ON THE ORIGIN OF CULTIVATED LETTUCE

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IN connection with cytological and genetical investigations within the *serriola* group of *Lactuca*, results of which have been published in earlier papers (LINDQVIST, 1956, 1958, 1960 a, 1960 b), material was obtained of a number of *Lactuca* forms, the identity of which was at first obscure. They had been given various names, but as the investigations progressed it became clear that they should be considered as primitive types of *L. sativa*, although none of them had been received under that name. The purpose of this paper is to provide taxonomic and cytogenetic evidence in support of this opinion and to consider the bearing of the existence of these forms on the theories about the origin of cultivated lettuce.

I. TAXONOMY OF THE SERRIOLA SECTION

1. Delimitation of species

The genus *Lactuca* belongs to the tribe *Cichoriae* of the *Compositae* family. It embraces about a hundred species with the haploid chromosome numbers 8, 9 or 17. These species are divided into a number of sections, one of which is the *Scariola* section, which includes the *serriola* group (THOMPSON, WHITAKER and KOSAR, 1941; THOMPSON, 1943), consisting of the four 9-chromosome species *L. saligna*, *L. virosa*, *L. serriola* and *L. sativa*. THOMPSON, WHITAKER and KOSAR (*l.c.*) included in this group also *L. altaica* FISCH. and MEY. which will be discussed later in this paper.

The above mentioned authors found that the *serriola* group occupies an isolated position within the genus *Lactuca*. Among numerous attempted crosses with other species only one combination was successful, namely *L. graminifolia*×*virosa*, producing one partly fertile F_1-hybrid. It is, of course, not impossible that other species, not yet investigated cytogenetically, bridge the gap between the *serriola* group and other species groups.

The four species of the *serriola* group may be identified with the aid of the following key:

- Plant biennial; achenes purplish black, wing-margined, rugose but not spiculate or setose .... *L. virosa*
- Plant annual or winter annual; achenes brown, grey or white, not wing-margined, not or very slightly rugose, but more or less spiculate or setose towards the apex.
  - Panicle spike-like; beak of pappus longer than the achenes; achenes spiculate, but not setose .... *L. saligna*
  - Panicle open; beak of pappus same length as the achenes; achenes more or less setose but not spiculate.
    - Involucre reflexed when achenes ripe, panicle pyramidal .... *L. serriola*
    - Involucre erect when achenes ripe, panicle flat-topped .... *L. sativa*

With the exception of the involucre character used to separate *L. serriola* and *L. sativa*, these key characters are well established and generally accepted (*cf.* GRENIER and GODRON, 1850; BISCHOFF, 1851; HEGI, 1929; STEBBINS, 1939). The involucre characters have been found to provide a very reliable means of separating *L. sativa* and *L. serriola*. In the course of this study a large number of cultivated lettuce varieties have been examined with regard to involucre characters and all were found to have the erect involucre (*cf.* MC COLLUM, 1953; WHITAKER and MC COLLUM, 1954). This character was not found on any specimen of a very large amount of material of *L. serriola*, which was studied partly in cultivation, partly in natural populations and partly on herbarium specimens. If the character exists in this species it can be only as a very rare exception.

Most authors agree that *L. virosa* and *L. saligna* are species, which are well separated from *L. serriola* and *L. sativa*. BENTHAM and HOOKER (1947), however, point out that forms exist which are intermediate between *L. saligna* and *L. serriola*. Specimens agreeing with *L. saligna* with regard to general habit and with regard to length relation between pappus and achenes, but having the open panicle typical of *L. serriola*, have been encountered by the writer in various herbaria. As an example may be mentioned a specimen with the name '*L. Scariola* L, var. *adulterana* GR. et GODR.' at the Botanical Museum, Lund, Sweden.

There is some controversy as to whether *L. sativa* should be considered as a separate species or as a variety of *L. serriola*. It was given specific rank by LINNEAEUS (1753) and this has been accepted by many authors, *e.g.* HEGI (1929), and GRENIER and GODRON (1850). The opinion that *L. sativa* is only a cultivated form of *L. serriola* was held by BISCHOFF (1851) and was shared by BOISSIER (1875), HOOKER (1875—1897), FIORI (1925—1929) and others.

Cytogenetic investigations by THOMPSON, WHITAKER and KOSAR (1941), THOMPSON (1943) and LINDQVIST (1960 a) have given a picture of the relationships between the species of the *serriola* group, which agrees very well with that based on taxonomic evidence. There are clear differences between *L. virosa* and the other species with regard to chromosome morphology, and gene exchange appears to be almost impossible. Strong sterility barriers exist between *L. saligna* on one side and *L. serriola* and *L. sativa* on the other, and also minor differences in chromosome morphology, but gene exchange is still possible. *L. sativa* and *L. serriola*, finally, have chromosomes which appear to be identical morphologically and largely homologous, and there are no obstacles to gene flow between these two species. In biosystematic terminology the *serriola* group thus consists of three cenospecies, namely *L. virosa, L. saligna* and *L.sativa-serriola.*

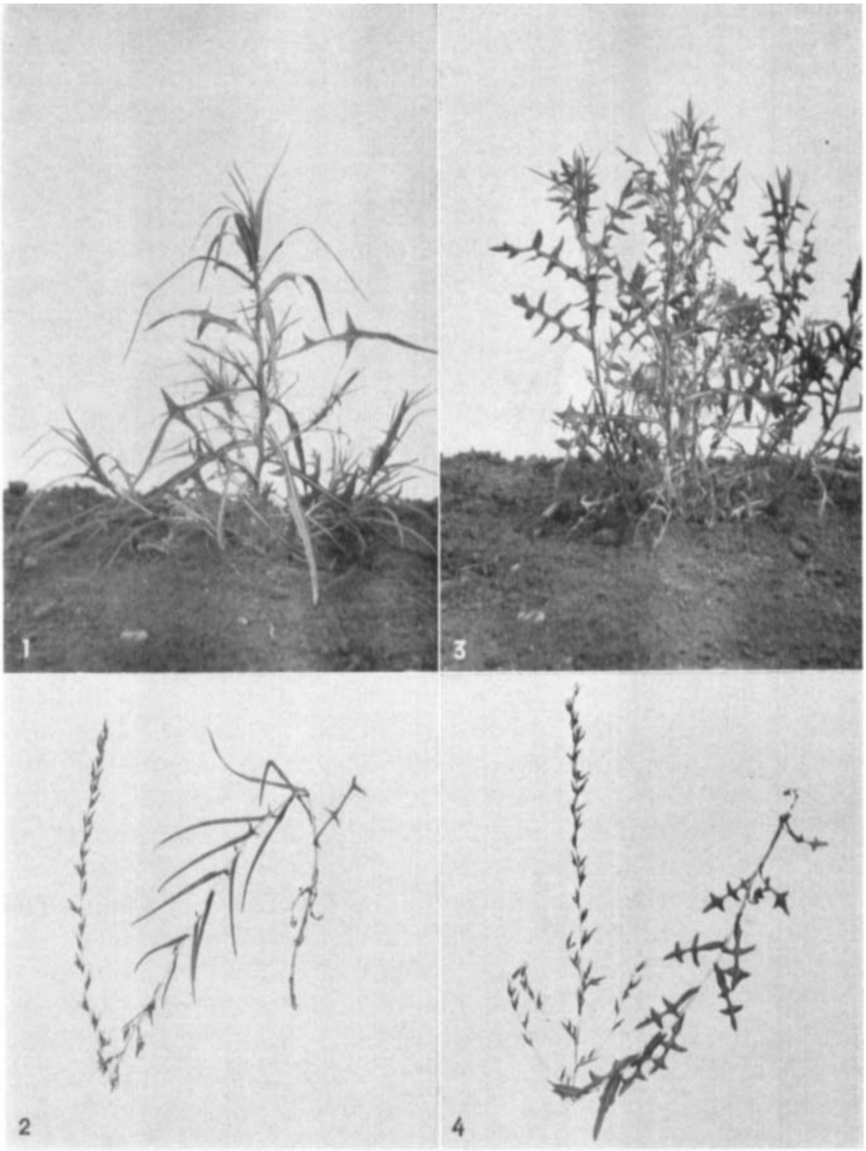
There is no indication of natural hybridization between *L. virosa* and *L. serriola* or *L. saligna* (*cf.* STEBBINS, 1939), but some evidence of the occurrence of spontaneous hybrids between *L. saligna* and *L. sativa-serriola* (LINDQVIST, 1960 a), and fertile derivatives have in experiments been obtained from hybrids between *L. saligna* and *L. sativa*, in spite of a very high degree of sterility in F_1. It is thus possible that some exchange of genes takes place in nature between *L. saligna* and *L. sativa-serriola*, and that the intermediate forms mentioned above are of hybrid origin. Spontaneous hybridization takes place occasionally between *L. sativa* and *L. serriola*. OWNBEY (1949) found hybrids with *L. sativa* in a natural population of *L. serriola* and the hybrid nature of these plants was confirmed by MC COLLUM (1953). Other cases have been reported by PAMMEL (1918) and by BOHN and WHITAKER (1951), who state that the occurrence of a few natural hybrids with *L. serriola* is not uncommon in commercial lettuce fields. The spontaneous hybrid described by NAUDIN (1875) as *L. sativa*×*virosa* was in all probability another example (*cf.* LINDQVIST, 1960 a, p. 132). No hybrids have been observed by the writer in natural populations.

