

DOI 10.18699/VJ15.118
УДК 631.9+581.6

THE LOST ANCESTOR OF THE BROAD BEAN (*Vicia faba* L.) AND THE ORIGIN OF PLANT CULTIVATION IN THE NEAR EAST

© 2014 г. О.Е. Kosterin

Institute of Cytology and Genetics SB RAS, Novosibirsk, Russia,
e-mail: kosterin@bionet.nsc.ru;
Novosibirsk State University, Novosibirsk, Russia

Поступила в редакцию 29 августа 2014 г. Принята к публикации 1 сентября 2014 г.

The broad bean (*Vicia faba* L.) was among the founder crops of the Near East; nevertheless, its wild close relatives remain unknown. Presumably, its missing wild progenitor had a small range within the Levant and was associated with restricted habitats, so that it was domesticated entirely as a species. Its habitats are supposed to have been situated along floodplain/slope borders (“transeluvial-accumulative barriers”) providing favorable edaphic conditions. These restricted natural habitats of the broad bean could be foci of early cultivation activities, thus becoming nascent fields. It is hypothesized that the broad bean, a conspicuous plant with large seeds and restricted habitats, could be the Near Eastern “primer crop”, which provoked the first emergence of the idea and practice of plant cultivation and “invention” of the field.

Key words: *Vicia faba* L., Near East, origin of plant cultivation, plant domestication, founder crops, primer crop, slope/floodplain joint.

INTRODUCTION

The broad bean, *Vicia faba* L., is known as a cultivated plant from the very onset of agriculture (Hanelt, 1972; Zohary, Hopf, 2000) and is an important crop until the present. According to the most recent revision, *V. faba* represents a monospecific section in its genus, nearly warranting upgrade to generic rank (Maxted, 1993). Until the present, neither wild representatives of this species nor any closely related species have been found (Ladizinsky, 1975; Maxted *et al.*, 1991; Maxted, Kell, 2009). The absence of a link to the extant wild flora made the broad bean scarcely considered in reconstructions of the origin of plant cultivation and domestication in the Near East. However, the absence of a wild relative of some specific crop may be as such meaningful and indicative, as discussed below.

BROAD BEAN AMONG FOUNDER CROPS

The broad bean has been found in quite a number of the earliest archaeological sites in the Levant, namely in ten sites referring to the Pre-

Pottery Neolithic B (PPNB, ca 8,700-6,000 BC), the time of early plant cultivation: three in the Jordan basin: Jericho II (Hopf, 1983), Yiftahel (Kislev, 1985), “Ain Ghazal (Rollefson *et al.*, 1985); one at the Orontes: Tell el-Kerkh (Tanno, Willcox, 2006a); four in the upper Euphrates basin: Tell Abu Hureyra II (Hillman, 1975; de Moulins, 2000), Tell Halula, Dja’de (Willcox, 1996), Nevali Çori (Pasternak, 1998), Cafer Höyük IX-XIII (de Moulins, 1997) and one at the upper Tigris: Çayönü (van Zeist, de Roller, 1992). The broad bean was also reported for two sites in the Jordan valley referring to the earlier Pre Pottery Neolithic A (PPNA, ca 9,800–8,700 BC), when nascent plant cultivation was probably arising, namely Jericho I (dating range 9,150–8,350 BC) and, less surely, Iraq ed-Dub (9,700–8,800 BC), but these records remain dubious with respect to exact archaeological layer and species identification (Colledge, 2001). There is some uncertainty with respect to identification of *V. faba* seeds, which in some cases could not be distinguished from those of *Vicia narbonensis* L. and were identified as *Vicia* sp., so the actual number of Neolithic sites where *V. faba* was found may

be greater (Kislev, 1985; Tanno, Willcox, 2006a). The broad bean seeds found in archaeological sites provide no information if the plant was collected in the wild or cultivated. It is noteworthy that in Yiftahel (Kislev, 1985) and Tell el-Kerkh (Tanno, Willcox, 2006a), broad bean seeds were found in very large quantities. *V. faba* was not included in the set of the so-called “founder crops” of the Near East (Zohary, Hopf, 2000; Weiss, Zohary, 2011). Fuller *et al.* (2012) referred to it as one of the “lost crops”, although it was the ancestor which is lost, not the crop. Tanno and Willcox (2006a) and Abbo *et al.* (2013. P. 816) reasonably proposed to include broad bean into the founder crop set: “We see no reason why the broad bean cannot be added to the classical eight “founder” crops list (Zohary, Hopf, 2000), as advocated earlier by Tanno and Willcox (2006b). We presume that Zohary and Hopf (2000, and in earlier editions) refrained from doing so simply because the wild ancestor of broad bean is still elusive (Zohary, Hopf, 2000)”.

The area of the broad bean domestication is supposed either very broadly as “between Afghanistan and East Mediterranean” (Hanelt, 1972; Maxted, Kell, 2009. P. 133) or as two options: “the Near East, which is the centre of diversity of section *Faba* [in a broad sense by Kupicha], and Afghanistan, where the most primitive forms of *V. faba* occur” (Maxted *et al.*, 1991). The second option (Afghanistan), proposed by Ladizinsky (1975) is, however, unlikely since the archeological records of cultivated *V. faba* in the Near East far predate the onset of agriculture in Afghanistan (Cubero, 1984). The diagnostic characters of *V. faba* subsp. *paucijuga* Murat., cultivated in Afghanistan, Pakistan and N India, namely, the greater number of leaflet pairs per leaf (3–4) and flowers per inflorescence (4–11), were supposed to be plesiomorphic (Muratova, 1937; Maxted *et al.*, 1991; Maxted, Kell, 2009) but the arguments are not convincing. Moreover, the very necessity of subspecies division of *V. faba*, is not well justified (Cubero, 1973, 1984). The substantial diversity found in recent broad beans has most probably been accumulated already under cultivation, by mutation, isolation during expansion of the crop, and selection, since little intraspecies divergence was found in the entire species (“a strong nucleus, which carries the maximum of potentialities of the species and from which different populations branch”) (Cubero, 1973. P. 59).

