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From the Cradle of Agriculture a Handful of Lentils: History of Domestication

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Abstract Literature on lentil domestication is reviewed, particularly considering archeobotanical, phylogenetic, and molecular evidence.

Lentils are one of the oldest crops cultivated and domesticated by man. Carbonized small lentil seeds have been found in several archaeological remains starting from the Neolithic. It is probable, however, that the most ancient remains refer to wild lentils; this is difficult to ascertain since seed size was probably selected after the establishment of a domesticated lentil. It is general opinion that cultivation occurred before domestication, but for how long is still an open question. It is now well accepted that the domestication of lentils was accomplished in the Near East, in an area called "the cradle of agriculture". The genus *Lens* is very small, containing only 6 taxa. A wide range of morphological and molecular evidence supports the idea that the lentil wild progenitor is *Lens culinaris* ssp. *orientalis*. On the other hand, the most distantly related species within the genus appears to be *L. nigricans*, whose domestication was also attempted without success.

The first characters involved in lentil domestication were pod dehiscence and seed dormancy. These traits are under a simple genetic control, and therefore mutants must have been fixed in a relatively short time. These and other morphological traits possibly involved in lentil domestication have been mapped in several linkage maps. However, generally these maps are not easily integrated since they are based on a limited number of markers. Newer

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maps, mainly built on different kinds of molecular markers, have been more recently produced. A consensus map is needed to fill the gap in lentil breeding and, at the same time, endow with deeper information on the genetics of lentil domestication, giving new insight into the origins of this crop, which present fragmented knowledge is unable.

Keywords lentils, *Lens* domestication, domestication syndrome to do molecular maps, phylogeny archaeological remains

Subject Codes L11006, L24027, L24051

1 Which crop was first domesticated?

Agriculture was born independently in several different places and at different times over the world, so we will concentrate on the origin of Near East agriculture only, probably the earliest area of this new human activity. For decades lentils have been considered the first species ever domesticated by man and the starting point of what has been defined the Neolithic revolution. Nevertheless this conviction has recently found some opponents who think that cereals like rye were probably the first plants to be cultivated (Nesbitt and Samuel 1998). The followers of this theory argue that cereals were more abundant and much easier to domesticate than legumes and even the pre-agricultural use of wild lentils was erratic, due to the fact that the relative rarity of this species did not provide enough food.

Whatever the truth, the use of lentils and their following domestication has provided human beings with a source of noble proteins that have surely helped the dietary subsistence of those Neolithic populations.

At the end of the last glaciation (also known as the Würm, $\sim$ 70,000–10,000 years before present) human populations started migrating northward in order to follow the game which represented the most important part of their diet. They used to inhabit small settlements during their migrations which were periodically re-used. In these settlements seed remains demonstrate that humans used to collect from the wild and store seeds for their own consumption. After a period known as the “Younger Dryas”, a short (ca. 1,000 years) colder period (approximately between 12,700 and 11,500 ybp), there was a dramatic increase of the size of those settlements which actually became small villages. In these sites seed remains of cereals and pulses resembling domesticated materials (plumper and larger seeds) are found and they are therefore considered villages of agriculturalists. For this reason nowadays there are some scientists that consider the temporary unfavourable conditions of the Younger Dryas the trigger that actually forced man to become sedentary.

Archaeological remains indicate that wheat, rye and lentils were domesticated in the so-called Fertile Crescent after the Younger Dryas, and that they were probably already used collecting them from the wild, or by means of pre-agricultural practices. How long man took to learn elementary agricultural practices, like seeding or ploughing, is still a matter of debate (Harris and Hillman 1989; Lev-Yadun et al. 2000). Some support a rapid transition (Ladizinsky 1987), others, instead, think that the build-up of such knowledge was a long course made of trials-and-errors (Pringle 1998; Fuller 2007). The process by which a wild species becomes a crop may be divided into three phases: gathering, cultivation, and domestication. In the first phase people gathered seeds from wild stands; in the second some plant genotypes were unconsciously selected and systematically sown in fields or stands, possibly close to human settlements; in the final phase mutant plants with desirable characteristics were selected and raised, thus transforming them into a crop (Weiss et al. 2006). In this view, the whole process leading to domestication would require hundreds of years.