The three wild species all occur as weeds of road sides and waste places, but *L. virosa* is also found in half-wild habitats, such as sand dunes and rock crevices. *L. serriola* is by far the most common and 'aggressive' of the three. They all originate from the Old World, where they have their main distribution centre round the Mediterranean. With increasing world communications they, particularly *L. serriola*, have spread to all parts of the world. In U.S.A. this species, which was first recorded in 1863 (PAMMEL, 1894) is a very common weed, which is much more troublesome than anywhere in Europe, whereas *L. saligna* and *L. virosa* have a very limited distribution in U.S.A. *L. virosa* is, in various parts of Europe, cultivated on a small scale for the sake of its milk juice, which has narcotic properties and which in dried form finds a use in medicin under the name of Lactucarium.

2. Variation within the species

L. saligna. — The typical form of this species has long, narrow, pointed almost linear leaves. The basal leaves are pinnatifid, but leaves on the seed stalk almost entire. A form with somewhat broader, clearly lobed leaves on the seed stalk is var. *runcinata* (GRENIER and GODRON, 1850; HAUSSKNECHT, 1895), which by GRENIER and GODRON (*l.c.*) was suspected to be a hybrid between *L. serriola* and *L. saligna.* Lines which fit the description of the two forms have been studied cytogenetically by the writer (LINDQVIST, 1960 a) and where found to be very similar, but they differed with respect to viability of F_1-hybrids with *L. sativa.* Specimens of these forms are illustrated in Figs. 1—4. A prickly form (f. *Ruppiana* WALLR.) and a non-prickly form (f. *Wallrothi* SPRENG) are mentioned by HEGI. All specimens of *L. saligna* examined by the writer had prickles along the dorsal side of the midrib of the leaf, but these prickles were fewer and softer than in *L. serriola*, and they did not continue down on to the stem, which is the rule in the latter species. This spination is similar to that produced by the allele sp_1 in the primitive *L. sativa* form Altaica (LINDQVIST, 1960 b). With regard to anthocyanin pigmentation, typical specimens of *L. saligna* belong to the tinged type (THOMPSON, 1938) and no variations have been reported.

L. virosa. — Within this species there is variation with regard to leaf form, spination and anthocyanin pigmentation. Non-lobed forms exist and forms with lobing similar to that of *L. serriola.* Some forms are completely non-prickly, others have degrees of prickliness similar to that produced by the alleles sp_2 or Sp in *L. sativa-serriola.* Anthocyanin pigmentation may be lacking or it may be present in varying degrees, with or without spots on the leaves. All specimens examined in cultivation, in natural habitats or as herbarium specimens had broad leaves with blunt apices. Specimens of *L. virosa* are illustrated in Figs. 5—7.



Figs. 1—4. *L. saligna*, cultivated specimens. — Figs. 1—2. Line Sal.C. Figs. 3—4. Sal.R (f. *runcinata*). Figs. 1 and 3. Growing plants. Figs. 2 and 4. Pressed specimens.

Variations such as those described here appear in botanical literature under various names. A green-leaved form (presumably lacking anthocyanin) has been referred to as *L. virosa* f. *flavida* JORD. (GRENIER and

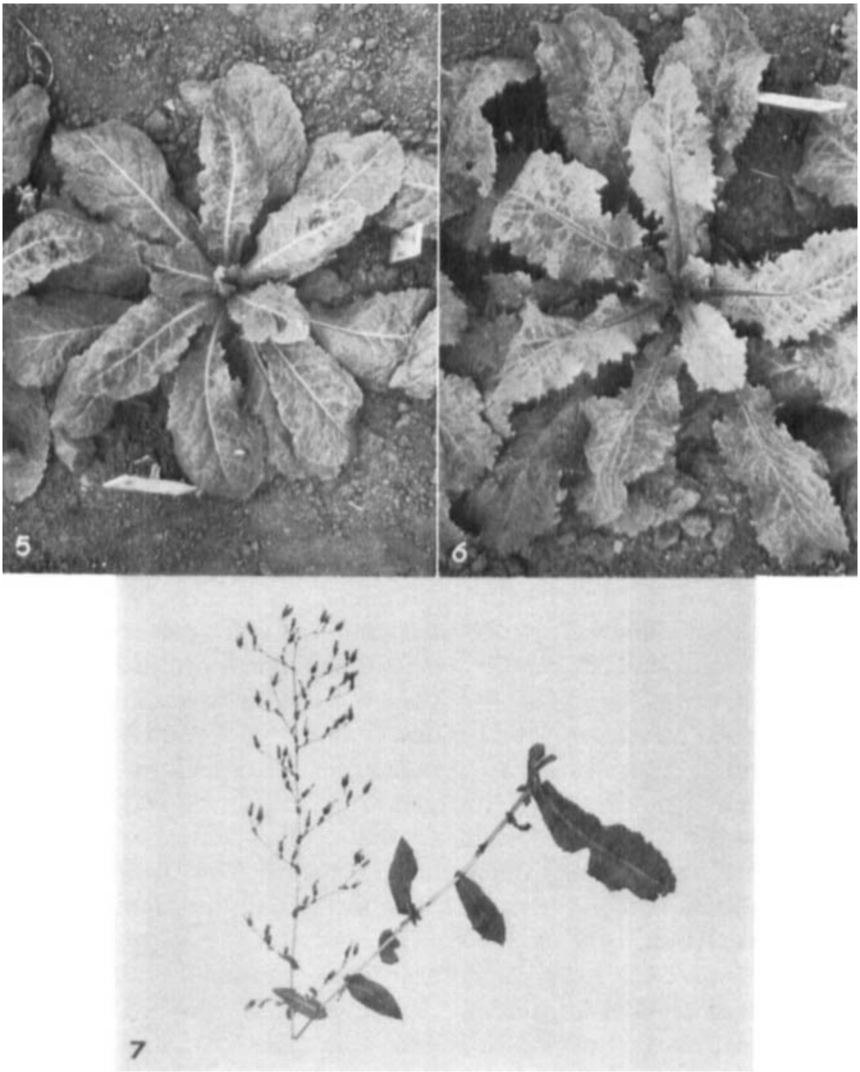
Godron, 1850), and forms with spotted leaves as *L. virosa* f. *maculata* (de Candolle, 1838) and *L. virosa* var. *cruenta* Nobis. A form which is very close to *L. virosa* was described by Boissier (1839—1845) under the name *L. livida* Boiss. and Reut. It differed by having more deeply lobed leaves and anthocyanin pigmentation of a violet shade in the whole plant.

