Salads for Everyone—A Look at the Lettuce Plant[1]

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This discussion is concerned with the history and development of a humble, obscure, roadside weed which later became cultivated lettuce, *Lactuca sativa*. The leaves of this species at the present time grace the plates of many millions of Americans at least once every day. It is no wonder that in our country the word salad has become synonymous with lettuce. Furthermore, lettuce is equally relished as a salad in other parts of the western world and even in the countries behind the iron curtain. The rise from obscurity of this inoffensive but unattractive weed is a success story of some significance to those of us with a vital interest in economic botany. A plant that today is used in this country, in freight car-lot quantities of approximately 300 units, or about 6,000,000 heads daily, and which had a farm value of a little over $200,000,000 in 1967, is not a minor factor in our agricultural economy.

How did it happen that such an unprepossessing plant as lettuce was chosen over dandelion or chicory, also roadside weeds, and, in their original state equally attractive for food as lettuce? The other two never found the favor as salad constituents that lettuce did. For what reasons? We can only guess at the answers to these questions, but our speculations in this domain have a reasonable degree of validity.

Dandelion, for example, is locked in an evolutionary *cul de sac* through its reproductive system. Abandoning sexual reproduction for the safe but non-deviating system of diplospory,[3] the dandelion has managed to survive and become a persistent and noxious weed, but little else. Chicory and endive were probably too tough or too bitter to have universal appeal. Moreover, these two species lack the adaptability of lettuce to different conditions of culture. On the other hand, lettuce, in spite of being a self-fertilizing species, has demonstrated within its genome an enormous plasticity of a peculiar kind. This plasticity is shown in an endless array of variation. Most of the variation is expressed in the size, shape, color and texture of the leaves, and, to a lesser extent, in their arrangement on a shortened stem to form a head or a compact group of leaves. This is what we would anticipate, for the leaves are the economic portions of the plant and probably caught the eye of primitive plant breeders and later their modern counterparts. This variation under the guidance of man has been exploited for food to satisfy the various tastes of different ethnic groups. In contrast with the variable vegetative structures, the reproductive structures of lettuce are relatively stable. There are, however, variations in the size and color of the achene, in the size and shape of the panicled inflorescence, and in the color of the ligulate ray florets.

Domestication and Early History

Nearly all authorities are agreed that *Lactuca sativa* and the closely related species, *L. serriola* and *L. saligna*, are indigenous to the southern shores of the Mediterranean Basin from Egypt eastward into Asia Minor. Lindqvist (2) who has thoroughly researched the subject suggests that lettuce was first domesticated in Egypt. The main support for this idea comes from paintings found on Egyptian tombs dated about 4500 BC. These paintings depict a cultivar of lettuce with elongate, pointed leaves. These leaves appear to be similar to the present day cos or romaine type of lettuce. From Egypt, lettuce cultivation spread across the Mediterranean, north into Rome and eastward into Greece.

According to Sturtevant (4) lettuce was a popular food item among the early Greeks. He offers, as evidence, the fact that lettuce

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[3] Asexual reproduction from an unfertilized diploid egg cell.

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is mentioned in the writings of Hippocrates (450 BC.), Aristotle (356 BC.), Theophrastus (322 BC.) and Dioscorides (60 AD.). Lettuce was even more popular among the Romans, and it was mentioned by a host of their writers, and it was also the subject of a discourse by Palladius in 210 AD., who implied that different cultivars were grown. Lettuce appears in English literature and scientific writings about 1340 AD. Sturtevant quotes a passage from Chaucer in which lettuce, garlic and onions are mentioned.

Until about the sixteenth century the lettuce cultivated by the Greeks, Romans, and generally in western Europe was most likely of the cos and leaf types. There is no evidence that the heading type, or as it is sometimes called, "cabbage" or "iceberg" lettuce, existed until the herbal or "Krauterbuch" of Leonard Fuchs was published in 1543. This herbal has a plate depicting a lettuce plant in full bloom, which is probably that of a cultivar of head lettuce, since it is labeled *Lactuca capitata*.