Another debate regards the place of domestication. Some authors support the idea that the discovery only happened once and later spread out to neighbouring settlements, others consider that it took place almost contemporarily in different places. Recent studies based on the intersection of data on the domestication of different species, like einkorn wheat, pea, and lentil, strongly suggest that this happened in a single small region of the Southern Levant; moreover botanical, genetic, and archaeological evidence point to a small core area within the Fertile Crescent, in present-day South Eastern Turkey – Northern Syria, near the springs of the Tigris and Euphrates rivers. This area is supposed to be the real cradle of agriculture (Lev-Yadun et al. 2000).

2 Origin of lentils

2.1 Relationships within the genus Lens and the wild ancestry of lentils

Lens is a small but genetically diverse genus (Ladizinsky and Abbo 1996) belonging to the family Leguminosae, subtribe Papilionaceae, tribe Vicieae. All the *Lens* species possess the same chromosome number ($2n = 14$). At first *Lens* was included in the genus *Ervum*, but later it was considered a separate genus. The correct scientific name for cultivated lentils is *Lens culinaris* published by Medikus in 1787, while the other name once used (*L. esculenta* Moench) was abandoned since it was assigned later (Westphal 1974; see also Hanelt 2001). The composition of the genus has been revised several times. Initially, five species were included: *L. culinaris, L. ervoides, L. montbretii* (now *Vicia montbretii*)*, L. nigricans, L. orientalis*. In 1974 Willams et al. considered *L. culinaris* and *L. orientalis* as subspecies of *L. culinaris* (ssp. *culinaris* and *orientalis* respectively). On the basis of cross and cytological analyses, Ladizinsky et al. (1984) recognized two pools of *L. nigricans*, one with horizontal stipule type, and the second one with upright stipules. The former one could be readily crossed with the cultigen, and its name was therefore changed into *L. culinaris* ssp. *odemensis*. Ladizinsky et al. (1984) considered that the genus *Lens* was composed of the species *L. culinaris* with three subspecies (ssp. *odemensis*, *orientalis*, *culinaris*), and the species *L. nigricans* with two subspecies (ssp. *nigricans* and *ervoides*). More recently, van Oss et al. (1997) proposed seven taxa for the genus *Lens*: *L. culinaris* Medik. ssp. *culinaris*, *L. culinaris* ssp. *orientalis* (Boiss.) Ponert, *L. odemensis* Ladiz., *L. ervoides* (Brign.) Grande, *L. nigricans* (Bieb.) Godr., and two newly recognized species, *L. tomentosus* Ladiz., and *L. lamottei* Czefr., separated from the ssp *orientalis* and from *L. nigricans* respectively (Ladizinsky 1997). On the basis of recent studies, Ferguson et al. (2000) assigned again *L. odemensis* a subspecific rank within *L. culinaris*, which therefore would contain three subspecies on the basis of their classification, but these results are contrasted by cytogenetic (Galasso 2003) and molecular (Sonnante et al. 2003) evidence. In the present paper we will therefore refer to the nomenclature of van Oss et al. (1997).

The distribution of wild *Lens* taxa is Mediterranean (Table 1), even though some differences in each species range are observed. In particular, *L. culinaris* ssp. *orientalis* is distributed from Greece to Uzbekistan, and from the Crimean Peninsula to Jordan (Ladizinsky 1979; Cubero 1981). *Lens nigricans* is distributed along the Mediterranean coasts, from Israel to Spain, including the Canary Islands and northern Africa. *Lens ervoides* has a similar, but more restricted distribution, although it reaches Ethiopia and Uganda (Smartt 1990). *Lens odemensis* is basically distributed in the Middle East (Ladizinsky 1986). *L. tomentosus* Ladz. is distributed in the Middle East, especially Syria and Turkey and *L. lamottei* in Morocco, France and Spain.

Table 1 The wild *taxa* of the genus *Lens* (according to van Oss et al. 1997) and their distribution.