AN ANCESTOR MISSING

Since Alphonse de Candolle (1882), the standard logic for locating the area of plant domestication, at least in the Near East, was the search for areas where all or most of wild relatives of the founder crops still exist until the present (Lev-Yadun *et al.*, 2000; Abbo *et al.*, 2011a, 2012). This approach has to leave aside a founder crop which no longer has its extant wild representatives or close relatives. One may, however, suppose that such a species was domesticated entirely as is, rather than was “taken for cultivation from nature”, so that its natural range and habitats were small and entirely converted to nascent agrocenoses.

The wild progenitor of the broad bean is supposed to be either extinct (Hanelt, 1972; Schäfer, 1973; Abbo *et al.* 2013) or not yet found (De Wouw *et al.*, 2001; Abbo *et al.*, 2013). However, perhaps the simplest explanation could be that it had a restricted natural range and habitat and so was domesticated entirely. Its cautious version is found in literature: “... material in the centre of origin was bred extensively so obliterating the remains of the original forms” (Maxted *et al.*, 1991. P. 136).

A PUTATIVE HABITAT

What conjectures can we make about the lost broad bean wild ancestor based on the present day crop? This is a large and conspicuous annual herb with stiff erect stems and broad foliage. It is hygrophilous and demands heavy clayey humid soils rich in humus and carbonates (Muratova, 1937). These traits suggest for the broad bean wild progenitor an open habitat with fertile soil and a good water supply. This kind of habitat is far from widespread in the Near East. In spite of a considerable variability of the seed size among present day cultigens, and although the earliest cultivated forms were rather small-seeded (Maxted, 1993), the broad bean is still a champion for this parameter among legume crops of Near Eastern origin. Thus there is little doubt that its wild ancestor was among wild Near Eastern herbaceous legumes with the largest seeds.

The large seeds may be advantageous in growth competition of seedlings among annual plant species; or an adaptation to drought after germination as allowing early growth of a deep root. At last, it

may be supposed to serve for successful germination in conditions of relatively deep burial (note the broad bean has a hypogeal type of germination). Domestication of a crop was usually followed (or accompanied) by gradual seed enlargement, which was supposed to be an adaptation to deeper seed burial under cultivation than achieved with natural seed dispersal (Harlan *et al.*, 1973; Smith, 2006; Fuller, 2007), with germinating ability at deep burial experimentally shown to correlate with seed mass for five of eight grain legume species tested (Kluyver *et al.*, 2013). Analogous situations of deeper burial can be found in nature, for instance, beneath occasional alluvium deposited by sudden floods in river floodplains. In pre-agricultural times, the floodplains of major rivers received seasonal delivery of thick alluvium. They were swampy and dominated by large perennial plants propagating via rhizomata or stolons, with participation of tiny “floodland ephemeratum” (annual plants with very short life span specific to floodlands). However, we may suppose that natural growth of the broad bean progenitor occurred at the most elevated levels of floodplains along their margins, where they meet the valley slopes, thus locally rimming the slope bases. In terms by the seminal work by B.B. Polynov (1937) considering soil chemistry in a geomorphological context, this position was the border between the transluvial position of a hill/mountain slope and the accumulative position of floodplain. This transitional landscape position, once termed “transluvial-accumulative barrier” (Glazovskaya, 1964; Stebaev *et al.*, 1993), is an ecotone known for its very high biological productivity because of soils enjoying permanently sufficient amount of ground water (provided by springs at slope bases as well as by the river), oxygen and nutrients (Stebaev *et al.*, 1993). It is irregularly (not every year) reached by the highest floods and the soil is expected to be irregularly and moderately disturbed by slope creeps and linear erosion as well as by occasional deposit of thin alluvium.

It is noteworthy that many species of the plant communities of the slopes are usually found still growing along the slope bases, partly because of accumulation of seeds washed down or fallen from above, so the slope bases are the habitats richest in species across a valley. In the Near East they could include wild progenitors of other annual founder crops, with seeds smaller than those of the broad

bean. Moreover, there they could undergo some natural selection for greater seed mass which increases the chances of a seed descending the slope by gravitation and ensures its germination from under the thin alluvial deposit. Various species from the slope plant communities could facultatively grow at the slope margins, however the characters of the contemporary broad bean tempts us to suppose its wild progenitor to be specialised to this very habitat. Judging from the archaeological evidence from the Levant cited above, the wild broad bean progenitor’s native range could comprise the valley(s) of some of the upper Orontes, Euphrates and Tigris Rivers or their major tributaries, but unlikely spread over all these valleys.

It is not possible to indicate at a plant association in which the faba bean wild progenitor once participated; moreover, the below hypothesis on its role in the origin of plant cultivation implies that this association, as a nascent agrocoenosis, disappeared in its natural state together with the progenitor itself.

INVENTION OF THE FIELD

Origin of agriculture associated with domestication of plants, together with domestication of animals comprising the so-called Neolithic Revolution, was followed by a dramatic rise in human population density and hence was one of the main pre-requisites of civilisation. No doubt it took place several times in different continents, independently and non-synchronously (Vavilov, 1951; Harlan, 1971; Zohary, 1999; Smith, 2006; Abbo *et al.*, 2010a; Fuller *et al.*, 2012). Naturally, these crucial events used to inspire a great interest as to why and how they happened, giving rise to hypotheses about factors, both natural and social, which lead to the origin of plant cultivation and domestication. Such attempts, however, often look too deterministic as implying that domestication must have taken place as soon as necessary conditions appeared, such as useful plant species and soils, and would better be reformulated in terms of factors which made appearing of agriculture possible rather than inevitable.

