Seed Dispersal in Relation to the Domestication of Middle East Legumes[1]

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Modification of seed dispersal was perhaps one of the most important steps towards domestication of seed crops. Among the legumes of the Middle East, four patterns of such modification can be distinguished in the process of domestication. The initial stage of domestication of lentil, pea and grass pea was apparently due to a single mutation in a major gene that prevented pod dehiscence. In chick pea the domesticated type was formed by accumulation of several mutations in minor genes that reduced the amount of pod dropping and shattering. From a seed dispersal point of view, fenugreek was preadapted to cultivation since the wild species do not shatter their seeds. In the bitter vetch and common vetch partial seed shattering apparently was tolerable and desirable under cultivation since the seed served merely for sowing the next year crop.

The Neolithic revolution in the Middle East was associated with plant and animal domestication. The role of cereals, wheat and barley in particular, in that agricultural beginning is unquestionable. Remains of legume seeds unearthed in various excavations of early settlements of Neolithic man suggest that pulses have been utilized by man almost since he began to exploit cereals (Renfrew, 1969, 1973). It is difficult to estimate the proportion of pulses in the grain sack of the Neolithic farmer but it apparently was small in comparison with wheat and barley. Even today, in the traditional agricultural belt of the Middle East, the pulses are grown on relatively small scale, less than 1% in comparison to wheat and barley cultivation. Since legumes are crops of secondary importance, it is surprising how many of them were domesticated in that area. The edible legumes, lentil, pea, chick pea, grass pea and fenugreek, are all of Middle East origin. Occasionally the broad bean is also regarded as originating in the Middle East, but the evidence for this is very slim (Ladizinsky, 1975). In addition, two fodder legumes, common vetch and bitter vetch, were apparently domesticated in the Middle East.

Wild plants are usually equipped with various means for assuring effective seed dispersal. In seed crops, domestication is, in part, considered as a modification of the seed dispersal mechanism of the wild plant which allows regular and extended harvest with minimal loss of yield. By comparing the mode of dispersal of the wild progenitors of the pulses to that of their cultivated counterparts the following patterns of domestication can be distinguished:

Complete modification of the seed dispersal mechanism

Lentil, *Lens culinaris*, is an important field legume in many Asiatic countries and it is grown extensively also in Ethiopia, northern Africa and southern Europe. The plant is small and characteristically a short season crop. In a recent study the wild species *L. orientalis* was proved to be the wild progenitor of the cultigen

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(Ladizinsky, 1979a). These two lentils are cross compatible and their hybrids are almost fully fertile. The cultigen is cross compatible also with another wild lentil, *L. nigricans*, but the hybrids in that case are much less fertile due to irregular chromosome pairing at meiosis. Plants of *L. orientalis* are tiny, producing several pods which dehisce and immediately shatter their seeds when dry. In the cultivated lentil the dry pods remain intact for a long time and thus can be harvested and threshed.

The behavior of *L. culinaris* × *L. orientalis* F_1 hybrids and the segregation pattern of F_2 populations indicate that pod indehiscence of the cultivated type is governed by a single recessive gene (Ladizinsky, 1979b). Thus, domestication of lentil apparently occurred as a result of man selecting a spontaneous indehiscent pod mutant from his field of *L. orientalis*. Once that happened new relationships emerged between man and the mutant lentil. Unlike *L. orientalis* which had to be harvested before maturity in order to avoid loss of seeds, the pods of the mutant remained closed for a longer time allowing an extended harvest and consequently greater yield. On the other hand, that mutant became totally dependent upon man for dissemination.

From a genetic point of view, primary lentil domestication was a single step event due to mutation in a major gene and it is fully comparable to the initial domestication of wheat and barley.

A similar domestication pattern apparently occurred also in pea. The cultivated pea, *Pisum sativum* originated from the *P. elatius–P. humile* complex of species (Lamprecht, 1951; Ben-Ze'ev and Zohary, 1973). These wild species shatter their seeds immediately after desiccation of the mature pods. In the cultivated pea the dry mature pods remain closed. Mature pods also remain intact in the grass pea, *Lathyrus sativus*, and seed dispersal in the wild *Lathyrus* species, botanically related to the cultigen, is similar to that of wild pea and lentil.