Taxa	**Distribution**
L. culinaris subsp. *orientalis*	Greece to Uzbekistan, and from the Crimean Peninsula to Jordan
L. odemenisis	Middle East
L. tomentosus	Middle East (esp. Syria and Turkey)
L. lamottei	Morocco, Spain, France
L. ervoides	Israel to Spain, Ethiopia, Uganda
L. nigricans	Mediterranean coasts: Israel to Spain, including Canary Islands and Northern Africa

2.2 Archaeological remains

The oldest carbonized remains of lentils (Table 2, Fig. 1) are from the Franchthi cave in Greece dated to 11,000 BC and from Tell Mureybit in Syria dated 8,500–

Table 2 Some of the oldest archaeological remains of lentil.

Locality/area	**Country/continent**	**Period**
Franchthi cave	Greece	11,000 BC
Tell Mureybit	Syria	8,500–7,500 BC
Yftah-el	Israel	6,800 BC
Tepe Sabz (*larger seeds*)	Iran	5,500–5,000 BC
Khirokitia	Cyprus	5,500 BC
Danube valley	Europe	ca. 5,000 BC
—	Georgia	5,000–4,000 BC
Prastio	Cyprus	3,500–2,800 BC
Indian sub-continent	Asia	2,500–2,000 BC

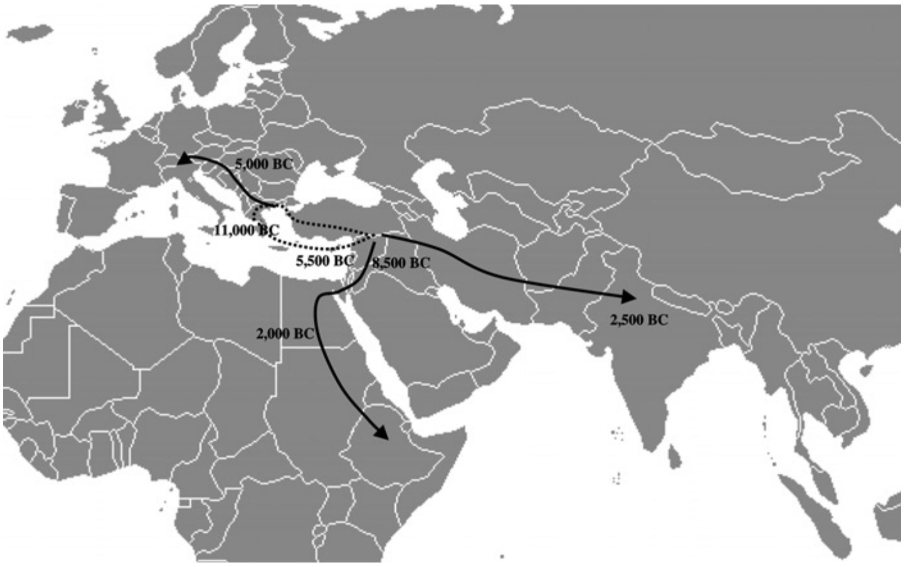

Fig. 1 Early archaeological remains and the diffusion of lentils in the Old World.

7,500 BC (van Zeist in Zohary 1972; Hansen and Renfrew 1978; Zohary and Hopf 1993). It is not possible to distinguish the state of domestication of these and other carbonized remains from villages of the 7th millennium BC in the Near East, since wild and small-seeded cultivated types are morphologically undistinguished. At Yiftah-el (Israel) a large store of lentils dated to 6,800 BC was discovered, suggesting domestication or at least intense cultivation (Zohary 1992). The oldest discovery of larger lentil seeds, therefore domesticated (Helbaek 1969), was at Tepe Sabz, Iran (5,500–5,000 BC). Indications that lentils were domesticated in the Near East come from the overlapping distribution of wild lentils and early archaeological remains.

The crop spread in Neolithic times to Cyprus. The oldest remains are from the Khirokitia excavations dated 5,500 BC (Erskine et al. 1994). Lentils are also present in some 60% of samples collected in excavations at Prastio (ca. 3,500–2,800 BC). In this latter archaeological material it is not possible to ascertain the state of wild or domesticated, since it is of small seed size. The use of the gradual change in size as an indication of wild or domesticated status of lentils has often created uncertainty on early sites, especially in areas, such as Cyprus, which also host several wild species. Most likely the assemblage found in early sites probably suggests the use of both wild and domesticated samples (Rupp et al. 2000).