The seminal N.I. Vavilov’s concept of plant domestication centres (Vavilov, 1951) faced the main theoretical problem in explaining why agriculture origin and plant domestication was localised in

space and time (Harlan, 1971). And indeed, some Vavilov's disciples found it possible to expand the centres to "regions" (Sinskaya, 1969) or "mega-gene-centres", the latter eventually occupying nearly the entire land except for the extreme North (Zhukovskiy, 1970). A pre-existing fortunate set of especially useful plant species is a bad candidate for a specific factor restricting the area of agriculture origin: in most speculations of that kind (e.g. Diamond, 1998), advantages of plant species which have been domesticated used to be reasoned *ad hoc* while advantages or disadvantages of edible species which have not been domesticated are not (and could hardly be) considered comparatively.

Currently a hot debate goes on concerning the origin of plant cultivation and domestication in the Near East. One party suggests that their origin was singular, rather fast (hundreds of years), and took place in the so-called "core area" about 250 × 150 km situated at the sources of the Euphrates and Tigris in NE Turkey (Dijarbakyr and Mardin Vilayets); this was followed by cultural evolution of domesticated crops improving their quality (Levyadun *et al.*, 2000; Gopher *et al.*, 2001; Abbo *et al.*, 2010a, 2011a, 2012, 2013). Adherents of the contrary so-called protracted model of plant domestication argue that both cultivation and domestication had multiple origins over the Fertile Crescent, went on slowly and in parallel, with pre-domestication cultivation for 1–1.5 thousand years preceded domestication (as a genetical phenomenon) which was gradual, lasted for not less than 3,000 years and was crowned by fully domesticated crops (Willcox, 2005; Tanno, Wilcox, 2006b; Weiss *et al.*, 2006; Fuller, 2007; Allaby *et al.*, 2008; Brown *et al.*, 2009; Glémin, Battailon, 2009; Fuller *et al.*, 2011, 2012; Asouti, Fuller, 2012). Both parties agree that plant cultivation emerged as a conscious practice but disagree whether selection for the domestication traits was conscious and exploited variation pre-existing in wild population (the "Core Area party") or non-conscious and utilised spontaneous mutations occurring in already cultivated crops (the protracted domestication party).

While arguments of both parties about domestication, essentially genetic changes of crops, are strongly supported and diverse, those concerning the origin of cultivation as an idea and practice are not. This is not surprising since it would hardly leave archaeological remnants (Willcox, 2007).

Thus, arguments in favour of pre-domestication cultivation are largely based on finding seeds of cultivation weeds admixed with those of non-domesticated crops, or remnants of "pre-domestication granaries" (Colledge, 1998; Willcox *et al.*, 2008). It may be argued that such evidence depends on the methods of yield processing and may not reflect the origin and spread of cultivation as an idea. So the issue is far from being solved whether the invention of cultivation in the Near East happened once or many times over.

The very nature of the invention of cultivation can still be put into question: was it

- "a cultural conscious and deliberate choice" (Abbo *et al.*, 2005. P. 495), "a fully conscious socio-cultural move based on a well-educated choice of specific food sources" (Abbo *et al.*, 2010a. P. 325) and based on "deep cultural traditions of plant tending" among hunter-gatherers (Fuller *et al.*, 2012. P. 642), as both parties believe;
- or a "cultural mutation", a "meme" in Richard Dawkins's (1982) sense supported by "natural selection of ideas" in Karl Popper's (1978) sense?

These options are rather aspects of our attempts to speculate on motivations of the most primitive farmer than mutually exclusive alternatives. But there is a high danger of involving too much of actualism while reconstructing motivations of pre-historic people. All primitive societies are characterised, if not to say overloaded, by numerous and diverse traditions and rituals; it may be said that rituals were the main mode of existence of early humans. Some of them seem senseless from the modern human's point of view, while some are obviously harmful biologically, such as body modification, human sacrifice etc. From an evolutionary biologist's perspective, traditions and rituals can be viewed as the heredity of a society, the diversity of which looks as if it resulted from random "mutations". Only societies with more or less harmless traditions would survive and those with useful traditions would propagate. (Some biologically harmful traditions, e.g. body modification, of course bring about social advantage to those who execute them, but only within the context of these traditions themselves, and a society is still viable only if the biological harm is tolerable.) There is a well-known example of a kind of useful traditions found in most of the known societies including our

own: those preventing inbreeding and promoting exogamy. It is noteworthy, however, that in primitive societies, the actual harm of inbreeding is not realised and is too weak to be noticed in practice, and that traditions providing outbreeding are usually too overcomplicated for this purpose (Lévi-Strauss, 1966). Such traditions most probably appeared by chance and independently in some local societies but were positively selected and enhanced throughout the world by the benefit of avoiding inbreeding. Analogously, plant cultivation can be imagined to originate from some ritual appearing by chance and positively selected because of the gain of food.

Some hypotheses refer to such usual evolutionary scenario as change of function and derive the nascent agricultural technologies from otherwise aimed human activities. For instance, primitive agricultural habits could result as a by-product of some complex ritual of a religious or magic nature. Such rituals were indeed described as focused on maize, considered by primitive farmers not just food but also a magic plant (Anderson, 1952). Initial practices leading to plant cultivation could be rituals associated with e.g. sacrificing food, burial imitations etc., probably unconscious in respect of gain in food supply and perhaps quite odd from our point of view. In fact it is fairly difficult to reconstruct if the initial motivation of the most primitive farmer was mostly trophic or spiritual, or combining these components in a manner which modern people would hardly understand. Anyway, such speculations can by no means be tested.

