The Wild Progenitor and the Place of Origin of the Cultivated Lentil: *Lens culinaris*

DANIEL ZOHARY [1]

Introduction

The last decade has seen a renewed attempt to clarify the mode of origin of the Old World cultivated plants. Rather than reliance on surveys of varietal diversity in crops (i.e., the classical approach of Vavilov and his school), students of the origin of cultivated plants focused their attention on the following two analytical tools: (*1*) assessment of carbon-dated plant remains in the rapidly growing number of archaeological excavations, (*2*) identification of the wild progenitors of cultivated plants and delimitation of the geographic distribution and ecological specificities of the wild progenitor stocks.

A new synthesis based on the combined evidence from these two disciplines is now available for wheats and barley (Helbaek, 1966; Harlan and Zohary, 1966; Zohary, 1969, 1971). But while the Old World cereals were extensively analyzed, its legumes remained almost untouched. *Lens* is no exception. Economic botanists still refer to the classic monograph of Barulina (1930) as their standard guide to lentils and frequently repeat her conclusions (based on examination of diversity among cultivars) that (*a*) cultivated lentils originated in the mountainous region between Hindu Kush and the Himalaya, and (*b*) the wild progenitor of cultivated lentil is yet unknown (see Zhukovsky, 1964).

In the last few years the present author examined wild lentils in their natural habitats in Israel, Turkey and Iran, and supplemented these field observations by survey of herbarium collections placed at the Hebrew University Jerusalem, Kew Botanic Gardens, Edinburgh Botanic Garden and the Conservatoire et Jardain Botanique, Geneva. Also the available archaeological information on lentils was critically evaluated. This paper summarizes the results obtained and aims at (*a*) identification of the wild progenitor of cultivated lentils, and (*b*) delimitation of the geographic area where domestication probably took place.

The Morphological and Ecological Evidence

Five species are grouped in the genus *Lens* Miller (Barulina, 1930; Davis and Plitmann, 1970). All are small annuals. As pointed out by Davis and Plitmann (*l.c.*) this rather specialized genus holds an intermediate position between *Vicia* and *Lathyrus*.

The cultivated lentil, *L. culinaris* Medik. [=*L. esculenta* Moench], is a characteristic component of the Old World Belt of Mediterranean Agriculture. Numerous varieties of lentils are described, and cultivars are conventionally grouped in two integrading clusters: (*i*) small-seeded lentils (subsp. *microsperma* Barul.) with small pods and small seeds (diameter 3–6 mm), (*ii*) large-seeded lentils (subsp. *macrosperma* Barul.) with larger pods and with seed attaining 6–9 mm.

The four wild species of *Lens* are delicate, ephemeral small-flowered annuals distributed over southwest Asia and the Mediterranean Basin. No cytogenetic data are available on affinities between the wild lentils and their domesticated relatives. Indeed because of the

[1] Laboratory of Genetics, the Hebrew University, Jerusalem, Israel.

Submitted for publication February 17, 1972.

small size of flowers and prevalence of cleistogamy, crosses in *Lens* are technically very difficult to make. Assessment of affinities between tame and wild depends primarily on comparative morphology. The following information on the wild lentils seems pertinent for our analysis:

1. *L. montbretii* (Fisch. & May) Davis & Plitm. [=*L. kotschyanum* (Boiss.) Nab.; *L. kotschyana* (Boiss.) Alef.]

This is a precumbent, villose-sericeons annual with relatively large (20–22 mm) densely villose pod. Seeds are ovoid and large. Confined in its distribution to southeastern Turkey and adjacent northern Iraq. As already stressed by Davis and Plitmann (1970) *L. montbretii* differs widely in its pod and seed morphology from all other lentils, and it is even doubtful whether it should be placed in the genus *Lens*.

2. *L. nigricans* (Bieb.) Godr. [=*Ervum nigricans* Bieb.]

This is a slender (8–15 cm tall) densely pilose wild lentil, with semi-hastate stipules, conspicuously aristate peduncles and mauve flowers. Pods are small (10 mm) and glabrous, usually containing two tiny (2.0–2.5 mm) lenticular seeds. A typical Mediterranean ephemeral, growing, usually in diffuse small colonies, on stony hillsides and shallow rocky soils, particularly in maqui and pine-forest clearings. Distributed from Spain and Morocco in the west to the Aegean region and further east to Crimea and the eastern shore of the Mediterranean Sea.

L. nigricans is morphologically much more closely related to cultivated *L. culinaris* — compared with the previous wild species. Yet it is distinctly separated from the cultivated pulse by several characters such as the toothed semi-hastate stipules and the strongly aristate peduncles. Intergrading individuals between *L. nigricans* and *L. culinaris* were not observed.