L. serriola. — The typical form of this species has lobed leaves with blunt apex, prickles on stem and leaves and anthocyanin pigmentation of the tinged type. A non-lobed form, f. *integrifolia* Bogenhard occurs more or less frequently throughout the distribution area of the species, and mixed populations of the typical and the non-lobed forms are not uncommon. A non-lobed, non-prickly form from Val d'Aosta, Italy, was described by Allioni (1786), who gave it specific rank under the name *L. augustana* All., but it has been included in f. *integrifolia* by many authors, *e.g.* Bischoff (1851). The writer had had an opportunity of studying populations of *L. serriola* in Val d'Aosta, and has found that all four combinations of the characters lobed, non-lobed, prickly and non-prickly occur together there. Lobed, non-prickly forms have been seen also in other parts of Italy. Progenies of non-lobed, non-prickly plants from Val d'Aosta have been grown side by side with progenies of *L. serriola* f. *integrifolia* from England and France. Apart from the absence of prickles in the Italian progenies no essential differences were noted. There is thus every reason to consider *L. augustana* All. merely as a variety of *L. serriola* f. *integrifolia*. Specimens of a lobed form, a non-lobed form from England and *L. augustana* from Val d'Aosta are shown in Figs. 8—11.

Lobing in *L. serriola* is normally of the runcinate type produced by the allele U_{lob} (Lindqvist, 1958), but some herbarium specimens with the oakleaved type (allele U_{oak}; Lindqvist *l.c.*) have been encountered, *e.g.* a specimen with the name *L. plicata* in Herb. F. Negri at the Botanical Institute at Turin, Italy. This specimen which had been collected in Val d'Aosta, was a form of *L. serriola* with the typical reflexed involucre, lacking prickles and having leaves of the oakleaf type.

Typical specimens of *L. serriola* have the blunt leaf apex caused by the recessive gene p (Lindqvist, 1960 b) and only one exception to this rule is known, namely a form from Idaho, U.S.A., used by Mc Collum (1953) in his cytogenetic study. It is obvious from the description and illustration in Mc Collum's paper that this form has the leaf type resulting from interaction of the genes U_{lob} and P (Lindqvist, 1960 b).

All specimens of *L. serriola* examined by the writer have had the



Figs. 5—7. *L. virosa*, cultivated specimens. — Figs. 5 and 6. 1st year plants of two different lines. Fig. 7. Line Vir.L; pressed twig of flowering plant.

tinged type of anthocyanin pigmentation produced by the allele *r* in the *R-r′-r* series (THOMPSON, 1938) *i.e.* anthocyanin is present only at the leaf margins, but there are no spots or red coloured areas on the lamina, and there is no reliable evidence that any of the other alleles occur in this species. Form with spotted leaves are, however, mentioned by BISCHOFF (1851), namely *L. scariola* var. *β* LINN. and *L. scariola β ma-*

culosa DE C. Both LINNAEUS (1753) and DE CANDOLLE (1838) refer to a description and illustration by PAUL HERMANN (1705) of a form called *Lactuca sylvestris Italica, costa spinosa, sanguineus maculis adspersa.* The illustration agrees, however, better with *L. virosa* than with *L. serriola.* The form is described as having '*semina nigra*' which indicates that it really belongs to *L. virosa.*

The very exceptional occurrence of the alleles U_{lob}, P and possibly R or r' in *L. serriola* is probably a consequence of natural hybridization with forms of *L. sativa* carrying these alleles. MC COLLUM (1953) states that his Idaho form, which had pointed leaf apex, also had bigger achenes than the other *L. serriola* form with which he was working, and that the ligules of the Idaho form had a much deeper yellow colour. Both these characters might well have been introduced from *L. sativa* (see page 331 below concerning size of achenes). MC COLLUM (*l.c.*) discusses the possibility that the non-lobed form of *L. serriola* is a derivative of a hybrid between lobed *L. serriola* and non-lobed *L. sativa.* This possibility suggests itself, particularly with regard to *L. augustana* ALL., which has also the non-prickly condition in common with *L. sativa.* However, as pointed out by MC COLLUM there is no certain evidence that the lobed condition is more primitive than non-lobed in *L. serriola.*

L. sativa, cultivated forms. — Within this species there is a tremendous variation. The classification of the multitude of different cultivated varieties has been dealt with by several authors, most recently by HELM (1954). Four types are generally recognized, namely asparagus lettuce, cos lettuce, cabbage lettuce and leaf lettuce. Among these, cos and cabbage lettuce are the most important. They form two distinct groups which by some authors are believed to have separate origin (STURTEVANT, 1886; HELM, 1954).

In *asparagus lettuce* the young fleshy stems are used, not the leaves, which are coarse and unpalatable. Some varieties of asparagus lettuce have long lanceolate leaves with pointed apex. These varieties have been confused with ALLIONI's *L. augustana* (STURTEVANT, 1886; HELM, 1954, p. 100), and they often appear under the name *L. augustana* or *L. angustana.* The true *L. augustana* ALL., however, has leaves with the blunt apex typical of *L. serriola,* and there is, in fact, little similarity between this form and lanceolate-leaved asparagus lettuce. Another type of asparagus lettuce is represented by Chinese varieties of which the most well-known is Burpee's Celtuce. These varieties are characterized by a light grey leaf colour not found in any other lettuce varieties. In leaf shape they resemble the next group of varieties.

Figs. 8—11. *L. serriola.* — Figs. 8 and 9. Line Sc.H. Fig. 10. Sc.J. Fig. 11. Sc.aug.All. Figs. 8 and 10. Growing plants, Figs. 9 and 11. Pressed specimens. Figs. 8—10. Cultivated specimens, Fig. 11. Specimen collected on natural habitat.

The *cos lettuce* varieties have oblong, upright leaves with a prominent midrib, running almost to the apex which is rounded. The lamina is rigid and rather coarse in texture. Most cos varieties grown to-day are self-folding, forming loose oblong hearts. In Egypt a form with oblong leaves, known as f. *aegyptiaca* is widely grown. Material of this form has been obtained by the courtesy of Prof. V. LAURENT TÄCKHOLM, Cairo. It can be described as a primitive cos variety which forms no hearts whatsoever.

Cabbage lettuce varieties have broad, almost orbicular leaves which are more prostrate than those of cos lettuce. The midrib branches into smaller veins before reaching the apex of the lamina. Cabbage lettuce varieties have more tender leaves than cos lettuce, and they form more or less firm hearts. These develop in a different way to those of cos lettuce, and the process is controlled by different genes (LINDQVIST, 1960 b).

The *leaf lettuce* varieties are with regard to leaf texture and appearance of the midrib similar to cabbage lettuce, but differ in their inability to form hearts. They constitute a very heterogeneous group, which includes some extremely curly and fringed varieties (*e.g.* Grand Rapids).

There is much disparity between varieties of the four types with regard to a number of morphological and physiological characters. Comprehensive descriptions of lettuce varieties have been compiled by TRACY (1904), VILMORIN-ANDRIEUX (1920), MORSE (1930) and general surveys have been made by BRIAN (1936), LENANDER (1951) and HELM (1954). Only certain characters, which are of importance for the further discussion, will be considered here.

It has already been mentioned that some varieties of asparagus lettuce are characterized by leaves with pointed apex for which the dominant gene P is responsible, but the overwhelming majority of cos, cabbage and leaf lettuce varieties, probably all, have the rounded apex. Varieties with the red and spotted types of anthocyanin pigmentation (THOMPSON, 1938) are found among cos, cabbage and leaf lettuce. Whether they exist also in asparagus lettuce is not known. This type of lettuce is grown mainly in China, and little is known about its variability. BOIS (1927, p. 301) indicates that many varieties exist and that they differ, among other things, in anthocyanin pigmentation. Cultivated lettuce varieties normally have non-lobed leaves, but oakleaved and lobed varieties occur in the asparagus and leaf lettuce groups (TRACY, 1904; BOIS, 1927). Specimens of three varieties of *L. sativa* are illustrated in Figs. 12—14, mainly for comparison with the primitive forms to be described below.

Figs. 12—13. *L. sativa*, growing plants. — Fig. 12. Line K.driv. Fig. *13*. Line Maik.

3. Primitive forms of L. sativa

Source of material. — These forms which have been referred to in the introduction, were received from botanic gardens under various names listed below.