Another example of the change-of-function approach is the so-called “dump-heap hypothesis” suggesting that soil disturbance around human dwellings, its fertilisation by domestic wastes and dropping of edible seeds would result in abundant growth of useful annual plants and hence were pre-requisites of plant cultivation (Engelbrecht, 1916; Sauer, 1952; Anderson, 1952). However, it was heavily criticised by Abbo *et al.* (2005) with respect to the Near East cultivation. Note also that this hypothesis does not solve the problem why plant domestication was localised in space and time rather than took place at early stages of human evolution coherently throughout vast areas, as this hypothesis predicts (Hawkes, 1983). Indeed, most of the land was inhabited by humans and everywhere they used to utilise some plants for food. Abbo *et al.* (2005)

additionally argued against the dump-heap hypothesis noting that some of wild representatives of the Near Eastern founder crops are not ruderals and can hardly tolerate substantial human disturbance of their natural ecosystems. In fact, as soon as a plant species had been domesticated, the still wild and already domesticated forms became subjected to disruptive selection favouring them to retain either wild or domesticated characteristics (Zohary, 2004; Glémin, Battailon, 2009).

If practices of plant cultivation appeared by chance as a cultural mutations, it is their low probability which could explain why centres of plant cultivation origin, although quite a few worldwide, were mostly localised in space and time in spite of hunter-gatherers immense and intimate knowledge of the surrounding nature and availability of some useful plants wherever people lived. Still one can consider objective pre-requisites favouring appearance of such cultural mutations (subjective in essence) and/or providing their selective advantage over non-farming societies, that is a common approach in the Darwinian theory of biological evolution.

The amount of seasonal labour invested into plant cultivation should have been associated with dramatic changes in societies of hunter-gatherers which transited from utilising diverse but limited food resources to cultivation of crops as a staple (Fuller *et al.*, 2010; Asouti, Fuller, 2012, but see Tzarfati *et al.*, 2013). So cultivation most probably could not appear readily as soon as it became possible and beneficial in principle. Some additional factor is necessary to facilitate invention of cultivation.

Hunter-gatherer societies depended on diversified activities and used diverse food resources distributed over considerable areas (Kelly, 1995; Fuller *et al.*, 2010; Asouti, Fuller, 2012). Perhaps a crucial event in the transition to farming was the “invention of the field”, that is investment of large amount of labour focused to certain restricted land plots. Little is known about the earliest fields since they used to leave no archaeological traces, so that the archaeological record of nascent agriculture is based on remnants of crop processing sites, dwellings and burials (Fuller *et al.*, 2010).

It is logical to suppose that the field invention would be facilitated if some very useful food plant was confined to restricted habitats in the wild, especially if this plant was conspicuous and formed

pure growth. Let us call it *the primer crop*. Such a situation would bring about natural focusing of human attention to a special plant and of their foraging activity to a restricted area. Addition of some practice of soil treatment facilitating plant growth either intentionally aimed at gain in food or of a ritual nature, or most probably combining both options, would result in converting these habitats into fields. Hence a single primer crop is supposed to trigger plant cultivation rather than a set of founder crops.

Note this would to some extent solve the first problem of plant domestication: the wild type seed dormancy, a trait considered critical for domestication (Abbo *et al.*, 2011b, 2012), which lead Ladizinsky (1987) to his challenging concept of “domestication before cultivation” in case of lentil: sowing is efficient only with non-dormant seeds. The inefficiency (because of dormancy) of sowing wild-type seeds without scarification was proved by Abbo *et al.* (2011b) by experimental cultivation of wild peas. If the earliest fields evolved from natural habitats of a primer crop, harvesting seeds could hardly be total, and the failure of sowing dormant seeds would be compensated to some extent by the soil seed bank. And if natural habitats of the primer crops were scarce and restricted in some large area, the focused human activity would convert them all into nascent fields, thus solving the second problem of plant domestication: gene flow from the wild ancestor. Such a primer crop would then undergo rather a rapid domestication, that is genetic changes towards acquisition of the so-called “domestication syndrome” (Hammer, 1984), characteristic for seed crops, in contrast to slow domestication of those nascent crops which co-existed with their wild relatives and hence demonstrated the protracted pattern of acquisition of the domesticated syndrome, because of gene flow from the wild relatives (Jones, Brown, 2007; Allaby, 2010) or just recurrent mixture with those still being gathered from the wild (Barker, 2006; Abbo *et al.*, 2012) or entering fields through field shifting and fallowing (Fuller *et al.*, 2010).

Fuller *et al.* (2012) argued that many independent cases of plant cultivation and domestication were based on solitary crops, e.g. rice, Chinese millet, pearl millet etc. Those solitarily domesticated crops mostly were conspicuous plants confined to specific habitats. A scenario with natural habitats

converted to fields could be suspected for the above mentioned crops, and also maize. Note that the bottleneck during maize domestication was estimated to last 500–2000 years with the population size of 500–4000 maize individuals that suggests a fairly small population of early farmers existing for about a thousand years in isolation (Eyre-Walker *et al.*, 1998; Doebley, 2004). As supposed below, the Near East plant cultivation may not have been an exclusion and started from cultivation of a single plant species serving as a primer crop”.

Whatever be the origin of the idea or tradition of plant cultivation, it could spread over societies via sociocultural influences (Braidwood, 1967; Abbo *et al.*, 2010a) even decoupled from crops themselves, allowing recruitment elsewhere of suitable species as crops from local wild floras (Jet, 1973). Abbo *et al.* (2010a) noted that there is no proof of independence of domestication of common bean (*Phaseolus vulgaris* L.) and maize (*Zea mays* L.) in Mesoamerica, which had taken place in an area just several hundred kilometres away (Matsuoka *et al.*, 2002; Kwak *et al.*, 2009), so that a sociocultural influence cannot be excluded. We may at least consider as an option, and a version of the Core Area hypothesis by Lev-Yadun *et al.* (2000), that in the Near East, cultivation as an idea and practice had a singular origin even if it was followed by multiple domestication events. On the other hand, this supposition agrees with the protracted model of plant domestication in assuming that the founder crops may not have entered cultivation simultaneously.

