle and dog fit this anomalous pattern fairly well.

It may be worth while to mention the concept of transdomestication. It was originally applied to guar by Hymowitz (1972). In this case, the crop is grown in India and Pakistan, but the nearest relatives are all African. One species that might be progenitor is reported in Arabia as well. Some think the tomato might fit the pattern with wild races in Peru and Ecuador and domestication taking place in Mexico and Guatemala. Sesame is another possibility, but its progenitor has not been identified with certainty. It is easier to think of modern examples, however, such as rubber, coffee, cinchona, oil palm and cacao. The last was, of course, domesticated in ancient Mexico, but much of the plantation material in Africa and Asia is derived from wild races of South America. Transdomestication may not be a major factor but can explain some anomalous distributions.

Perhaps, I have presented enough examples to show that the processes of domestication do not follow neatly set pathways. Each species is a case of its own. Domesticates that were highly successful with widespread distributions tend to show different variation patterns from those with more restricted ranges. The relationships of weedy and feral races to domesticated ones may be complex and take on a variety of forms. It is clear that some crops are derived from weeds and that some weeds are derived from crops. In recent history, horses, cattle, and camels escaped into the wild in the U.S.A. where they were introduced. They behaved as though they were a part of the native fauna and did not require any help or interference by man. Feral dogs and cats are common, and how is one to classify the pigeons of Trafalgar Square? They appear to be weedy, but encouraged by those who feed them. On the other hand, the house mouse, brown rat, house sparrow, starling, roaches, and fruit fly seem to thrive under human disturbance despite active prejudice against them. The feral or weedy adaptation may or may not be an intermediate state of semidomestication.

The point is that some domesticates can become undomesticated and that some variation patterns can be confounded by intermediate states and conditions. This is to be expected, since domestication is an evolutionary process, but the history of domestication of a species can often be traced by a detailed study of the distributions of its wild relatives and of the domesticated races and breeds. When this is not possible, it is usually because of insufficient studies or because the necessary information has disappeared.

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