Designation	Origin	Name under which received
Altaica	Kew, England	*L. altaica* Fisch. and Mey.
LC	Copenhagen, Denmark	*L. livida* Boiss. et Reut.
SL	Lund, Sweden	*L. saligna*
SP	Palermo, Italy	*L. sagittata*
„	Pisa, Italy	„ „
„	Tabor, Czechoslovakia	*L. augustana* Reichb.
SB	Brünn, „	*L. virosa*
SM	Modena, Italy	*L. dregeana* D.C.
SN	Nancy, France	*L. virosa*
ST	Turin, Italy	*L. serriola*

Cytogenetic data. — With the exception of the lines called SN and ST, these forms have all been studied cytogenetically (Lindqvist, 1960 a). The results showed that they are only remotely related to *L. saligna* and *L. virosa*, but that they agree with *L. sativa* and *L. serriola* in chromosome morphology and that hybrids with these species have normal meiosis and are highly fertile. They must therfore be considered as belonging to the *L. sativa-serriola* ecospecies.

Designation. — The fact that these forms were received under such a variety of names, shows that they have not been recognized as an entity in spite of their very close relationship. Most of these names cannot with justification be used for forms of the *L. sativa-serriola* complex. The names *L. saligna* and *L. virosa* must obviously be ruled out. *L. livida* was used by BOISSIER (1839—1845) for a form very close to *L. virosa* (*cf.* p. 324). Judging from BOISSIER's description, the only similarity between this form and the line LC is in the anthocyanin pigmentation. The names *L. sagittata* and *L. augustana* REICHB. are synonyms of *L. quercina* L subsp. *Chaixii* VILL., which is entirely different from these forms. DE CANDOLLE (1838) introduced the name *L. dregeana* for a South African species close to *L. virosa.*

FISCHER and MEYER (1846) described under the name *L. altaica* a form intermediate between *L. saligna* and *L. serriola* and originating from the Altai region. The leaves were described as entire, dentate or runcinate. The form from Kew has leaves which are too deeply lobed to be described as runcinate, but agrees otherwise in many respects with FISCHER's and MEYER's description. No herbarium specimens have been available for comparison and it is impossible to say whether the two forms are identical. If that is so, there is some reason for using the name *L. altaica* for the whole group, which is here referred to as primitive forms of *L. sativa.* THOMPSON, WHITAKER and KOSAR (1941) used, in their cytogenetic study, a form called *L. altaica* FISCH. and MEY. originating from Egypt, which probably also belongs to this group. Their illustrations show that it differs from the form from Kew in having non-lobed leaves. Whether it agrees with the form described by FISCHER and MEYER cannot be decided. From the above it is clear that there is no obvious choice of name for this group of forms.

Comparison with L. sativa and L. serriola. — There is considerable disparity between the different forms with regard to general morphology as shown by the following classification for presence of alleles for some of the most important characters.

Designation	Involucre	Anthocyanin	Spination	Leaf apex	Leaf form
Altaica	*b*	*CTr'i*	sp_1	*P*	U_{lob}
LC	*b*	*CTri*	*sp*	*P*	*u*
SL	*b*	*CtRI*	sp_2	*P*	*u*
SP	*b*	*CTRI*	sp_2	*P*	*u*
SB	*b*	*CtrI*	*Sp*	*p*	*u*
SM	*b*	*CTRI*	*sp*	*P*	*u*
SN	*b*	*CTRI*	*sp*	*P*	*u*
ST	*b*	*Ct??*	sp_2	*p*	U_{lob}

The reader is referred to an earlier paper (LINDQVIST, 1960 b) for an account of the phenotypical manifestation of the various alleles and for a summary of their occurrence in *L. sativa* and *L. serriola.*

The new forms have all the allele *b* for erect involucre and thus agree with *L. sativa* with regard to this key character. Several of these forms have the allele *P* for pointed leaf apex and the alleles *R* or *r′* for the red or spotted type of anthocyanin pigmentation. These alleles occur in many forms of *L. sativa* but not at all in *L. serriola* or only as very rare exceptions, probably as a result of spontaneous hybridization with *L. sativa* (*cf.* page 326). Altaica and LC also have the recessive anthocyanin gene, *i*, which is common in *L. sativa* but not known in *L. serriola.* With regard to spination, all the four types described by LINDQVIST (1960 b) are found. Spination is often used as a character separating *L. serriola* and *L. sativa*, but it cannot be considered as a reliable key character since non-prickly forms occur also in *L. serriola* (*cf.* p. 324).

There is considerable variation with regard to shape of the panicle which in some forms, *e.g.* Altaica, approaches the flat-topped shape typical of *L. sativa* and in others, *e.g.* ST, is more pyramidal.

Presence of fine white hairs towards the apex of the achenes is one of the characters which distinguish *L. sativa* and *L. serriola* from the other species of the *serriola* group. Observations on the material used for this study have shown, that cultivated varieties are variable with regard to this character but they all have decidedly less hairy achenes than the *L. serriola* lines. Among the primitive forms, some agree with the most hairy of the cultivated forms, others agree with *L. serriola* and one, namely Altaica, has achenes which are even more hairy than those of *L. serriola.*

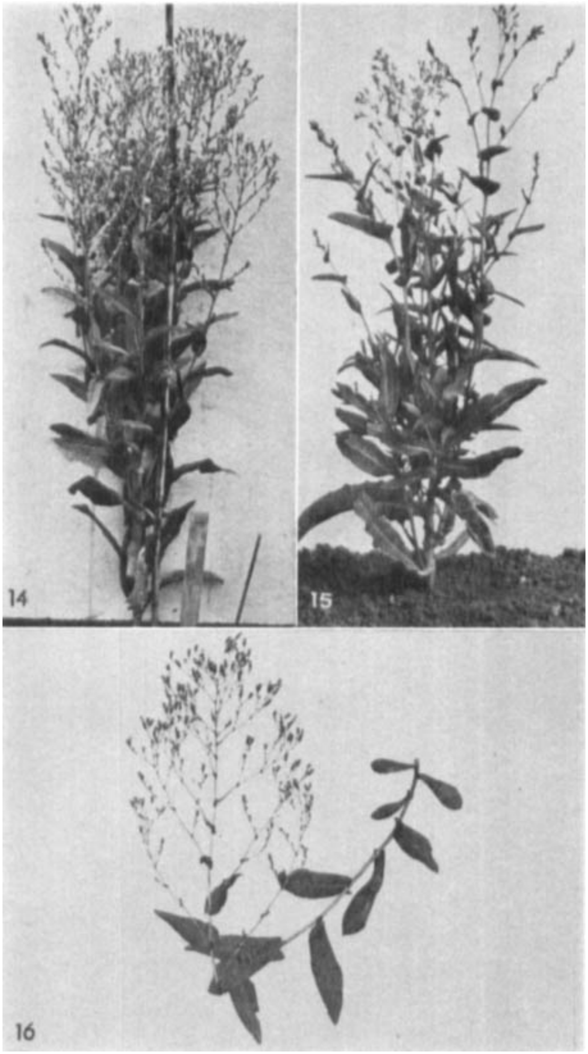
There are consistent differences between *L. sativa* and *L. serriola* with regard to some characters not mentioned earlier. Flower heads and achenes, or seeds as they will be called hereinafter for convenience, are decidedly larger in the cultivated species and the seeds germinate more rapidly and evenly when sown in the normal way. These statements are based on observations made on a large number of different lines over several years and the differences are exemplified by the data presented in Table 1. These data were obtained from plants grown in the same greenhouse and treated alike in every respect. The average diameter of 10 flower heads, with florets fully open, has been used as measure of flower head size, the length of the petals usually being closely related to the size of other floral parts. The line LC is exceptional in this