BROAD BEAN AS A PRIMER CROP?

The European/West Asian civilisation sprouted from the so-called “Neolithic revolution” following the onset of plant cultivation in the Near East. This centre of cultivation origin is characterised by quite a number of founder crops: eight “traditional” ones from three families: einkorn wheat (*Triticum monococcum* L.), emmer wheat (*T. dicoccum* (Schrank) Schuebl), barley (*Hordeum vulgare* L.), lentil (*Lens culinaris* Medic), pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), bitter vetch (*Vicia ervilia* (L.) Willd.) and flax (*Linum usitatissimum* L.) (Lev-Yadun *et al.*, 2000; Zohary, Hopf, 2000; Abbo *et al.*, 2010a, b; Weiss, Zohary, 2011), plus broad bean (*V. faba*) (Abbo *et al.*, 2013), plus maybe some lost crops (Melamed *et al.*, 2008; Fuller *et al.*, 2011,

2012 but see Abbo *et al.*, 2013). It is noteworthy that these crops are quite dissimilar in ecological and biological respects demanding different ways of treatment under cultivation: the cereals are characterised by highly competitive determinate growth, the legumes by indeterminate growth and low competitive ability, with the pea being a tall climbing plant, the broad bean a tall erect plant and lentil and chickpea (Abbo *et al.*, 2009, 2011b). For this reason, the set of founder crops was supposed to be complementary and deliberately chosen “on the basis of intimate knowledge of their nutritional value and potential to contribute to the nutritive welfare of consumers” (Abbo *et al.*, 2008. P. 928) and because of “a very good yield buffering ability” (Abbo *et al.*, 2010b, 2012. P. 21).

However, such a variety of potential crop progenitors, most of which grew over broad areas, would hardly motivate transition from diverse gathering activity to cultivation which demanded extraordinary concentration of attention and labour (Fuller *et al.*, 2010). It may be supposed that among those Near Eastern founder crops there was one which served as the primer crop, to provoke an idea and/or practice of plant cultivation and of the field as its focus. This could be the broad bean. It is suggested above that the putative natural habitat along the rims of river valleys was quite narrow and probably patchy, and easy to convert into primary fields. The relief position it probably occupied was very favourable for cultivation, allowing a naturally sufficient amount of ground water, nutrients and oxygen. The broad bean is a tall conspicuous plant. Its large seeds were not only useful for food but also allow a clear observation of a plant germinating from a seed and hence comprehension or stressing the causal link between sowing and growing. (Note that these are beans which are used for this very purpose at present, as a model object` in school education. Ironically, our hypothesis connotes with the sacred nature of beans proclaimed by the earliest philosopher of Pythagoras.) Absence of extant wild relatives of the broad bean suggests that the wild progenitor was not a common and widespread plant. If so, all its scarce natural populations would be soon converted into primary fields and then, without gene flow from wild relatives, it would undergo rapid domestication, leaving no remnants of the wild ancestor. Wild progenitors of other founder crops were scattered over much larger

areas, as they still are at present, that would hardly favour the emergence of the idea of cultivation at a restricted field. At the same time, presence of other potential crops in the habitat of the broad bean wild progenitor, being converted into primary fields, as discussed above, would lead to their involvement into cultivation as well. Moreover, conversion of the broad bean natural habitats into primary fields would most likely result in mixed species cultivation. Probably this was an initial type of plant cultivation in the Near East where the founder crop set included so many species altogether. In this respect, the set of founder crops could be balanced rather ecologically than nutritionally (as supposed by Abbo *et al.*, 2008, 2010b). If so, their involvement into cultivation could be interpreted in terms of endogenous ecological succession of a biogeocenose which included humans and plants being domesticated as its constituents: human culture and genomes of several plant species coevolved bringing about drastic changes in the biogeocenosis structure and appearance – an approach related to consideration of the plant cultivated origin in terms of symbiosis (Rindos, 1980).

The proposed scenario would shape the pattern we are observing: the founder crop, with the largest seeds among others, known only as a cultivated plant recorded archeologically from quite a restricted area of the Levant. The hypothesis is in line with supposition by Kislev and Bar-Yosef (1988), based on favourable nutritional properties and patchy distribution of wild legumes, that domestication of pulses could predate domestication of cereals in the Near East. It may draw attention of archaeologists to a certain relief position where the traces of the earliest fields could be sought for if there appear methods to detect them. Finding of archaeological remnants of a pre-agricultural society using broad bean as a staple would be decisive but there is little hope for this since this hypothetical society, if existed, should have occupied a very restricted area and for a short time, to rapidly evolve to an early agricultural society using the founder crop set.

ACKNOWLEDGEMENTS

I am grateful to Dr. Shahal Abbo and four anonymous referees for valuable critical comments, to Dr. N.P. Goncharov for fruitful discussion

and to Dr. D. Thomas for the same and linguistic corrections. This work was supported by the Russian State Program VI.53.1.3. "Genetic control of mechanisms of incompatibility between plant taxa and their adaptation to unfavourable environmental conditions".