More or less at the same time, lentils diffused to South-Eastern Europe and, via the Danube, to Central Europe. The repeated finding of lentils in early agricultural settlements of the 5th millennium BC in Europe indicates that domestication had already taken place. Lentils were also diffused to the Nile valley in Neolithic times, and from there they reached Ethiopia following invasions from the North.

Eastward lentils spread to Georgia in the 5th and early 4th millennia BC, and appeared in India and Pakistan around 2,500–2,000 BC. On linguistic grounds, de Candolle (1883) wrote “It may be supposed that the lentil was not in this country (India) before the invasion of the Sanskrit-speaking race”, which occurred before 2,000 BC (Erskine 1997).

Lentils were well know to the antiques. Reference to lentils is found in old Egyptian documents of the 12th dynasty (2,000–1,167 BC) and on an inscription of the reign of Ramses III (Friedrich et al. 1989).

Theophrastus wrote about lentil cultivation methods. From numerous classical sources we learn that lentils were part of the poor man’s diet and were used admixed with barley in the making of bread during adversities. The lentil’s status of staple food for the poorer layer of the Greek population is also evidenced by classical literature: in the comedy Plutus by Aristophanes (*c*. 455–387 BC), we hear the character Chremylus state “now he is rich, he no longer cares for lentils”.

Apart from the well known episode of Esau selling his birthright to Jacob for a dish of lentil soup, narrated in the Bible (Genesis 25:34), Lucius Giunius Moderatus Columella, the famous Roman agriculturist of the 1st Century AD, in his “De Re Rustica, Liber secundus” gives very precise indications on lentil cultivation practices, harvesting and seed conservation to prevent weevils damage. To this end he suggests the use of “Silphium”, an extinct species probably of the genus *Ferula*, which was highly considered for its presumed medical properties. Silphium was so important to the economy of the province of Cyrene that the effigy of this plant was impressed in Cyrenaic coins. The proposal to employ such a precious resource in lentil seed preservation suggests the great importance the Romans gave to this crop. Moreover, Columella gives a very precise estimation of the economic values regarding lentil cultivation, demonstrating a deep knowledge not too far from that of the present day.

The value of lentils at Roman times as staple food is further testified by their presence in Roman graves as ritual offerings (Collis 1978). In a Gallo-Roman burial place in the French province of Moselle, seeds of lentils were repeatedly found, all of which being of small seed size. It is supposed that lentils and other plant remains found in the graves, like barley or pea seeds, came from plants locally grown, and were possibly consumed in a ritual dinner during burial ceremonies (Preiss et al. 2005).

It is interesting to notice the origin of the names lentil and pulse. Due to seed shape, *Lens* and lentil come from the Latin “lens” meaning lens! Pulse, instead, a common name for many legume species used by man, derives from the Latin “puls” meaning thick gruel, porridge (The American Heritage Dictionary of the English Language, ed. 2006). The Romans, to denigrate the barbarian populations of Gallii, called them “pulentarios”, that is eaters of “puls”, which was made of a ground mixture of cereals and legumes. From this same word derives the Italian “polenta”, a porridge made of maize flour. This neotropic crop replaced the old mixture but the name of the dish was retained.

2.3 Genetic evidence on the origin of lentils

For years students have investigated the origin of lentils and the relationship among the taxa of the species of the genus *Lens* by means of different approaches.

Due to morphological similarities, Barulina (1930) supposed that the now called *L. culinaris* ssp. *orientalis* could be the wild progenitor of the cultigen, and, of the wide distribution area of this taxon, she selected the region between Hindu Kush and the Himalaya as the place where the small seeded lentils evolved. Renfrew (1969, 1973) hypothesized that lentils originated from *L. nigricans* and that its domestication could have been placed in Southern Europe. Zohary (1972) accepted Barulina’s idea that the lentil’s wild progenitor is *L. culinaris* ssp. *orientalis*, and also considering the fact that carbonized lentil seeds from the Neolithic were found in the Middle East, he suggested that lentils were domesticated in the Fertile Crescent. Recent molecular and biochemical evidence confirms that the ssp. *orientalis* is the taxon from which the crop was domesticated.