TABLE 1. *Flower head size and seed characters of L. serriola and L. sativa.*

Species	Line	Size of flower heads in mm	Average weight of seeds in mg	% germination in darkness 6-day count
L. serriola	Sc.L	14.3	0.78	5.5
,,	Sc.H	10.6	0.62	16.4
,,	Sc.R	13.1	0.73	8.9
,,	Sc.Fr.	10.8	—	—
,,	Sc.S.Afr.	11.3	0.58	8.0
,,	Sc.J.	13.8	0.80	18.9
L. sativa				
1. cultivated	Berl.	20.1	1.34	72.2
,,	R.rouge	17.8	1.13	95.8
,,	Oakl.	19.5	1.28	47.8
,,	Asp.	17.7	1.25	91.8
2. primitive	Altaica	15.1	1.10	97.6
,,	SP	19.3	1.38	92.3
,,	SL	17.7	1.37	95.3
,,	SB	19.0	1.39	93.0
,,	LC	12.7	1.48	86.4

respect, the petals being much shorter than usual in relation to other floral parts, and the figures for this line are therefore, in one sense, misleading. The germination tests were carried out in darkness at room temperature in petri dishes filled with sand. It is known that seeds of *L. serriola* are light-sensitive whereas most varieties of *L. sativa* germinate equally well in light and in darkness (HEGI, 1929). There are also differences with regard to temperature requirements, temperatures favouring the germination of one variety inhibiting the germination of another variety, and these differences can be eliminated if the seeds are exposed to low temperature during the initial stages of germination (BORTHWICK and ROBBINS, 1928; MC COLLUM, 1953). The conditions of the tests referred to here favoured the germination of cultivated varieties and retarded the germination of the *L. serriola* lines. The data in Table 1 show, that the primitive forms behaved in the same way as the cultivated forms of *L. sativa*.

On the strength of the above considerations, bearing in mind particularly that the new forms, like *L. sativa*, all have the erect involucre, it has been considered justified to include them under this name. Some of them are illustrated in Figs. 15—24. They all have a short period of

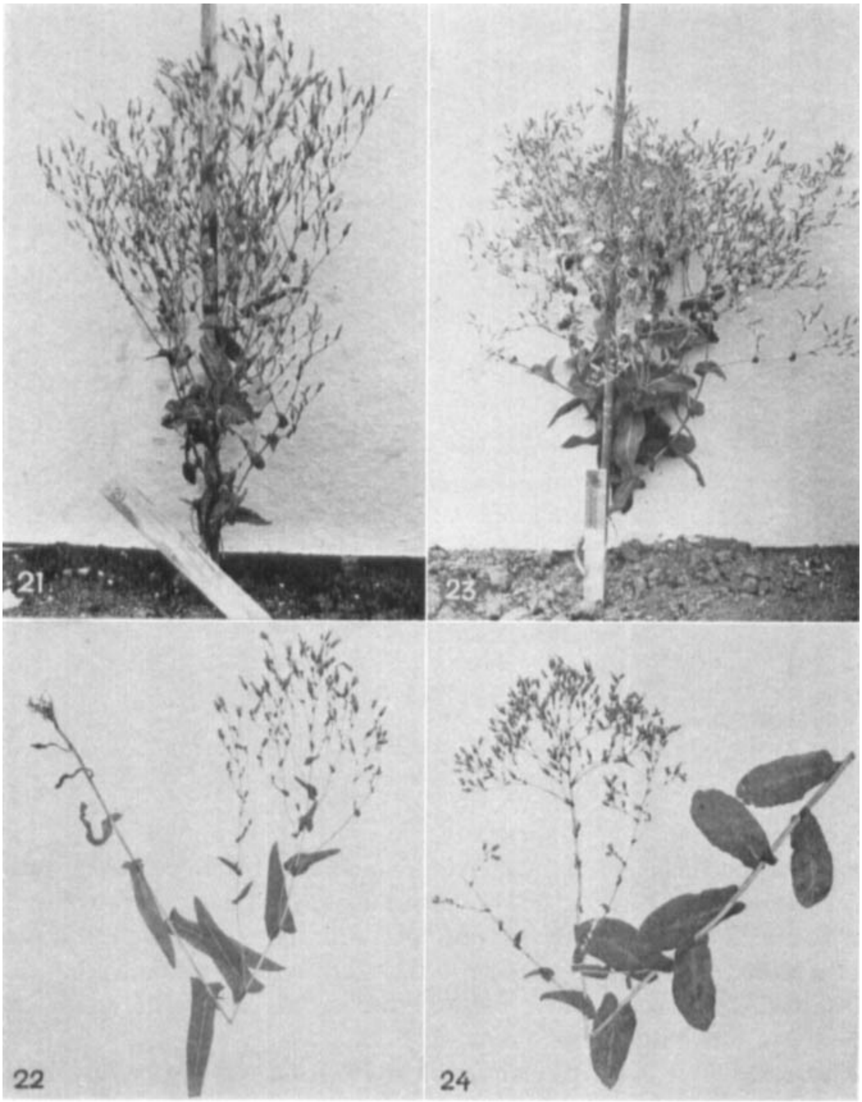


Figs. 14—16. *L. sativa*, cultivated specimens. — Fig. 14. Aspargus lettuce, line Asp.; growing plant. Fig. 15—16. The primitive form SL. Fig. 15. Growing plant. Fig. 16. Pressed specimen.

vegetative development, running to seed without a marked rosette stage. As plants for human consumption they appear to have very little to offer. In this connection it may be of interest to mention, that a similar form has recently been received from Aswan, Egypt, where it occurs in a state of semi-cultivation and is used as fodder for sheep, not for human consumption. This form is illustrated in Figs. 25 and 26. It is

Figs. 17—20. *L. sativa*, primitive forms, cultivated specimens. — Figs. 17 and 18. Line LC. Fig. 19 and 20. Line Altaica. Figs. 17 and 19. Growing plants. Figs. 18 and 20. Pressed specimens.

possible that the other forms have been, and perhaps still are, used for similar purposes, but it has not been possible to obtain from the various botanic gardens any information about their initial origin.



Figs. 21—24. *L. sativa*, primitive forms, cultivated specimens. — Figs. 21 and 22. Line SM. Figs. 23 and 24. Line SB. Figs. 21 and 23. Growing plants. Figs. 22 and 24. Pressed specimens.

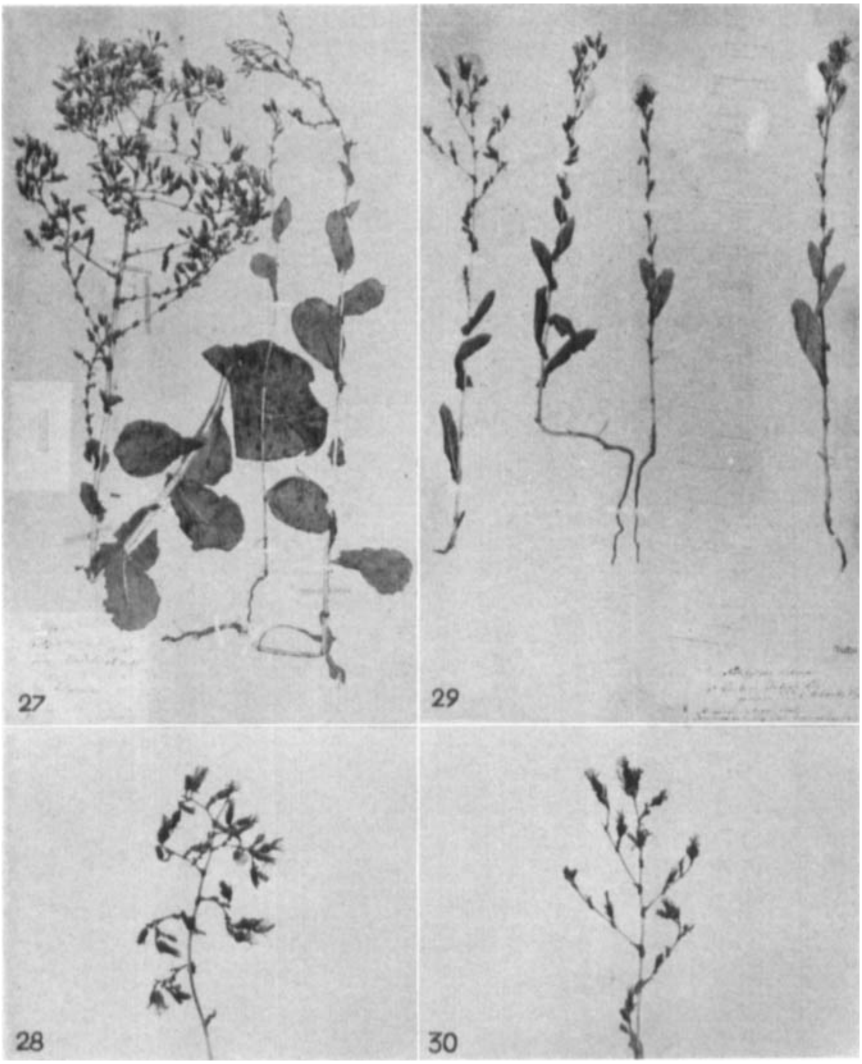
Similar forms in herbaria and literature. — A number of similar forms have been seen in various herbaria and are exemplified by the specimens listed below.