REFERENCES

- Abbo S., Gopher A., Rubin B., Lev-Yadun S. On the origin of Near Eastern founder crops and the "dump-heap hypothesis" // *Genet. Res. Crop. Evol.* 2005. V. 52. P. 491–495.
- Abbo S., Zezak I., Schwartz E., Lev-Yadun S., Gopher A. Experimental harvesting of wild peas in Israel: implications to the origins of Near East farming // *J. Archaeol. Sci.* 2008. V. 35. P. 922–929.
- Abbo S., Saranga Y., Peleg Z., Lev-Yadun S., Kerem Z., Gopher A. Reconsidering domestication of legumes versus cereals in the ancient Near East // *Quant. Rev. Biol.* 2009. V. 84. P. 29–50.
- Abbo S., Lev-Yadun S., Gopher, A. Agricultural origins: centres and noncentres; a Near Eastern reappraisal // *Critl. Rev. Plant. Sci.* 2010a. V. 29. P. 317–328.
- Abbo S., Lev-Yadun S., Gopher A. Yield stability: an agronomic perspective on the origin of Near Eastern agriculture // *Veg. Hist. Archaeobot.* 2010b. V. 19. P. 143–150.
- Abbo S., Lev-Yadun S., Gopher A. Origin of Near Eastern plant domestication: homage to Claude Levi-Strauss and "La Pensée Sauvage" // *Genet. Res. Crop. Evol.* 2011a. V. 58. P. 175–179.
- Abbo S., Rachamim E., Zehavi Y., Zezak I., Lev-Yadun S., Gopher A. Experimental growing of wild pea in Israel and its bearing on Near Eastern plant domestication // *Ann. Bot.* 2011b. V. 107. P. 1399–1404.
- Abbo S., Lev-Yadun S., Gopher A. Plant domestication and crop evolution in the Near East: on events and process // *Critl. Rev. Plant. Sci.* 2012. V. 31. P. 241–257.
- Abbo S., Lev-Yadun S., Heun M., Gopher A. On the "lost crops" of the neolithic Near East // *J. Exp. Bot.* 2013. V. 64. P. 815–822.
- Allaby R.G. Integrating the processes in the evolutionary systems of domestication // *J. Exp. Bot.* 2010. V. 61. P. 935–944.
- Allaby R.G., Fuller D.Q., Brown T.A. The genetic expectation of the protracted model of the origin of domesticated crops // *Proc. Natl Acad. Sci. USA.* 2008. V. 105. P. 13982–13986.
- Anderson E. *Plants, Man and Life.* 1952. Little, Brown and Co., Boston.
- Asouti E., Fuller D.Q. From foraging to farming in the southern Levant: the development of the Epipaleolithic and Pre-pottery Neolithic plant managing strategies // *Veg. History Archaeobot.* 2012. V. 21. P. 149–162.
- Barker G. *The Agricultural Revolution in Prehistory, Why did Foragers Become Farmers.* Oxford Univ. Press, Oxford, 2006.
- Braidwood R. *Prehistoric Men,* 7th edition. 1967. Scott, Foresman and Company, Glenview.
- Brown T.A., Jones M.K., Powell W., Allaby R.G. The complex origins of domesticated crops in the Fertile Crescent // *Trends Ecol Evol.* 2009. V. 24. P. 03–109.
- Candolle de A. *Origine des plantes cultivées.* Germer Baillière, Paris, 1882.
- Colledge S. Identifying pre-domestication cultivation using multivariate analysis // *The origins of agriculture and crop domestication / Eds A.B. Damania, J. Valkoun, G. Willcox, C.O. Qualset.* ICARDA, Aleppo, 1998. P. 121–131.
- Colledge S. Plant excavation on Epipaleolithic and early Neolithic sites in the Levant // *Brit. Archaeol. Rep. Intern. Ser.* Archaeopress Oxford: Archaeopress, 2001. V. 986.
- Cubero J.I. Evolutionary trends in *Vicia faba* // *Theor. Appl. Genet.* 1973. V. 43. P. 59–65.
- Cubero J.I. Taxonomy, distribution and evolution of the faba bean and its wild relatives // *Genetic Resources and their Exploitation / Eds J.T. Witcombe, W. Erskine.* Chickpeas, Faba Beans and Lentils. 1984. Springer Netherlands. P. 131–143.
- Dawkins R. *The Extended Phenotype.* Oxford: W.H. Freeman, 1982.
- De Wouw M. van, Enneking D., Robertson L.D., Maxted N. Vetches (*Vicia L.*) // *Plant Genetic Resources of Legumes in the Mediterranean / Eds N. Maxted, S.J. Bennett.* Kluwer, Dordrecht, 2001. P. 132–157.
- Diamond J. *Guns, germs and steel.* Vintage-Random House, London. 1998. 480 p.
- Doebly J.F. The genetics of maize evolution // *Annu. Rev. Genet.* 2004. V. 38. P. 37–59.
- Engelbrecht T.H. Über die Entstehung einiger feldmäßig angebauter Kulturpflanzen // *Georg. Z.* 1916. V. 22. P. 328–334.
- Eyre-Walker A., Gaut R.L., Hilton H., Feldman D.L., Gaut B.S. Investigation of the bottleneck leading to the domestication of maize // *Proc. Natl Acad. Sci. USA.* 1998. V. 95. P. 4441–4446.
- Fuller D.Q. Contrasting pattern in crop domestication and domestication rates: recent archaeological insights from the Old World // *Ann. Bot.* 2007. V. 100. P. 903–924.
- Fuller D.Q., Allaby R.G., Stevens C. Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops // *World Archaeol.* 2010. V. 42. P. 13–28.
- Fuller D.Q., Willcox G., Allaby R.G. Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East // *World Archaeol.* 2011. V. 43. P. 628–658.
- Fuller D.Q., Willcox G., Allaby R.G. Early agricultural pathways: moving outside the "core area" hypothesis in Southwest Asia // *J. Exp. Bot.* 2012. V. 63. P. 617–633.
- Glémin S., Bataillon T. A comparative view of the evolution of grasses under domestication // *New Phytol.* 2009. V. 183. P. 273–290.
- Glazovskaya M.A. *Geochemical bases of typology and methods of investigation of natural landscapes.* M.: Nauka, 1964. (in Russian).
- Gopher A., Abbo S., Lev-Yadun S. The "when", the "where" and the "why" of the Neolithic revolution in the Levant // *Documenta Praehistorica.* 2001. V. 27. P. 49–62.
- Hammer K. The domestication syndrome // *Kulturpflanze.* 1984. V. 32. P. 11–34.
- Hanelt P. Die infraspezifische Variabilität von *Vicia faba L.* und ihre Gliederung // *Kulturpflanze.* 1972. V. 20. P. 75–128.