In carbonized material, unearthed in archeological excavation, domesticated wheat and barley can be distinguished from the wild types by their non-brittle rachises and hence the time and place of domestication can be estimated rather accurately. Identification of this kind is very difficult, if not impossible in lentil and pea. These legumes are identified according to seed size and seed shape, characteristics that were changed very little by domestication, at least in the first stages. The contemporary small-seeded lentils are almost indistinguishable by their seed size and shape from *L. orientalis* and to some extent from *L. nigricans* (Fig. 1). The large-seeded lentils are apparently a late development in this cultigen (Renfrew, 1973). Zohary and Hopf (1973) concluded that lentil seeds found in the pre-pottery B level in Jericho must be of the domesticated type since no wild lentil grows in the vicinity of Jericho. But *L. orientalis* is found even today in the Judean hills, about 20 miles west of Jericho where it often forms sizeable populations. Thus, the possibility that lentil seeds found in Jericho were collected elsewhere in the wild and brought to the site, cannot be eliminated.

Reduction of the efficiency of the dispersal mechanism

The seed dispersal mechanism of the wild chick pea species is different from that of wild pea and lentil. Dry mature pods of wild chick peas remain attached to the plant for a relatively long time before they finally shed, burst on the ground and shatter their seed. The cultivated chick pea, *Cicer arietinum*, is perhaps the

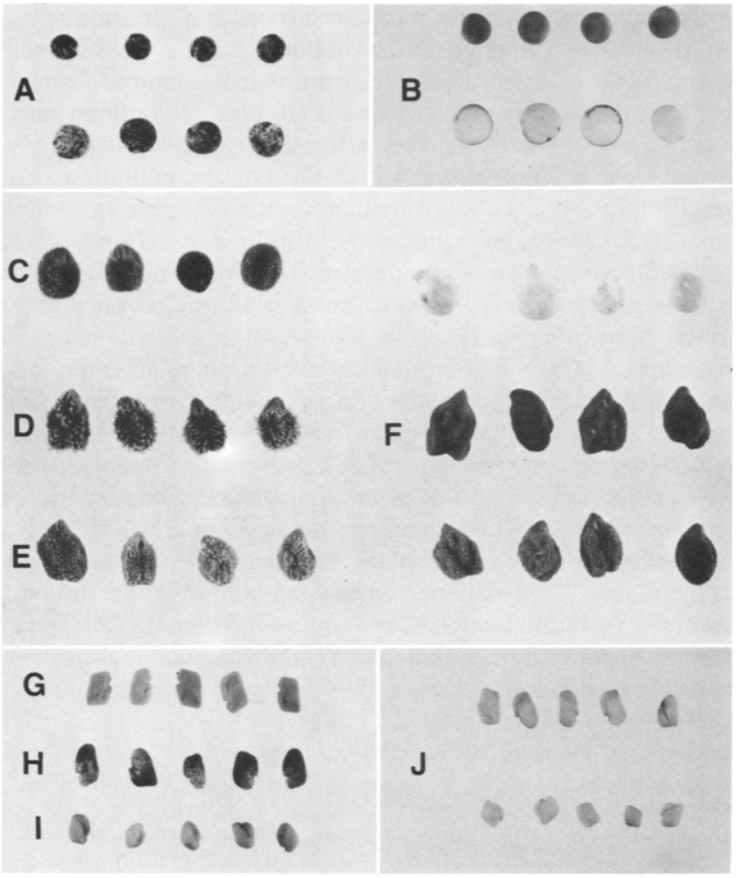

Fig. 1. Seeds of cultivated (B, F, J) and wild (A, C, D, E, G, H, I) legumes (natural size). A. *Lens orientalis*, B. *Lens culinaris*, C. *Cicer bijugum*, D. *Cicer echinospermum*, E. *Cicer reticulatum*, F. *Cicer arientinum*, G. *Trigonella berythea*, H. *Trigonella macrorrhyncha*, I. *Trigonella gladiata*, J. *Trigonella foenum-graecum*.

most important field legume in the traditional Mediterranean agriculture. The pods of the cultigen usually do not shed and have a much smaller tendency to shatter their seeds.

Cytogenetical and biochemical evidence indicate that the recently discovered species *Cicer reticulatum* is the wild progenitor of the cultigen (Ladizinsky and Alder, 1976a). This species disperses its seeds like all other wild chick peas. The F_1 hybrid between the cultigen and its wild progenitor is intermediate between its parents regarding seed dispersal. The segregation pattern in F_2 indicates that several genes determine the cultivated phenotype. Hence, it can be concluded that chick pea domestication was not a clear cut event as in lentil, but rather a gradual selection for types with less tendency for seed dispersal.

It is possible that due to their seed dispersal, wild chick peas were a much more reliable source of food for the plant gatherers of prehistorical times than wild pea and lentil. For the same reason wild chick pea may have been a better candidate for sowing in the field of the Neolithic farmer. It is, therefore, surprising

that relatively few chick pea seeds have been found, so far, among plant remains in excavations of prehistorical sites in the Middle East. A possible reason for the scarcity of chick pea seeds in these excavations is the limited distribution of the wild species *C. reticulatum*. Its present distribution is confined to a small area in southeast Turkey (Ladizinsky and Adler, 1976b). If that distribution range existed also in prehistoric times the agricultural experimentation with chick pea was presumably more limited in comparison with wild pea and lentil which are distributed over extensive portions of the Middle East. In other words, while cultivation and domestication of pea and lentil could occur independently in several places throughout the Middle East, cultivation of chick pea apparently was initiated in a single nuclear area.