Figs. 25—26. *L. sativa*, primitive form from Aswan, Egypt, cultivated specimens. — Fig. 25. Growing plant. Fig. 26. Pressed specimen.

Herbarium	Name	Origin
Kew	*L. augustana*, Allioni	Aegypt sup.
,,	*L. scariola*, *β sativa*	Egypt 1881. Escape?
,,	*L. scariola*, L	Egypt 1867
Turin Herb Balbis	*L. Chaixii*	?
Lund	*L. altissima* M.B.	cultivated at St. Emiland, France
,,	*L. cracoviensis* Bueck in herb.	,, ,, ,, ,, ,,
,,	*L. sagittata* W & K	,, ,, ,, ,, ,,

These specimens all had the erect involucre and were certainly forms of *L. sativa*, but there is no evidence that any of them were collected from uncultivated habitats. According to Boissier (1875) a curly leaved form called *L. scariola β crispa* was found by Haussknecht in Kurdistan. Haussknecht (1895, p. 31), however, makes it quite plain that this form was an escape from cultivation.

Interesting forms have been described by Haussknecht (1895) under the name of *L. sativa* f. *spontanea* Hauskn. and by Alefeld (1866) under the name of *L. sativa* var. *Schulzii* Alef. Specimens of the former from the Haussknecht herbarium at Jena are illustrated in Figs. 27 and 28 and specimens of the latter from Naturhistorisches Museum, Vienna, in Figs. 29 and 30. Both forms clearly have the erect involucre. *L. sativa* f. *spontanea* is strikingly similar to the line SB. The achenes are stated to be much more hairy than those of cultivated forms. Haussknecht's specimens of f. *spontanea* were cultivated by Dieck in an



Figs. 27—30. Herbarium specimens of primitive forms of *L. sativa.* — Figs. 27—28. *L. sativa* f. *spontanea* HAUSSKN. from Jena. Figs. 29 and 30. *L. sativa* var. *Schultzii* ALEF. from Vienna.

experimental garden in Zöschen, Germany. HAUSSKNECHT (1895) writes about the origin of this form '. . . einer Lactuca . . ., deren Samen er (*i.e.* DIECK) aus den Bergen von Nerczynsk mit anderen Sämereien dort wild wachsender Pflanzen erhalten hatte'. On this evidence alone the possibility can, however, not be excluded that f. *spontanea*, like the form received by the writer from Aswan, Egypt, was not a genuine wild form, but a primitive cultivated form.

ALEFELD (1866) was more definite concerning the wild form status of *L. sativa* var. *Schultzii*: 'Wild gewachsene Exemplare von dem Berge Arask Cool im westlichen Kordofan sammelte KOTSCHKY und bestimmte C. H. SCHULTZ BIPONTINUS ...'

The following information is, however, found on the specimen (no. 765) from Kulturhistorisches Museum, Vienna: 'In montem Arasch Cool. Spontanea in cultis Sorghi frequens.' This, together with the fact that three similar specimens from Egypt were seen in the herbarium at Kew, one with the note Escape ?, and the fact that the form received from Aswan occurs in a semi-wild state, suggests that a form of *L. sativa* is found as a weed or in semi-cultivation in that part of the world. Another form growing in Egypt under similar conditions is *L. scariola* f. *oleifera* LAM., about which SICKENBERGER (1901) writes: 'spontanée dans la haute Egypte et la Nubie ... Les indigènes laissent cette plant se propager et en recueillent les semances pour en retirer l'huile. Il n'y a pas de culture proprement dite'. Reference to oil extraction from *Lactuca* seeds is made also by KEIMNER (1924).

L. sativa apparently occurs in Egypt in a semi-wild state and is encouraged, rather than cultivated, for the purpose of extracting oil from the seeds or as fodder for animals. It is not difficult to imagine that the primitive forms referred to in this paper are used for similar purposes, perhaps in other parts of the world, but whether this is really so must for the present remain a matter of conjecture.

ALEFELD (1866) brought together in the Var — Gr — *silvestris* four varieties of *L. sativa:* var. *Schultzii* ALEF., var. *pallida* ALEF., var. *rufescens* ALEF. and var. *maculata* ALEF. and considered that this group of varieties represented wild forms of the species. The origin of var. *Schultzii* has already been discussed but ALEFELD gives no information about the origin of the other three varieties. The varieties *rufescens* with red leaves and *maculata* with spotted leaves are very interesting, because these pigmentation types are found also among the forms received by the writer from botanic gardens.

VAVILOV (1949—1950) states that *L. sativa* occurs as wild and cultivated in the Near Eastern centre of origin of cultivated plants, but no details are given about the wild forms referred to. As a result of literature studies HELM (1954, 1955) arrived at the conclusion that primitive forms of *L. sativa* once existed, which were characterized by long, entire, more or less pointed leaves and absence of a rosette stage. He believed that such forms were common in LINNAEUS' days, and that they constituted his type for *L. sativa*. HELM (1954) calls these forms *L. sativa* provar. *sativa*, but thinks that they have gone out of cultivation and no longer exist.

There is reason to believe that the forms received by the writer from botanic gardens are similar to those described by ALEFELD, HAUSSKNECHT and HELM. It is possible that similar forms occur in a wild state, but there is no definite evidence on this point.

Are the primitive forms derivatives of crosses L. sativa×L. serriola? In view of the occasional occurrence of spontaneous hybridization between *L. sativa* and *L. serriola* the possibility must be considered that the presumed primitive types of *L. sativa* are products of such crosses. As an argument in favour of this assumption might be mentioned that they are in several respects intermediate between the two species and that they have been obtained from botanic gardens where opportunities exist for hybridization, and where hybrid products stand a much better chance of survival than in a natural habitat. There are, however, also a number of facts which argue against such an origin. It is difficult to understand why the alleged hybrid derivatives should consistently agree with *L. sativa* in the characters which separate the two species, *i.e.* the involucre character, size of flower heads and seeds and mode of germination of the seeds, unless these characters are strongly correlated, which according to preliminary investigations does not appear to be the case. If they were derivatives of *L. serriola×sativa* hybrids, some recombination of the characters would be expected. Nor is it easy to understand why they should all be characterized by very rapid development. Further, it is on general grounds more likely that these forms represent intermediate stages in the evolution of *L. sativa* than hybrids between the end result of this evolution and *L. serriola*. The latter alternative implies that all forms intermediate between cultivated lettuce and its ancestors have disappeared, which is difficult to accept, when forms exist, which have the expected characters. It is much more likely that the forms concerned really are primitive types of *L. sativa*.

II. ORIGIN OF CULTIVATED LETTUCE

1. History

The first records of lettuce as a vegetable come from Egypt. LAURENT TÄCKHOLM (1951) refers to tomb paintings from 4500 B.C. which show that a long leaved form of lettuce was in cultivation already then. KEIM-

NER (1924) classified the forms grown in ancient Egypt as belonging to *L. sativa* var. *longifolia*, *i.e.* the cos lettuce group, and points out that the illustrated specimens often have lanceolate, pointed leaves. From Egypt the cultivation of lettuce spread to Greece and Rome. Long leaved forms, presumably of the cos type, were used and probably also leaf lettuce types (HELM, 1954), but the cabbage lettuce did not appear until much later. The first incontestable record of the existence of cabbage lettuce comes according to HELM (1954, p. 124) from the 'Kräuterbuch' of L. FUCHS in 1543.