It is surprising how quickly lettuce reached the New World. As early as 1494, barely two years after Columbus' first voyage, lettuce was cultivated on one of the islands of the West Indies. By 1565 it was abundant in Haiti, and about a century later, in 1647, it was being cultivated in Brazil. In our country, McMahon, in his garden catalogue of 1806, lists 16 different kinds of lettuce, which we can probably equate with cultivars.

Lettuce was not introduced into China until 600–900 AD., and here a distinctive type evolved with a large stem. Thus the stem was used for food and the leaves discarded. Stem lettuce is known under several names such as asparagus lettuce, Chinese stem lettuce, or simply as stem lettuce. Celtuce, a cultivar of stem lettuce, is occasionally grown in this country as a novelty.

Sources of Variation

Lettuce is a diploid, self-fertilized species with nine pairs of chromosomes. Usually, we like to think of self-fertilized species as relatively stable with a narrow range of variability. The reason for this is that self-fertilizers are victims of their own breeding system, since they are denied access to the full range of the species gene pool available to cross-fertilized species.

Stebbins (3) has shown that self-fertilization is a derived condition originating from cross-fertilizing ancestors. Self-fertilization, however, need not be an evolutionary dead-end street. As Stebbins points out, the more aggressive self-fertilizers have not produced radical adaptive devices that would lead to new genera or families. Nevertheless, self-fertilizers have produced many mutations and recombinations at the species level. This seems to be the course followed by cultivated lettuce.

It is clear from even the most casual inspection that there exists an enormous amount of variability within *Lactuca sativa*; otherwise lettuce would not be the popular vegetable it is today. The source of this variation poses some fundamental problems relevant to studies of the origin of cultivated plants. It is to these problems that I expect to devote the remainder of the discussion.

There are two all-important questions for which we must seek answers if we intend to identify the sources of variation currently found in *Lactuca sativa*: 1) Is *L. sativa* the product of interspecific hybridization? 2) Is *L. sativa* a derivative by selection from prickly lettuce, *L. serriola*?

In attempting to answer the first question, we find that in *Lactuca* there is a group of four species with nine pairs of chromosomes capable of exchanging genes with each other, but with different degrees of difficulty. These four species, *L. sativa* L., *L. serriola* L., *L. virosa* L., and *L. saligna* L., are isolated genetically within the genus.

There is no evidence for natural hybridization between the *L. sativa*-*L. serriola* complex and *L. virosa*. They can, however, be hybridized artificially, but generally only with great difficulty, and only when forms of *L. sativa* or *L. serriola* are used as the female parent (6). The F_1 plants from such matings are usually highly sterile. My colleague, the late Dr. Ross Thompson, polyploidized one of these sterile hybrids, producing a fertile amphidiploid. The amphidiploid was then backcrossed to several lettuce cultivars in succession. From this program, Thompson finally obtained a diploid cultivar, later given the name Vanguard (5). Compared to other cultivars of lettuce,

TABLE I
MORPHOLOGICAL DIFFERENCES BETWEEN LACTUCA SATIVA AND L. SERRIOLA

	Size of seed (achene)	Seed emergence	Shape of involucre at maturity	Head formation
L. sativa	large	even	cup-shaped	present
L. serriola	small	uneven	reflexed	absent

Vanguard is quite distinctive, no doubt because of a favorable recombination of genes from *sativa* and *virosa*. Thus, a new and distinct source of variation was artificially introduced into lettuce.

The other non-cultivated species in the group, *L. saligna*, will hybridize with elements of the *L. sativa-L. serriola* complex, but normally with great difficulty, and again the F_1 hybrids are sterile. Fertile derivatives, however, have been obtained from this cross, and Lindqvist (2) has data suggesting that natural hybridization may occasionally occur.