3. *L. ervoides* (Brign.) Grande [=*L. lenticula* (Schreb.) Alef.]

A very slender wild lentil, 10–30 cm tall, with semi-hastate stipules and long, filiform peduncles. Pods are very small (6–9 mm) and puberulent; seeds are lenticular. This wild lentil too is a typical Mediterranean element. Its distribution overlaps considerably with that of the former species: South Europe, Northwest Africa, West and South Turkey, West Syria, North Palestine, Crimea and Caucasia. Also *L. ervoides* occupies gravelly places and shallow soils. It is sporadically distributed in cleared maquis, garigues and pine forests. Occasionally it colonizes edges of cultivation.

Also *L. ervoides* is morphologically much more closely related to *L. culinaris* — compared to *L. montbertii*. But it is distinctly separated from the cultivated lentil by several diagnostic traits (structure of the peduncle and stipule; size of the pod and seed, floral shape). Furthermore, no intergradation between the two species has been noticed.

4. *L. orientalis* (Boiss.) Hand.-Mazz.

This is a slender, pilose annual, 10–30 cm tall, that shows striking resemblance to *L. culinaris* — both in vegetative traits and the structure of the flower and fruit: stipules are entire, obliquely lanceolate, unappendaged. The calyx is 4–6 mm long with teeth much longer than tube. Pods are glabrous, 8–11 mm long; seeds are lenticular, 2.5–3.0 mm in diameter. All in all, *L. orientalis* looks strikingly like a miniaturized *L. culinaris* (Fig. 1). Both lentils also contain the same chromosome number ($2n=14$).

L. orientalis is a Near Eastern plant. It is distributed over Turkey, Syria, Israel, North Iraq, West and North Iran, Transcaucasia and Transcaspia. Several collections are reported also from Greece. It grows primarily in gravelly

Fig. 1. Representative specimen of *Lens orientales* (Boiss.) Hand.-Mazz. (flowering and fruiting stage). Note the size of the seed in the mature pods (arrow).

hillslopes and stony habitats in steppe-like herbaceous formations. In the Judean and Samarian hills it is a rare plant but it is locally common on the stony south and east facing slopes of Mt. Hermon (alt. 1100–1600 m) and it grows in similar habitats in Syria, in the oak parkforest belt of South Turkey and in the Zagros range of Iran (450–1200 m alt. in Turkey; 700–1700 m alt. in Iran). In addition to such more-or-less primary habitats, *L. orientalis* spills

over also into secondary places such as cleared-up maquis in the typical Mediterranean vegetation belt and into disturbed ground and stone heaps bordering grain cultivation and orchards.

Finally it should be pointed out that the morphological boundaries between *L. orientalis* and *L. culinaris* are occasionally blurred. Already Davis and Plitmann (1970) report some intergradation between the two species in Turkey. The present author found similar series of intermediates in several localities in the Judean hills and in Galilee, Israel. Significantly such variation patterns were sporadically encountered at edges of cultivation: in places where lentil cultivation is practiced in the arable land, and *L. orientalis* grows wild on the adjacent stony slopes.

All in all the morphological evidence indicates:

(*i*) The four wild *Lens* species are, taxonomically speaking, "good species." They seem to be separated from one another by substantial morphological discontinuities and this very likely reflects an effective reproductive isolation between species.

(*ii*) Taxonomically, *L. montbretii* is too remote to be considered as a possible ancestor of the domesticated lentil. In contrast, *L. orientalis* manifests the closest morphological similarity to *L. culinaris*. Furthermore it is also occasionally interconnected to it by intermediates. There are no indications of similar intergradations between *L. culinaris* and *L. nigricans* or *L. culinaris* and *L. ervoides*.

(*iii*) *L. ervoides* and *L. nigricans* grow under typical Mediterranean climatic conditions and are distributed over the entire Mediterranean Basin. *L. orientalis* grows under more continental, steppe-like climate and is centered in the Near East.