There is no certain evidence that the asparagus lettuce was used by the Egyptians, Greeks or Romans (HELM *l.c.*). These varieties are grown almost exclusively in China, where the lettuce was introduced between 600 and 900 A.D. (BREITSCHNEIDER, from HELM, 1954).

2. Previous theories

This subject has recently been reviewed by HELM (1954) and will therefore only be summarized briefly here.

The generally accepted theory is that cultivated lettuce originates from *L. serriola*. This opinion has been expressed among others by BISCHOFF (1851), DE CANDOLLE (1883) and more recently by DURST (1930), who considered that the differences and also the large variety of forms in the cultivated species are the result of accumulation of mutations due to selection during cultivation. This hypothesis has been accepted also by STEBBINS (1950, p. 292).

Different opinions have been expressed by ALEFELD (1866), who considered his var. *Schultzii* as the ancestor of *L. sativa* and by HAUSSKNECHT (1895) who believed that cultivated lettuce originates from *L. sativa* f. *spontanea* (see page 336). STURTEVANT (1886) believed that the three 'form-species', the lanceolate-leaved form (*i.e.* asparagus lettuce), cos lettuce and cabbage lettuce, originate from different wild forms which have been brought into cultivation in different regions. HELM (1954, p. 75) raises the question whether the cultivated forms have originated from pure *L. serriola* or from hybrids between this and other species, and cites as evidence for the latter alternative the marked morphological differences between cos lettuce varieties on one hand and leaf and cabbage lettuces on the other. According to FOCKE (1881, p. 221) LINNAEUS also considered the possibility that some of the cultivated lettuce varieties have hybrid origin.

Thus three different theories have been advanced concerning the origin of cultivated lettuce, namely, 1: origin from wild forms of *L. sativa*, 2: origin through direct descent from *L. serriola* and 3: origin through hybridization between different species.

3. Discussion of different theories

Origin from wild forms of L. sativa. — With regard to this theory it has already been shown that there is no reliable evidence for the existence of genuine wild forms of *L. sativa*.

Origin through direct descent from L. serriola. — If it is understood by this theory that cultivated lettuce has originated from the species *L. serriola* as we know it to-day, two problems are involved, namely 1: why a species like *L. serriola*, which appears to have so little to offer as a crop plant, was taken into cultivation and 2: whether the polymorphism of *L. sativa* can be the result of mutations which have accumulated as the result of relaxation of natural selection.

With regard to the first question it is very interesting that *L. sativa* is known to occur in Egypt in a semi-wild state, being used, not for human consumption, but for extraction of oil from seeds or as fodder for animals. No information has been found about the properties of the *Lactuca* oil or the purpose for which it is used, and it is not known whether oil of similar quality is present in seeds of *L. serriola*. If this is so and if the wild species was used for the sake of this oil, there would be an obvious selective advantage for mutation from the dominant to the recessive allele at the *B*-locus, resulting in plants with the erect involucre and better seed retaining capacity. Non-prickly forms like ALLIONI's *L. augustana* might have found a use as fodder plants. Mutations towards a longer duration of the vegetative phase and more luxurious growth, might have led to forms similar to the long leaved Egyptian lettuce, f. *aegyptiaca*, and between this and the cos or asparagus lettuce the gap is not wide. However, the fact pointed out by KEIMNER (1924) that specimens of lettuce in ancient Egyptian tomb paintings invariably are illustrated with lanceolate, pointed leaves, does not very well fit into this picture, as it indicates that the character pointed leaf apex is a primitive trait in cultivated lettuce, although this character is hardly ever found in *L. serriola* as pointed out above. It may be argued that ancient paintings are not reliable evidence for the existence of morphological traits, but in this case authorities like KEIMNER and SCHWEINFURTH (quoted by KEIMNER *l.c.*) are in no doubt about the interpretation, and therefore the evidence cannot be ignored. SCHWEIN-

FURTH writes in a letter quoted by KEIMNER (*l.c.*): 'Man muss annehmen, dass in alter Zeit unter den Blattformen des angebauten Lattichs auch solche vorkamen, die durch gleichmässig spitz zulaufende Blätter ihre Abstammung von der Urpflanze *Lactuca scariola* L deutlich bekundeten. Auch in Europa haben wir in der als „Spargelsalat" bezeichneten Lattichform, in der *L. scariola* L. var. *angustana* ALL. eine der Stammform näherstehende Kulturvarietät mit spitz auslaufenden Blättern ...' Like many other authors (*cf.* p. 326) SCHWEINFURTH has apparently confused asparagus lettuce and ALLIONI's non-lobed form of *L. serriola.* However, his statement about the pointed leaf apex in the ancient Egyptian forms is unequivocal, and as this character is found also in asparagus lettuce and primitive forms of *L. sativa*, it is not unreasonable to assume that it has been a primitive trait in cultivated lettuce and it is therefore not likely that this originated from pure *L. serriola*, as we know the species to-day.

The most recently developed form of lettuce is the cabbage lettuce (*cf.* p. 340). It is not easy to imagine that this type has originated directly from cos lettuce although the difference between non-hearting and hearting habit is due to a single gene (LINDQVIST, 1960 b). The cabbage lettuces, like the leaf lettuces, have rounded leaves of a more tender texture and a different type of venation, which to STURTEVANT (1886) and HELM (1954) has suggested two different lines of descent within *L. sativa.* If that is so, the original forms must have been very closely related, as hybrids between cos and cabbage varieties are normal in every respect (THOMPSON, 1937; LINDQVIST, 1960 a). In this connection attention is drawn to the form received under the name *L. altaica*, which has been found to have only one of the dominant genes for rosette habit (LINDQVIST, 1960 b) and which has leaves more tender than those of cos lettuce varieties. Unfortunately nothing is known about the origin of *L. altaica*, but the possibility cannot be ruled out, that it occurs in a wild state in the Altai region, or perhaps in a semi-wild state like primitive *L. sativa* forms in Egypt, and that it may have played a part in the origin of cabbage lettuce.

Another possible mode of origin of cabbage lettuce must, however, be considered. Plants, which must be classified as cos lettuce, have repeatedly appeared by mutation in the cabbage lettuce variety Tezier (LINDQVIST, 1960 b) and somewhat similar rogues recurrently appear in the variety 456 (PEARSON, 1956). Whatever the mechanism involved, the reverse process is not inconceivable, and would result in the origin of cabbage lettuce from cos lettuce by means of a single change.

When the polymorphism of *L. sativa* is considered, doubts arise, however, as to whether this can be accounted for entirely by mutation. It is not difficult to imagine that characters which are controlled by genes recessive to those in *L. serriola* and which have a selective advantage in cultivated forms, owe their origin to mutation. Such 'Kulturpflanzenmerkmale' are erect involucre, lack of spination, bigger and more rapidly germinating seeds, bigger more tender leaves etc. (*cf.* SCHWANITZ, 1957; DARLINGTON, 1956). It is more difficult to accept such an origin for characters like pointed leaf apex and the spotted type of pigmentation, which have no obvious selective advantage in cultivation, which are controlled by dominant genes and which are lacking in *L. serriola*, but present in related species (*P* in *L. saligna* and *r'* in *L. virosa*). The presence of these characters in *L. sativa* lends some support to the theory that hybridization between different species has played a part in the origin of *L. sativa*, and this raises the question of the relative importance of mutation and hybridization as creators of polymorphism.

Gene mutation versus hybridization as cause of variability. — There is much controversy concerning the parts played by gene mutation and by hybridization in creating the variability necessary for evolution of cultivated plants from wild species. Some different points of view will be presented here.

LOTZY (1916) believed that hybridization is always the cause of variability in domestication, whereas SCHWANITZ (1957) was of the opinion that gene mutation alone, is sufficient to account for this variability and for evolution from wild to cultivated forms. HEISER (1949) concluded that mutation and hybridization both must have played an important part, but that very critical data are necessary to assess their relative importance.