- Harlan J.R. Agricultural origin: centres and noncentres // *Science*. 1971. V. 174. P. 468–474.
- Harlan J.R., De Wet J.M.J., Price E.G. 1973. Comparative evolution of cereals // *Evolution*. 1973. V. 27. P. 311–25.
- Hawkes J.G. *The Diversity of Crop Plants*. Cambridge: Harvard Univ. Press, 1983.
- Hillman G. The plant remains from Tell Abu Hureyra: a preliminary report // *Proc. of the Prehistoric Soc.* 1975. V. 41. P. 70.
- Hopf M. Appendix B. Jericho plant remains // *The pottery phases of the Tell and other finds* / Eds K.M. Kenyon, T.A. Holland. Excavations at Jericho. British School of Archaeology in Jerusalem, London, 1983. V. 5. P. 578–621.
- Jones M., Brown T. Selection, cultivation and reproductive isolation: a reconsideration of the morphological and molecular signals of domestication // *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives* / Eds T. Denham, J. Iriarte, L. Vrydaghs. Left Coast Press, Walnut Creek, 2007. P. 36–49.
- Jett S.C. Comment on Pickersgill's "Cultivated plants as evidence for cultural contacts" // *Amer. Antique*. 1973. V. 38. P. 223–225.
- Kelly R.L. *The foraging spectrum: Diversity in hunter-gatherer lifeways*. Washington: Smithsonian Institution Press, 1995.
- Kislev M.E. Early Neolithic horsebean from Yiftahel, Israel // *Science*. 1985. V. 228. P. 319–320.
- Kislev M.E., Bar-Yosef O. The legumes: the earliest domesticated plants in the Near East? // *Curr. Anthropol.* 1988. V. 29. P. 175–179.
- Kluyver T.A., Charles M., Jones G., Rees M., Osborne C.P. Did greater burial depth increase the seed size of domesticated legumes? // *J. Exp. Bot.* 2013. V. 64. P. 4101–4108.
- Kwak M., Kami J. A., Gepts P. Center of *Phaseolus vulgaris* is located in the Lerma-Santiago basin of Mexico. // *Crop Sci.* 2009. Vol. 49, P. 554–563.
- Ladizinsky G. On the origin of the broad bean, *Vicia faba* L. // *Isr. J. Bot.* 1975. Vol. 24, P. 80–88
- Ladizinsky G. Pulse domestication before cultivation // *Econ. Bot.* 1987. V. 41. P. 60–65.
- Lev-Yadun S., Gopher A., Abbo S. The cradle of agriculture // *Science*. 2000. V. 288. P. 1602–1603.
- Lévi-Strauss C. *The Savage Mind*. Chicago: The University of Chicago Press, 1966.
- Matsuoka Y., Vigouroux V., Goodman M.M., Sanchez G.J., Buckler E., Doebley J. A single domestication for maize shown by multilocus microsatellite genotyping // *Proc. Natl Acad. Sci. USA*. 2002. V. 99. P. 6080–6084.
- Maxted N. A phenetic investigation of *Vicia* L. subgenus *Vicia* (Leguminosae, Viciaeae) // *Bot. J. Linn. Soc.* 1993. V. 111. P. 155–182.
- Maxted N., Kell S.P. Establishment of a global network for the *in situ* conservation of crop wild relatives: status and needs. FAO Commission on Genetic Resources for Food and Agriculture, Rome. 2009.
- Maxted N., Khattab A., Bisby F.A. Domesticated legumes and their wild relatives: newly discovered relatives of *Vicia faba* do little to resolve the enigma of its origin // *Botanika Chronika*. 1991. V. 10. P. 129–159.
- Melamed Y., Plitmann U., Kislev M.E. *Vicia peregrina*: an edible early Neolithic legume // *Veg. Hist. Archaeobot.* 2008. V. 17. P. 29–34.
- Muratova V.S. *Vicia* L. // *Kulturnaya Flora SSSR* / Ed. E.V. Vulf. IV. Zernovye bobovye. State Publishing House of State and Collective Farm Literature, Moscow, Leningrad, 1937. P. 79–122 (in Russian).
- Moulins de D. Agricultural changes at Euphrates and steppe sites in the mid-8th to the 6th millennium BC. *British Archaeological Reports, International Series*. Iss. 683. Oxford: Archaeopress, 1997.
- Moulins de D. Abu Hureyra 2: Plant remains from the Neolithic // *Village on the Euphrates. From foraging to farming at Abu Hureyra* / Eds A.M.T. Moore, G.C. Hillman, A.J. Legge. N.Y.: Oxford Univ. Press, 2000. P. 399–416.
- Pasternak R. Investigations of botanical remains from Nevali Çori PPNB, Turkey: short interim report // *Origin of Agricultural and Crop Domestication* / Eds A.B. Damania, J. Valkoum, G. Willcox, C.O. Quallset. ICARDA, Aleppo, 1998. P. 170–177.
- Polynov B.B. *The cycle of watering*. T. Murby, London. 1937.
- Popper K. Natural selection and the emergency of mind // *Dialectica*. 1978. V. 32. P. 339–355.
- Rindos D. Symbiosis, instability, and the origins and spread of agriculture: a new model // *Curr. Anthropol.* 1980. V. 21. P. 751–772.
- Rollefson G.O., Simmons A.H., Donaldson M.L., Gillespie W., Kafafi Z., Köhler-Rollefson I.-U., McAdam E., Rolston S.L., Tubb M.K. Excavation of the Pre-Pottery Neolithic B village of "Ain Ghazal (Jordan) // *Mitteilungen der Deutschen Orientgesellschaft zu Berlin*. 1985. V. 117. P. 69–116.
- Sauer C.O. *Seeds, Spades, Hearths, Herds. The Domestication of Animals and Foodstuffs*. Cambridge: The MIT Press, 1952.
- Schäfer H.I. Zur Taxonomie der *Vicia narbonensis* Gruppe // *Kulturpflanze*. 1973. V. 21. P. 211–273.
- Sinskaya E.N. *Historical Geography of Cultivated Flora (At the Dawn of Agriculture)*. Leningrad: Kolos, 1969. 480 p. (in Russian).
- Smith B.D. Eastern North America as an independent center of plant domestication // *Proc. Natl Acad. Sci. USA*. 2006. V. 103. P. 12223–12228.
- Stebaev I.V., Pivovarova Z.F., Smolyakov B.S., Nedelkina S.V. *General Biogeosystem Ecology*. Novosibirsk: Nauka, Siberian Branch (in Russian), 1993.
- Tanno K., Willcox G. The origins of *Cicer arietinum* L. and *Vicia faba* L.: early finds from Tell el-Kerkh, north-west Syria, late 10th millennium B.P. // *Veg. Hist. Archaeobot.* 2006a. V. 15. P. 197–204.
- Tanno K., Willcox G. How fast was wild wheat domesticated? // *Science*. 2006b. V. 311. P. 1886.
- Tzarfati R., Saranga Y., Barak V., Gopher A., Korol A.B., Abbo S. Threshing efficiency as an incentive for rapid domestication of emmer wheat // *Ann. Bot. London*, 2013. V. 112. P. 829–837.
- Vavilov N.I. The origin, variation, immunity and breeding of cultivated plants // *Selective Writings of N.I. Vavilov. Chronika Botanica*. 1951. V. 13. P. 1–364.
- Weiss E., Kislev M.E., Hartmann A. Autonomous cultivation before domestication // *Science*. 2006. V. 312. P. 1608–1610.