RFLP analyses revealed that the taxon showing the highest genetic identity with the cultigen was *L. culinaris* ssp. *orientalis*, followed by *L. odemensis*, *L. ervoides* and *L. nigricans* (Havey and Muehlbauer 1989). Moreover, *L. nigricans* from a wide geographic range displayed a low level of polymorphism, thus supporting the idea that also this species could have possibly undergone a domestication process (Ladizinsky et al. 1983).

Chloroplast DNA was analyzed by restriction analysis by Muench et al. (1991) who found a high degree of fragment length conservation especially between the cultigen and its presumed wild progenitor, and also between these two taxa and *L. odemensis*. Mayer and Soltis (1994) also performed a cpDNA restriction analysis and observed that out of 114 cultivated accessions analyzed, only three revealed a distinct restriction pattern. Four accessions of *L. culinaris* ssp. *orientalis* were analyzed, and three of them shared an identical pattern with the cultivated lentil, thus confirming that this wild taxon is the progenitor of the cultigen. The other taxa analyzed, even though considered at subspecific level were included in another clade of the tree based on Nei and Li (1979) parameters, with *L. nigricans* being the most divergent species. In a more recent paper on cpDNA restriction analysis, van Oss et al. (1997) found a higher variation in the restriction pattern of *L. culinaris* ssp. *orientalis*, probably due to the use of a higher number of samples originating from a wider geographical range. In the tree based on Nei and Li (1979) genetic distances, these samples were dispersed in clusters also including the cultigen, *L. tomentosus* and *L. odemensis*. *Lens ervoides* accessions formed a separate cluster including also *L. lamottei*, while *L. nigricans* was the most distantly related species.

In a RAPD analysis based on 45 polymorphic fragments (Abo-elwafa et al. 1995), ssp. *orientalis* was the most similar to the cultigen. *Lens odemensis* was grouped with *L. nigricans*, while *L. ervoides* appeared to be the species most distantly related to the cultigen. Large (*macrosperma*) and small (*microsperma*) seeded cultivated lentils, considered as subspecies by Barulina (1930), were not discriminated in this analysis, indicating a near simultaneous evolution of these two cultivated races from ssp. *orientalis*. On the other hand, an analysis based on AFLP markers (Sharma et al. 1996) suggested a closer affinity between *macrosperma* and ssp. *orientalis*.

Allozyme frequencies at 11 loci and phylogenetic analysis from them suggested that *L. odemensis* and *L. ervoides* evolved from a common ancestor. *Lens culinaris* ssp. *orientalis* later evolved from *L. odemensis*, and was the taxon from which the lentil was subsequently domesticated. The fact that the distribution of *L. odemensis* and *L. ervoides* overlap in Turkey, Syria and Palestine is in agreement with the idea that these two species evolved from a common ancestor (Ferguson and Robertson 2006).

Sequences of the ribosomal DNA spacers (ITS1 and ITS2) were analyzed to assess *Lens* phylogeny in two studies (Mayer and Bagga 2002; Sonnante et al. 2003). Both studies found that *L. nigricans* was the most divergent species, while *L. culinaris* ssp. *orientalis* was phylogenetically close to the cultigen. The paper by Sonnante et al. (2003) also demonstrated the validity of the assignment of specific rank to *L. lamottei* and *L. tomentosus*; moreover, variation was observed in *L. culinaris* ssp. *orientalis*, corroborating the idea that lentils were domesticated from a precise genetic stock of its wild progenitor (Ladizinsky 1999).

Sonnante et al. (2005) analyzed the variation of intronic regions of a cytosolic glutamine synthetase gene. Introns are generally highly variable regions within coding genes which are less subjected to evolutionary sieve; therefore, they can be considered neutral markers. In their contribution, they demonstrated that *L. culinaris* ssp. *orientalis* was the closest taxon to lentil, while the most distantly related was *L. nigricans*.

Two paralogous genes coding for Bowman Birk protease inhibitors were studied by Sonnante et al. (2005) in the taxa of the genus *Lens*. Although a coding region, therefore evolving at a lower rate, one of the genes showed to be almost identical in the cultivated material and in one sample of the ssp. *orientalis*, while other samples of this subspecies were differentiated. This further supports the idea that the domestication of lentils took place from a precise population or genetic stock; by means of such characters that are polymorphic in the wild progenitor, but monomorphic in the cultigens, it should be possible to identify the genetic stock from which the crop originated (Ladizinsky 1999).