Most of our crop plants are too old for their history to be unravelled, except by indirect means, but some of the ornamental plants are sufficiently young for their history to be accurately reconstructed. It must be assumed that the mode of evolution has been fundamentally the same for ornamental plants and for ancient crop plants. On evidence from the evolution of ornamental plants, DARLINGTON (1956, p. 165) concluded that cultivation by itself has never produced variability in a cultivated plant, but that new variation only arises as a consequence of a change in the breeding system, *e.g.* when cross-fertilizing species are forced to inbreeding, or when hybridization occurs between different races or species of self-fertilizing plants. He quotes three cases of ornamental plants in which a large number of very different varieties have originated from a uniform wild species, namely *Lathyrus odoratus*, *Primula sinensis* and *Hyacinthus orientalis*, but in all three cases the ancestral wild type was a cross-fertilizer and bursts of variation occurred after some generations of inbreeding. DARLINGTON's explanation is that unstable recessive segregates have been selected which were prone to mutation.

Hybridization has often been emphasized as a very important factor behind the polymorphism of cultivated or wild plants. GRIGGS (1937) for example, points out that polymorphic domestic types are invariably the result of hybridization, whereas stable cultivated types have no close relations in domestication, with which they could be crossed. MÜNTZING (1930, p. 279) is of the opinion that interspecific hybridization is the main reason for the polymorphism of *Galeopsis tetrahit* and *bifida*. ANDERSON (1949) attaches much more importance to hybridization than to mutation for creating and maintaining variability, and believes that hybridization has been one of the most potent factors in the origin of domesticated plants and weeds. He proposed a very interesting theory concerning the origin of cultivated plants and associated weeds (ANDERSON *l.c.*). According to this theory primitive man unconsciously encouraged hybridization between wild species by removing barriers which had previously kept them apart, and by creating new habitats in which hybrid derivatives had a chance to survive. Out of mixtures of hybrids there originated, partly forms which were useful to man and therefore were taken into cultivation, and partly weeds which occupied waste place habitats round human habitations (so called 'camp followers'). Both were spread by man, and they became increasingly adapted and specialized, one by artificial, the other by natural selection. Thus the fact that a wild species is closely related to a cultivated species need not necessarily mean, that it is the ancestor of the cultivated species. Occasional hybridization with the cultivated species has, in combination wth the action of natural selection, the effect of increasing the efficiency of the weed species as a colonizing plant. The visible effect of such hybridization is drastically reduced because of a delicate balance between habitat and genotype and the cohesive effect of linkage between multiple factors on the morphological character complexes of the parental species, and as a consequence, the weed and the cultivated species remain distinct. The result is a slight trickle of genes from one species to another, by ANDERSON (*l.c.*) termed introgression, and this is in his opinion 'many times more important than mutation in keeping up the basic variability of the parental species'.

Possible role of hybridization in the history of L. sativa-serriola. — It has been proved that at least one species in the *serriola* group, namely *L. saligna*, is sufficiently closely related to the *L. sativa-serriola* ecospecies to give fertile hybrid derivatives, and some of these derivatives resemble lanceolate-leaved primitive forms of *L. sativa*. This makes it a real possibility that hybridization has played a part in the process of differentiation and in creating the polymorphism of *L. sativa*. More knowledge is desirable about related species from the Near East and Egypt, the areas which according to VAVILOV (1949—1950) form the centre of origin of cultivated lettuce. It is possible that in this area other forms or species exist, which are capable of hybridizing with the *L. sativa-serriola* ecospecies giving fertile derivatives.

There are certain facts which suggest that interspecific hybridization might have taken place during the evolution of *L. sativa*. It has already been pointed out that the presence of the characters spotted leaves and pointed leaf apex are easier to understand as a result of hybridization than of mutation, as the genes concerned are dominant and the characters found in related species.

The partial pollen sterility in some hybrids between different forms of the *L. sativa-serriola* complex may also be a consequence of hybridization. MÜNTZING (1938) and BERNSTRÖM (1953) suggest that the presence in *Galeopsis* and *Lamium* respectively, of partial intraspecific sterility not associated with meiotic disturbances, is due to minute structural chromosome differences, which owe their origin to hybridization with species differing in chromosome structure. A similar explanation is feasible for the partial sterility within *L. sativa-serriola*, although the possibility that it is due to gene mutations or spontaneous small structural changes cannot be ruled out on present evidence.

The disturbed segregations which have been observed with regard to leaf form (LINDQVIST, 1958, 1960 b) can also be interpreted as the result of interspecific hybridization. The cause of the abnormality was found to be different fertilization efficiency of the pollen grains, which presumably is due to complementary action of genes or small structural differences in the parents. As emphasized by MÜNTZING (1930, p. 316) there is no difference in principle between certation phenomena and partial pollen sterility. Similar abnormal segregations were found by BAENZIGER and GREENSHIELDS (1958) in crosses between *Melilotus alba* and derivatives of crosses between this species and *M. dentata* and *M. officinalis*. The authors are of the opinion that minute structural chromosome differences, resulting from the interspecific hybridization, are responsible for differences in efficacy of the gametes.

The difference between *L. sativa* and *L. serriola* with respect to the viability of their hybrids with other species may also be a consequence of hybridization. It is easier to imagine that the genes, or structural differences present in *L. sativa* and causing lethality in interspecific hybrids, have been introduced from another species, than that they should have originated spontaneously.

All the species of the *serriola* group are self-fertilizers and it has been shown earlier in this paper that evidence of spontaneous hybridization is rare. This is, however, based on observations in North West Europe and in U.S.A. It is well known that many plant species *e.g.* the tomato (RICK and BUTLER, 1956) are more or less allogamous near their centre of origin, but change to autogamy towards the periphery of their distribution area. It is therefore quite possible that the species of the *serriola* group are more allogamous in their distribution centre round the Mediterranean and hybridization between species more frequent which would make hybrid origin of *L. sativa* much more probable.

Any theory concerning the origin of *L. sativa* must take into account the very close relationship with *L. serriola*, and if the theory of direct descent is ruled out other explanations of the similarity between the two species must be considered. Three possibilities suggest themselves. 1: that both species have originated from heterogeneous hybrid populations, which included forms of some use to primtive man and that *L. sativa* has developed through selection by man, and *L. serriola* through adaptation to man-made waste habitats. 2: that the progenitors of *L. sativa* were hybrids between *L. serriola* and some other species. 3: that *L. serriola* is a product of hybridization between cultivated forms of *L. sativa* and some other species, in the same way as teosinte according to MANGELSDORF (1947) is a product of hybridization between cultivated maize and species of the genus *Tripsacum*, and not the progenitor of *Zea Mays*. On present evidence it is futile to speculate about which of these three possibilities is the most likely.

Evidence of occasional spontaneous hybridization between *L. sativa* and *L. serriola* has been produced in this paper. If such hybridization results in introgression of genes potentially useful to the wild species, hybrid derivatives with a selective advantage will occur from time to time and gradually oust other forms. In this way a close relationship between the weed and the cultivated species will be maintained. According to ANDERSON's theory, natural selection will reduce the visible effect of hybridization in the wild species and maintain the morphological differentiation. Introgression of genes from *L. sativa* has by AN-

DERSON been suggested as the reason for the ubiquity and aggressiveness of *L. serriola*. The related species *L. virosa* and *L. saligna*, which are separated from *L. sativa* by strong sterility barriers, certainly have a much more limited distribution.

Admittedly this discussion has been somewhat speculative, but in summing up the facts and arguments presented in this and in previous papers it may be said, with regard to the origin of cultivated lettuce, that many facts indicate that *L. serriola* is not the progenitor of cultivated lettuce, but that other species have been involved in evolution of this polymorphic form group, but it is not possible to form an exact picture of the events on the evidence available at present. The primitive forms must be considered as representatives of the ancestors of cultivated lettuce. The possibility that *L. sativa* and *L. serriola* are associated as cultivated species and 'camp following weed' is interesting and deserves further investigation.

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SUMMARY

An account of the taxonomy of the *serriola* group of *Lactuca* has been given, with special reference to the characters separating *L. serriola* and *L. sativa* and to primitive forms of the latter species. The nature of these forms and their bearing on the origin of cultivated lettuce has been discussed in the light of cytological and genetical results presented in earlier papers. A theory entailing hybridization between different species and evolution along the lines suggested by ANDERSON (1949) is preferred to the generally accepted theory of direct descent of *L. sativa* from *L. serriola*.

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Contents