- Weiss E., Zohary D. The Neolithic Southwest Asian founder crops, their biology and archaeobotany // *Curr. Anthropol.* 2011. V. 52. Suppl. 4. P. S237–S254.
- Willcox G. Evidence for plant exploitation and vegetation history from three early Neolithic pre-pottery sites on the Euphrates (Syria) // *Veg. Hist. Archaeobot.* 1996. V. 5. P. 143–152.
- Willcox G. The distribution, natural habitats and the availability of wild cereals in relation to their domestication in the Near East: multiple events, multiple centres // *Veg. Hist. Archaeobot.* 2005. V. 14. P. 534–541.
- Willcox G. Agrarian change and the beginnings of cultivation in the Near East // *The emergence of agriculture. A global view* / Eds T. Denham, P. White. Routledge, N.Y., 2007. P. 217–241.
- Willcox G., Fornite S., Herveux L.H. Early Holocene cultivation before domestication in northern Syria // *Veg. Hist. Archaeobot.* 2008. V. 17. P. 313–325.
- Zeist van W.A., Roller de G.J. The plant husbandry of aceramic Çayönü, SE Turkey // *Palaeohistoria.* 1992. V. 33/34. P. 65–96.
- Zhukovskiy P.M. World Gene Fund of Plants for Selection. (Megagenocentres and Endemic Microgenocentres). Leningrad: Nauka, 1970. 88 p. (in Russian).
- Zohary D. Monophyletic versus polyphyletic origin of the crops on which agriculture was founded in the Near East // *Genet. Res. Crop Evol.* 1999. V. 46. P. 133–142.
- Zohary D. Unconscious selection and evolution of domesticated plants // *Economic Bot.* 2004. V. 58. P. 5–10.
- Zohary D., Hopf M. *Domestication of Plants in the Old World*, 3rd ed. Oxford: Clarendon Press, 2000.

«УТЕРЯННЫЙ ПРЕДОК» КОНСКИХ БОБОВ (*Vicia faba* L.) И НАЧАЛО ВОЗДЕЛЫВАНИЯ РАСТЕНИЙ НА БЛИЖНЕМ ВОСТОКЕ

О.Э. Костерин^{1,2}

¹ Федеральное государственное бюджетное учреждение науки Институт цитологии и генетики Сибирского отделения Российской академии наук, Новосибирск, Россия,
e-mail: kosterin@bionet.nsc.ru;

² Новосибирский национальный исследовательский государственный университет,
Новосибирск, Россия

Конские бобы (*Vicia faba* L.) принадлежат к набору культур, с которых начиналось культивирование растений на Ближнем Востоке, однако их дикий предок или близкие сородичи до сих пор неизвестны. Предполагается, что дикий предок бобов имел ограниченный ареал в Леванте и был тесно связан с растительным сообществом, ограниченным по площади, вследствие чего оказался одомашнен целиком как вид. Возможно, его местообитания были связаны с границей речной поймы и склона (так называемый «трансэлювиально-аккумулятивный барьер»), отличающейся благоприятными почвенными условиями. Эти ограниченные природные местообитания бобов могли стать фокусом приложения нарождающегося возделывания растений, становясь тем самым прообразом будущих полей. Предполагается, что конские бобы, будучи заметными высокими растениями с крупными семенами и ограниченным местообитанием, могли служить «стартовой культурой» для возникновения сельского хозяйства на Ближнем Востоке и способствовать самому возникновению идеи и практики возделывания растений и «изобретению» поля.

Ключевые слова: *Vicia faba* L., конские бобы, Ближний Восток, происхождение возделывания растений, domestикация растений, культуры-основатели, стартовая культура, трансэлювиально-аккумулятивный барьер.

Cite this article as:

Kosterin O.E. The lost ancestor of the broad bean (*Vicia faba* L.) and the origin of plant cultivation in the Near East. *Vavilov Journal of Genetics and Breeding.* 2014. Volume 18, No. 4/1, pp. 831–840.