Galasso et al. (2001) isolated two repeated DNA sequences from cultivated lentils, which allowed the construction of a lentil molecular karyotype. One of these sequences was unique to the genus *Lens*. Subsequently Galasso (2003) compared the molecular karyotypes of all *Lens* taxa demonstrating the identity of lentil and ssp. *orientalis* molecular karyotypes.

It is now evident that lentils derive from a specific stock of the ssp. *orientalis*, the one where the mutants that have triggered domestication first appeared, but it cannot be excluded that pre-domestication cultivation has been attempted also for other species of the genus.

3 The domestication of lentils

The domestication syndrome (Hammer 1984, 2003) refers to all modifications occurring in a crop when, from a wild plant, it becomes cultivated, and, therefore, dependent on man. Many are the traits involved in this process which depend on the species and the end use of it by man. These changes may include seed size, seed dispersal, seed dormancy, gigantism, plant architecture, etc. For lentils, two main traits were involved in the domestication process: pod dehiscence and seed dormancy, both of which are reported to be under the control of single recessive genes. A third major trait, seed size, appears to be under a more complex control.

Ladizinsky (1987) hypothesized that man first selected for the absence of seed germination constrains by means of cycle of cultivation/selection of wild material which lasted only few years, basing his ideas on assumptions that were not considered valid by other authors (Zohary 1989; Blumer 1991). Several authors consider that seed dispersal has been the first character object of selection by man, because of its consequences on harvest effectiveness, thus yield, and seed increase efficiency (e.g. Zohary 1999). For sure seed size increase was pursued later, since archaeological remains do not show seed size increase until the Bronze age (Fuller 2007). To answer these questions it is important to establish how and when domestication took place. Recent evidence tends to suggest that cultivation was carried out by man far before domestication traits were fixed (Pringle 1998; Balter 2007). The most probable pattern is that man cultivated wild species selecting in a more or less conscious way those plants carrying the genes targeted by domestication. In this framework, one can consider domestication as a guided evolution, in which natural selection is replaced by agricultural pressure. The evidence that domestication may not be a sudden process might also come from the observation that seed size increase is surely successive to the establishment of a real crop. The question on how the passage from gathering to cultivation happened remains unanswered. Many theories have been provided. The one that for many years has been prevalent is the weedy/dump-heap hypothesis (Abbo et al. 2005). In this view, humans brought wild seeds to their villages and unconsciously dispersed them to the proximities or to dump places: in these areas, thanks to better soil fertility, stronger plants were observed by the inhabitants, thus triggering the idea of cultivation. This hypothesis, though, contrasts with the intolerance of today's wild lentils to disturbed habitats and the characteristic, still present in modern lentils, of scarce competition with weeds. In other words, it appears improbable, at least for lentils, that the wild genotypes could compete and be productive in the highly disturbed habitats present around Neolithic villages (Abbo et al. 2005).

Wild lentils have very small seeds which are cumbersome to collect for human use. Co-domestication in the fields of already domesticated cereals, as discussed by Hammer (2004), would be another possibility for establishing relatively large-seeded lentil genotypes, easier to harvest and more attractive for human consumption. One of the founders of this idea was Vavilov (1917; see also Hammer 1990) who proposed the so-called secondary crops in his studies on rye. Even weeds have been domesticated in this way (Hammer 1988). A well known example of this is *Agrostemma githago* (Hammer et al. 1982). Wild lentils are not very successful in invading disturbed ground around human settlements but they can grow perfectly in cereal fields, especially in barley. Domesticated lentils have maintained this ability as can be seen from the newly established mixed cultivation type for lentil production (Horneburg 2003).

In another parallel view, men brought small seed masses as offerings to ritual places (Heiser Jr 1981). In this case, a large amount of seeds of wild lentils would be present in a given spot, producing a high concentration of a large number of conspecific individuals, so able to compete with weeds.