The most intriguing association in this quartet of species is that of cultivated lettuce and the so-called wild lettuce or prickly lettuce, *L. serriola*. The understanding of lettuce as a cultivated plant hinges largely upon the relationship between these two species. They hybridize readily through artificial pollination, and a certain amount of natural hybridization must occur, as judged by occasional plants found in commercial fields which appear to be F_1 hybrids between the two species.

Further proof of natural hybridization between *L. sativa* and *L. serriola* comes from Edgar Anderson (1, pp. 76, 77). He quotes Owenby as observing extensive introgression between garden lettuce and wild lettuce near Pullman, Washington. Introgression was measured by observing the behavior of a pigmented leaf character in garden lettuce. Anderson goes on to suggest that hybrids between *L. sativa* and *L. serriola* may be quite common but overlooked because of their similarity in appearance to wild lettuce.

The compatibility results just reviewed can be summarized by stating that in the genus *Lactuca* there is a group of three species allied to *L. sativa*, each having nine pairs of chromosomes. These non-cultivated species are capable of exchanging genes with the cultivated species complex, either naturally or by artificial means.

In developing a satisfactory answer to the second question, (namely, is cultivated lettuce, *Lactuca sativa*, derived by selection from *L. serriola*), we must have an accurate idea of their differences and similarities. The most obvious differences are shown in Table I. These differences are largely relative, except for the shape of the involucre. None of the cultivars of lettuce have other than the cup-shaped involucre which prevents shattering of the achene (7). On the other hand, some cultivars of lettuce have fairly small seed, and not all cultivars of lettuce produce a head. If examined closely we see that the four main differences between these species are survival-oriented; in other words, they have selection value under natural conditions. Small seed probably has a wider dispersal area than large seed; uneven emergence would definitely have selection value under natural conditions, and the reflexed involucre allows for an immediate and wide dissemination of the achenes, by means of the parachute-like pappus. Likewise, the tight head formation of many lettuce cultivars restricts the development of the inflorescence unless aided by artificial means, whereas non-headers do not have to cope with this problem. Curiously enough, the most significant and reliable difference between the two species, that is, the shape of the involucre at maturity, is controlled by a single gene (7).

From the evidence at hand it is reasonable to suggest that cultivated lettuce could be derived directly from *Lactuca serriola*, prickly or wild lettuce, by selection. The two species are easily hybridized and fully compatible. Furthermore, nearly all of the important characters that separate the two species, except the shape of the involucre, and possibly the more extreme forms of head formation, can be found in wild lettuce.

If the evidence I have presented is valid, it suggests that the marked variation apparent today in cultivated lettuce is a product of early interspecific hybridization, followed by intensive selection of mutations and recombinants after it became a cultivated plant. Even at the present time there appears to be some slight gene flow or leakage of genes into cultivated lettuce from *L. serriola.*

There is also a strong possibility that some of the variation we see in cultivated lettuce is due to chance mutants that attracted the attention and were later preserved by man. Since lettuce is a self-fertilized species, such mutants would become homozygous in several plants in the generation following their occurrence and would immediately attract attention.

Summary

If we examine in detail the origin, domestication and breeding system of cultivated lettuce, the following conclusions emerge:

1. The group of species from which lettuce originated is indigenous to the eastern Mediterranean Basin, probably Egypt.
2. Lettuce was most likely domesticated in Egypt, moving at an early date to Rome, Greece and later to China. It moved to the Americas shortly after their discovery, and as early as 1806 seedsmen listed more than a dozen cultivars from the United States.
3. Lettuce is a self-fertilized species which, under cultivation, has produced an abundance of variation, mostly in leaf size, shape, texture and color, and the arrangement of the leaves on the stem.
4. Variation in lettuce can be accounted for by early interspecific hybridization, and the protection of many mutants undesirable under natural conditions, but favorable under cultivation.
5. An analysis of the characters that separate these two species indicates that *L. sativa* could be derived from *L. serriola* by intensive selection.

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