Chick pea seeds can be identified mainly by their angular shape and prominent beak. Each of the wild species usually has a unique seed shape and size. The cultigen, on the other hand, exhibits great variation in seed shape and size which overlaps with most of the wild species. This overlap prevents clear distinction between wild and cultivated types in carbonized material. Perhaps the earliest chick pea seeds recorded so far come from Cayönü (Van Zeist, 1972; Stewart, 1976) and are assumed to be of the cultigen *C. arietinum*. Yet, even today in the immediate vicinity of Cayönü two wild chick pea species are found. *Cicer pinnatifidum* is common in the hills, and *C. bijugum* is found in the valleys and often as a weed in cultivation. The latter is harvested regularly by farmers who grow vetch and bitter vetch.

Domestication without modification of seed dispersal

Fenugreek, *Trigonella foenum-graecum*, is an Old World crop characterized by trifoliate leaves and long tapering pods. Unlike pea, lentil and chick pea, fenugreek seeds are rarely used for direct consumption but rather for seasoning purposes and as an ingredient of curry powder. Fenugreek seeds have been valued also as a medicine, particularly for their stimulating effect on the digestive process. The plant is often used as forage and the young tops as a vegetable.

Botanically, fenugreek belongs to section *Foenum-graecum* of *Trigonella* (Davis, 1970). This section includes another five wild species which are endemic to the Middle East. The wild progenitor of fenugreek has not been identified but it is apparently one of the wild species of section *Foenum-graecum*.

The wild species of that botanical section are not equipped with particular means for dispersal. The dry mature pods remain attached to the plant and dehiscence does not take place. The seeds are released only following disintegration of the pod in the next season. In cultivation, the seeds are released by threshing. Definition of the domesticated state in fenugreek cannot be related to modification of the seed dispersal pattern. Seed size is also inappropriate for this purpose since seed size and shape of the cultigen are within the range of the wild species (Fig. 1).

The earliest remains of fenugreek come from Tel Halaf, Mesopotamia, about 4000 B.C. These remains, however, are not necessarily of the cultivated species since Tel Halaf is within the distribution range of *T. macrorrhyncha*, a member of section *Foenum-graecum*.

The domestication process of fenugreek apparently was even less conspicuous than in chick pea. The cultivated type is distinguished from the wild species

mainly by erect growth habit, greater number of pods per plant, pod length and size.

Incomplete modification of seed dispersal

Bitter vetch, *Vicia ervilia,* and common vetch, *Vicia sativa,* are grown as fodder plants mainly in west Asia, southern Europe, and north Africa, and are used for hay production. For this purpose the entire plants are cut before maturity and air dried. In the traditional Mediterranean agriculture hay supplements the farm animals' diet particularly toward the end of the summer when there is a shortage of natural pasture, and at the beginning of the winter when the new stands of grass are still too small.

The common vetch is a member of a polytypic species often called *Vicia sativa* aggregate (Hollings and Stace, 1974; Ladizinsky and Tamkin, 1978). This aggregate includes wild weed and cultivated forms, occasionally with different chromosome numbers and chromosome shapes, which can still be crossed with one another (Ladizinsky and Tamkin, 1978). Upon maturity the wild and the weedy types shatter their seeds as in wild pea and lentil. In most of the modern vetch cultivars, the dry mature pods remain intact but it is quite common to find various amounts of shattering, particularly among land races and local varieties.

Bohrer (1972) discussed the possibility that the primary reason for plant collection by man was to provide fodder for the animals he captured in nature. Bitter vetch and common vetch apparently have always been utilized as fodder plants. The green plants were cut, air dried and stored for use during the dry season. The only reason for collecting seeds of these plants was for establishing a crop in the following year. The relatively small quantity of seeds needed could be obtained either by threshing the partially matured pods or by collecting seeds which dropped from open pods and accumulated on the floor of the storage room.

Since under domestication *V. ervilia* and *V. sativa* have not passed through the critical stage of complete maturation, partial pod dehiscence was apparently tolerable or even desirable. The partially matured seeds used for sowing the next crop seemingly had little effect on yield. This kind of seed in *Vicia* germinates as quickly as a fully ripe one and the expected reduced seedling vigor in this case is not crucial since the main growing time of these legumes is in the spring, about three months after sowing.

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