Another question is how primitive men would think of any sort of agricultural practice and how they could assure the optimal cultivation conditions for a wild species (Blumer 1991). Possibly, the answer is that Neolithic men, being hunter/gatherers had a very good knowledge of plant biology, since their survival was based on it. As for water supply, besides the climatic differences and the changing conditions of those years (11,000–9,000 ybp) possibly the small villages were set not far from natural water sources, and therefore the land in the proximity could have been particularly fit for a very primitive agriculture. Possibly we do not have at present the instruments to solve the question that remains still open, since from archaeological remains we cannot assess dormancy (the testa is lost on those remains), or the shattering level of pods (which are not found), but recent literature demonstrates that new research methods and multidisciplinary approaches are producing knowledge that was unthinkable only few years ago.

3.1 Genetics of domestication

In legumes, the genetic basis of the domestication syndrome has been well documented for the common bean (Gepts 1990; Sonnante et al. 1994; Koinange et al. 1996; Blair et al. 2006) and pea (Weeden 2007 and references therein). In particular, in common bean, the analysis of QTLs from a recombinant inbred population derived from a cross of wild × cultivated types revealed that these markers were clustered in some regions of the linkage map, called islands of domestication (Papa et al. 2007). In pea, some crosses between parents representing different stages of the domestication level (from wild to fully domesticated, passing through primitive landraces), allowed the recognition of 20 genes or QTLs as responsible for the modifications of plant form and function superintending pea domestication (Weeden 2007).

The genetics of traits involved in the domestication of lentil has not received the same attention as in other legumes. Ladizinsky (1979) analyzed the inheritance of some morphological traits in a cross lentil × ssp. *orientalis* and the segregation pattern of the derived F_2 populations (Table 3). In particular, he studied the inheritance of seed coat color (*Scp*), epicotyl color (*Gs*), growth habit (*Gh*), flower color, and pod dehiscence (*Pi*). Of these traits, the white flowers, erect growth, and pod indehiscence are typical of the cultivated lentil. Pod indehiscence was probably one of the first characters selected by man. Being a self-pollinator, the lentil, once the mutant was selected, could be easily maintained and became dependent from man for its reproduction. In this light, according to Ladizinsky (1979), the domestication of lentils was accomplished in a single-step event, due to one mutation. On the other hand, for seed size, the situation is more complicated, since the two cultivated lentils used in the cross were one small-seeded, and the other large-seeded. The wild lentil possessed seeds of similar size to the small seeded cultigen. The F1 hybrids showed a wide variation from small to larger seeds, never reaching the size of the large-seeded cultigen. As already stated, from carbonized seeds found in the archaeological remains, it is not possible to ascertain whether they are cultivated or wild lentil.

Table 3 Heritability of morphological traits involved in lentil domestication (modified from Ladizinsky 1979).

	Scp	*Gh*	Flower color	*Gs*	*Pi*
Lentil	yellowish-gray	bushy growth or erect sparse growth	white standard – pale bluish veins	green or purple	indehiscent
Wild (ssp. *orientalis*)	brown + dark spots	prostrate growth	bluish	Purple	dehiscent
F1 hybrids	brown + dark spots	intermediate growth	pale bluish	Purple	dehiscent
Segregation	3:1 (spotted: unspotted)	1:2:1 single gene with incomplete dominance	single gene (white recessive)	3:1 single gene, green recessive to purple	3:1 (dehiscent: indehiscent) single gene, indehiscent recessive

Scp: seed coat spotting; *Gh*: growth habit; *Gs*: epicotyl color; *Pi*: pod indeiscence

Ladizinsky (1985) also investigated the genetics of hard seed coat in lentil: while seeds of cultivated lentil can germinate shortly after maturation, wild lentil seeds undergo seed dormancy due to a hard seed coat. The results of crosses between cultivated lentil and the ssp. *orientalis* revealed that the hard seed coat of this wild lentil is controlled by a single recessive gene in homozygous condition. On the other hand, this trait is controlled by a single dominant gene in *L. ervoides*, as resulted from a cross between *L. ervoides* and *L. culinaris*. Together with pod indehiscence, the breakdown of seed dormancy is one of the first traits implied in lentil domestication. As this trait is governed by one recessive gene in ssp. *orientalis*, a mutant with a soft coat must have appeared during domestication in a relatively short time (Ladizinsky 1985).