The Archeological Evidence

As already succinctly expressed by Helbaek (1963), "the history of lentils reaches back as far as the history of agriculture itself." Lentils make their appearance in the earliest neolithic farming villages of the Near East arc (7000–6000 B.C.). Helbaek (1959, 1963) encountered several lentil seeds at Jarmo, Iraq, and later came across similar small-grain lentil in aceramic Hacilar, Turkey. Hopf (1969) reports on the presence of small-seeded (3 mm) lentil in the pre-pottery B level in Jericho. Van Zeist (1970) found even older remains. In the incipient (8000–7500 B.C.) settlement of Mureybit, northern Syria, he recovered very small (2–3 mm) lentil seeds. In the subsequent three millenia, lentils abound in plant remains of neolithic and bronze age sites — throughout the Near East. Numerous carbonized lentil seed were unearthed in Tell Ramad in Syria (6250–5950 B.C.; see Van Zeist and Bottema, 1966), aceramic Beidha in Jordan (see Helbaek, 1969) Ceramic Hacilar in Turkey (5800–5000 B.C.; see Helbaek, 1970) and in Tepe Sabz, West Iran (5500–5000 B.C., see Helbaek, 1969). Significantly Tepe Sabz lentils are already relatively large and attain 4.2 mm in diameter. This is a clear indication of domestication. As already stressed by Helbaek (1963) and by Hopf (1969), the size of the lentil increases gradually under domestication.

Also the subsequent expansion of lentils from the Near East center is amply documented. In Greece lentils appear (together with domesticated wheats and barley) in the founder (6000–5000 B.C.) neolithic settlements such as Argissa-Magula Tessaly (Hopf, 1962) and Nea Mikomedeia, Macedonia (Renfrew, 1969; Van Zeist and Bottema, 1971). Towards the end of the predynastic time lentils appear in Egypt (Matmur, El Omari, late 4th millenium, Helbaek,

1963). Lentils apparently reached central Europe via the Balkans and the Danube.

It is difficult to determine whether the earlier Near-Eastern lentils were collected from the wild or alternatively whether they already represent man-dependent, domesticated derivatives. (For definition of "collection stage" vs. "cultivation," see Zohary 1969, p. 59). In wheats or barleys the appearance of non-brittle spikes is a definite proof that cultivation was practiced. In remains of lentils, however, such tell-tale morphological distinction is not possible. In insipient Mureybit (Van Zeist, 1970) we obviously still face the collection stage — both in cereals and legumes. But in pre-pottery Jericho such supposition is already unlikely. Wild lentils are very rare and sparse in Judea; in the lower Jordan Valley they do not grow at all. On the other hand it is clear that the prepottery B settlers in Jericho cultivated cereals. It seems therefore most plausible to assume that also Jericho lentil remains (Hopf, 1969) represent a cultivated stock.

A similar line of reasoning should be valid for numerous other Neolithic and Chalcolithic finds. As already noted, wild lentils rarely form sizable stands. In most places collection of large amounts of seed from such tiny, sparsely distributed ephemeral plants with their fastly dehiscent pods would be practically impossible. Therefore any sizable finds in areas where wild lentils are rare or absent should be regarded as an indication of cultivation.

Discussion

It is clear from the archaeological evidence that the earliest signs of *Lens* domestication are centered in the Near East. Lentils are obviously closely associated with the domestication of einkorn, emmer and barley; and this pulse participated in the founding of neolithic agriculture in the Near East arc.

The most likely wild progenitor of cultivated *L. culinaris* is wild *L. orientalis*. As already stressed, *L. orientalis* is morphologically strikingly similar to the cultivated lentil. Furthermore it is the only wild lentil which shows interconnections to the cultivated *L. culinaris* by means of series of intergrading forms. The places where such intermediates are found (contacts at edges of cultivation, or fallow fields) are also indicative. This strongly implicates *L. orientalis* in the ancestry of the cultivated lentil, and suggests that we are confronted here with a pair of loosely interconnected wild and tame types. In other words, the situation in *Lens* resembles closely the "pairs of wild and tame types" characteristic for the West Asiatic cereals (Harlan and Zohary, 1966; Zohary, 1969, 1971).

The geographic distribution and the ecological specificities of *L. orientalis* fit admirably well with the archaeological evidence and with a model of Near Eastern origin. The semi-dry slopes of Mt. Hermon and the Anti-Lebanon, the limestone hills and basaltic escarpments in southern Turkey and the rocky flanks of the Zagros range constitute the main center for *L. orientalis*. It is here that this delicate wild pulse thrives in what seems to be primary habitats. Furthermore, only in this belt *L. orientalis* is occasionally locally common. This distribution corroborates the archaeological information and delimits the Near East arc as the most probable belt where lentil domestication could have happened.

Also worth mentioning is the fact that in the Near East arc *L. orientalis* occupies a relatively wide range of altitudes and soil types. If indeed *L. culinaris* and *L. orientalis* are genetically loosely interconnected by occasional hybridization, the diverse and contrasting

forms of *L. orientalis* could have rapidly enriched the initial domesticated genepool, and thus facilitated the rapid expansion of the domesticated pulse.