4 What do we still need to investigate?

The lentil's economic and nutritional importance, as for genetic studies, has been, for quite a long time, neglected compared to other pulses. However, in recent years, a lot of studies regarding the genetics of lentils have been performed and maps have been established. The construction of linkage maps allows genes to be mapped for important traits and the markers associated with them, thus permitting marker assisted selection without passing through field evaluation. The first linkage maps for lentils included a limited number of markers, such as morphological, isozyme and RFLP markers, in populations derived from crossing lentil × ssp. *orientalis* (Havey and Muehlbauer 1989); in that work, the authors found linkage between some isozymes and morphological characters, and the linkage *Pi-Gal1-Pdp* was particularly interesting because pod indehiscence (*Pi*) and pigmentation (*Pdp*) are also linked in pea.

Tahir and Muehlbauer (1993) found that three morphological traits involved in the domestication syndrome of lentil (epicotyl color, pod indehiscence, and growth habit) were associated with genes or factors which gave a selective advantage to cultivated lentil alleles during the development of the recombinant inbred lines. Weeden et al. (1992) developed a 560 cM map consisting of 64 morphological, isozyme and DNA markers, from an interspecific cross of *L. ervoides* × lentil, and found that in eight regions linkage among marker loci appeared to be conserved between lentil and pea. The observed synteny between lentils and pea could foster the genetic studies in lentils. A map obtained from a cross of lentil × ssp. *orientalis* included five morphological loci (seed-color pattern, cotyledon color, stem pigment, pod dehiscence-indehiscence, seed ground color), 71 RAPDs, 39 ISSRs, 83 AFLPs, and two SSRs (Durán et al. 2004). All the morphological traits analyzed in this study, except for pod dehiscence-indehiscence, were found to be linked to one or more molecular markers.

The first intraspecific linkage map for lentils was established by Rubeena et al. (2003), which was based on 114 molecular markers, including mainly RAPDs, but also ISSRs and three RGAs (Resistance Gene Analogues). The lentil map by Kahraman et al. (2004) was established in order to map winter hardiness genes and included a total of 175 molecular markers (RAPD, ISSR, AFLP) and covered 1192 cM within nine linkage groups (LG). Four QTLs were identified for winter hardiness: three located on LG1, and one on LG4. The previous linkage map by Eujayl et al. (1998) was enhanced by the use of microsatellite and AFLP markers for the localization of *Fusarium* vascular wilt resistance (Hamwieh et al. 2005). The map finally contained 283 markers covering about 751 cM, and the resistance was localized on LG6.

Lentil genetic maps are still lacking integration and this explains why in Table 4 the same character may be associated to different linkage groups.

Table 4 Assignment of traits involved in domestication to linkage groups in mapping studies.

Cross	Trait – Linkage group							Reference
	Pi	*Gh*	*Yc*	*Gs*	*Scp*	*Ggc*	*W*	
lentil × ssp. *orientalis*	I	I	III	IV	–	–	–	Tahir & Muehlbauer 1994
lentil × ssp. *orientalis*	II	–	–	–	III	–	III	Eujayl et al. 1998
lentil × *L. ervoides*	III	–	–	I	VII	–	–	Weeden et al. 1992
lentil × ssp. *orientalis*	*n.a.*	–	II	IV	I	V	–	Durán et al. 2004

Pi: pod indeiscence; *Gh*: growth habit; *Yc*: cotyledon color; *Gs*: epicotyl color; *Scp*: seed coat spotting; *Ggc*: seed ground color; *W*: flower color; *n.a.*: not assigned.

The integration of the available information thus appears to be a priority. Microsynthenic relationships between lentils and the model legume *Medicago truncatula* was established by Phan et al. (2006). The integration of present knowledge on lentil genetic maps in a consensus map, also including information from other legumes such as pea (Weeden et al. 1992), could serve as a groundwork for future studies in lentil genetics and genomics (Ford et al. 2007). This knowledge would surely provide a powerful tool for filling the gap in lentil breeding and at the same time provide more information on the genetics of lentil domestication, and thus insight into the origins of this crop which present fragmented knowledge is unable to do.

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