This is indeed a simple model of origin which seems to explain well the available information. But lest one is fully satisfied, it should also be emphasized that this model assumes that *L. orientalis* is indeed *genetically* closely related to *L. culinaris* and that most likely these two types are still interfertile. This has yet to be demonstrated! The present author does not underestimate the power of classical taxonomic assessment when it is coupled with examination of ecology and variation patterns in places of contact. Again and again such analysis proved very reliable in the identification of progenitors of cultivated plants. But obviously the story of the origin of the cultivated lentil will not be complete without cytogenetic verification, i.e., the study of interspecific hybrids between *L. culinaris* and *L. orientalis* and similar clarification of relationships with the other *Lens* species.

Summary

1. The wild species of the genus *Lens* were surveyed. Wild *L. orientalis* was found to be morphologically closest to cultivated *L. culinaris*. It is also the only wild species interconnected to the cultivated lentil by a series of intermediate types.

2. Archaeologically lentil was established as one of the primary domesticants that founded the neolithic agricultural revolution in the Near East arc.

3. The geographic distribution of wild *L. orientalis* is centered in the neolithic nuclear area of the Near East arc, i.e., northern Israel, Syria, South Turkey, North Iraq, and Western Iran.

4. The conclusion was reached that *L. orientalis* is the wild progenitor of cultivated *L. culinaris*, and that its domestication took place in the Near East arc.

Literature Cited

Barulina, H. I. 1930. Lentils of the U.S.S.R. and other countries. Bull. Appl. Bot. Genet. Plant Breed. (Leningrad) Suppl. 40, 1–319.

Davis, P. H. and U. Plitmann 1970. *Lens. In:* Flora of Turkey. Vol. 3. Edited by P. H. Davis. Edinburgh Univ. Press. pp. 325–328.

Harlan, J. R. and D. Zohary 1966. Distribution of wild wheats and barley. Science **153**: 1074–1080.

Helbaek, H. 1959. Domestication of food plants in the Old World. Science **130**: 365–372.

Helbaek, H. 1963. Late Cypriote vegetable diet in Apliki. Act. Instit. Athen. Reg. Sueciae. Ser. 4, **VIII**: 171–186.

Helbaek, H. 1966. Commentary on the phylogenesis of *Triticum* and *Hordeum*. Econ. Bot. **20**: 350–360.

Helbaek, H. 1969. Plant collecting, dry farming and irrigation agriculture in prehistoric Deh Luran. *In:* Hole, F., K. V. Flannary and J. A. Neely. Prehistory and Human Ecology of Deh Luran Plain. Mem. Mus. Anthrop. Univ. Michigan, No. 1, pp. 383–426.

Helbaek, H. 1970. The plant industry in Hacilar. *In:* Mellart, J. Excavations at Hacilar Vol. I. Occasional Publications No. 9 of the British Institute of Archaeology, Ankara. Edinburgh Univ. Press, pp. 189–244.

Hopf, M. 1962. Bericht Über die Untersuchung von Samen und Holzkohlenresten von der Argissa-Magula aus den präkermischen bis mittelbronzezeitlichen Schichten. *In:* V. Milojčić, J. Boessneck und M. Hopf: Die Deutschen Ausgrabungen auf der Argissa-Magula in Thessalien. I. Rudolf Habelt Verlag, Bonn. pp. 101–119.

Hopf, M. 1969. Plant remains and early farming in Jericho. *In:* The Domestication and Exploitation of Plants and Animals. Edited by P. J. Ucko and G. W. Dimbleby. Duckworth and Company, London. pp. 355–359.

Renfrew, J. M. 1969. The archaeological evidence for the domestication of plants: methods and problems. *In:* The Domestication and Exploitation of Plants and

Animals. Edited by P. J. Ucko and G. W. Dimbleby. Duckworth and Company, London. pp. 149–172.

Van Zeist, W. 1970. The Oriental Institute excavations at Mureybit, Syria: preliminary report on the 1965 campaign. Jour. Near East. Stud. **29**: 167–176.

Van Zeist, W. and S. Bottema. 1971. Plant husbandry in early neolithic Nea Nikomedeia, Greece. Acta Bot. Neerl. **20**: 524–538.

Zhukuvsky, P. M. 1964. *Cultivated Plants and Thier Wild Relatives.* Moscow (Russian).

Zohary, D. 1969. The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. *In:* The Domestication and Exploitation of Plants and Animals. Edited by P. J. Ucko and G. W. Dimbleby. Duckworth and Company, London. pp. 47–66.

Zohary, D. 1971. Origin of southwest asiatic cereals: wheats, barley, oats and rye. *In:* Plant Life of South-West Asia. Edited by P. H. Davis et al. Bot. Soc. Edinburgh. pp. 235–263.