A REVISION OF THE GENUS LACTUCA

(COMPOSITAE: LACTUCEAE) IN THE GREAT PLAINS

by

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Approved by:

[Signature]

Major Professor
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Acknowledgment is made to the curators and staff of the herbaria listed below. The symbols are those of Holmgren and Keuken (1974), and the numbers in parentheses indicate the number of specimens borrowed or critically examined at that herbarium.

UC. University of California, Berkeley (20).
KSC. Kansas State University, Manhattan (200).
KANU. University of Kansas, Lawrence (800).
MO. Missouri Botanical Gardens, St. Louis (81).
OKL. University of Oklahoma, Norman (155).
SD. University of South Dakota, Vermillion (44).
SMU. Southern Methodist University, Dallas (50).
INTRODUCTION

*Lactua* (Compositae: Lactuceae) is a cosmopolitan genus of about 100 species inhabiting north temperate regions worldwide and tropical Africa. Fifteen species occur in North America (8 native and 7 introduced), and seven of these (5 native and 2 introduced) occur in the Great Plains. *Lactucas* are known commonly as the 'wild lettuces', and *L. sativa* is the garden lettuce. These plants occupy a variety of habitats with some taxa being aggressive colonizing ('weedy') species and other taxa are natives with more narrow and ecological requirements.

As a member of the tribe Lactuceae of the Asteraceae, much of the taxonomic work on *Lactua* has been contained in tribal treatments. Early authors used selected morphological characters, especially papapus characters, which resulted in highly artificial treatments of the tribe (de Jussieu, 1789; Cassini, 1826; D. Don, 1828; Lessing, 1832; De Candole, 1839; Bentham, 1873; Hoffman, 1891). The two most recent treatments of the tribe are those by Stebbins (1953) using cytotaxonomy and geography and by Jeffrey (1966) who added microcharacters. These treatments are believed to be much more natural.

Babcock et al. (1937) did a cytotaxonomic study of *Lactua* and related genera and proposed a phylogenetic scheme based on chromosome number and karyotypic relationships. Stebbins (1937 a, b, 1939) studied some of the species relationships in detail and proposed several new species and combinations. The work of Babcock and Stebbins forms the modern foundation of systematic studies in the tribe Lactuceae.
Another important set of studies has been done because of the economic importance of the cultivated lettuce, *L. sativa*. Much genetic and cytotaxonomic work has been done with various species of *Lactuca* in the hope of improving the cultivar (Lindquist, 1956, 1958, 1960 a, b, c; Thompson, 1942, 1943; Thompson, Haney, & Kosar, 1948; Thompson & Kosar, 1938; Thompson, Whitaker & Bohn, 1958; Thompson, Whitaker & Kosar, 1941; Whitaker, 1944, 1950; Whitaker & Jagger, 1939; Whitaker & McCollum, 1954; Whitaker & Thompson, 1941). A taxonomic study of the North American *Lactuca* species has been done as a doctoral dissertation by Radloff (1961). However, Radloff’s treatment of the genus was a superficial alpha-taxonomic treatment and did not treat the biology of the group.

In the present treatment the North American species of *Lactuca* are considered to fall into four more or less distinct species groups\(^1\) (the basis for these groups will be discussed under Species Relationships). Formally dividing the genus into sections or subgenera must await a comprehensive study of the genus.

Below are listed the North American species of *Lactuca* studied under a group name that will be used for purposes of discussion.

<table>
<thead>
<tr>
<th>Serriola group</th>
<th>Canadensis group</th>
<th>Biennis group</th>
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<tr>
<td><em>L. serriola</em>(^2)</td>
<td><em>L. canadensis</em>(^2)</td>
<td><em>L. biennis</em>(^2)</td>
<td><em>L. oblongifolia</em>(^2)</td>
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<tr>
<td><em>L. saligna</em>(^2)</td>
<td><em>L. ludoviciana</em>(^2)</td>
<td><em>L. floridana</em>(^2)</td>
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\(^1\)Four additional species are recognized by Radloff (1961). However, I have not seen material of these taxa and will not consider them in my study. These taxa are *L. muralis* (L.) Gaertn., *L. Stolonifera* (Gray) Bentham and Hooker, *L. intybeacea* Jacq, and *L. terra-novae* fern.

\(^2\)Taxa present in the Great Plains.
L. virosa L. graminifolia
L. sativa L. hirsuta

It is important to note that the members of the Canadensis, Biennis, and Oblongifolia groups are indigenous to North America, and that the members of the Serriola group are introduced from Eurasia.

For the purposes of this study, the Great Plains is defined as the area extending from the beginning of continuous eastern deciduous woodlands west to the front range of the Rocky Mountains and from the Canadian border south to the Texas Panhandle and the northwest half of Oklahoma (Figure 1). This area includes the entire states of North Dakota, South Dakota, Nebraska, and Kansas. Extreme western Minnesota, Iowa, and Missouri form the eastern boundary, and the southern boundary is formed by the northwest half of Oklahoma, the Texas Panhandle, and extreme northeast New Mexico. The portions of Colorado, Wyoming, and Montana east of the front range of the Rocky Mountains form the western boundary of this study. This area encompasses a natural vegetation provenience composed mostly of prairie grasslands with the notable exception being the Black Hills of South Dakota. There is, however, only one species of Lactuca that can be referred to a prairie habitat, L. ludoviciana. This region (Figure 1) corresponds to the Flora of the Great Plains, currently in preparation by the Great Plains Flora Association, and the map is derived from the GPFA Atlas.

This study makes special reference to the Great Plains species of Lactuca, but data on all of the North American taxa are included in some chapters toward a more comprehensive study of the genus. The

3Cultivar and type species.
goals of this study are to clarify the taxonomy of the Great Plains species of Lactuca, and to use a synthetic, biosystematic approach to elucidate the relationships among the North American Lactucas.
THIS BOOK CONTAINS NUMEROUS PAGES WITH DIAGRAMS THAT ARE CROOKED COMPARED TO THE REST OF THE INFORMATION ON THE PAGE. THIS IS AS RECEIVED FROM CUSTOMER.
FIGURE 1
The Great Plains
TAXONOMIC HISTORY

The genus *Lactuca* has had a very involved nomenclatural history; therefore, the only names considered will be those that pertain to the species being studied.

Tournfort (1719) established the genus *Lactuca*, and Linnaeus published the name in the *Genera Plantarum* (1737) and the *Species Plantarum* (1753). Linnaeus placed species with filiform beaked achenes in this genus, and those with unbeaked achenes were placed in the genus *Sonchus*. For example Linnaeus placed *L. floridana* in *Sonchus*. This trend of placing the species without filiform beaked achenes in *Sonchus* or other specially created genera persisted for almost two centuries.

The genus *Cicerbita* was erected by Wallroth (1822) to include those species without filiform beaks and *L. canadensis*. The genus was revised by Beauverd (1910) to include the lactucas with a short outer pappus plus portions of *Sonchus* and *Prenanthes*.

The genus *Mulgedium* was erected by Cassini (1824) for those species of *Lactuca* without filiform beaked achenes, and the genus *Agathyrsus* was created by D. Don (1828) also to include those species of *Lactuca* without filiform beaked achenes. *Galathenium* was a curious genus erected by Nuttall (1841) in which he included the species of *Lactuca* with filiform beaks and some species of *Mulgedium*. Nuttall (1841) did not recognize any species of *Lactuca* in North America. He split what is here called *Lactuca* between *Mulgedium* and *Galathenium*. The genus *Wiestia* was erected by Schultz-Ripontinus (1841) and this name is a synonym for much of *Lactuca*. 
The nomenclatural history of this genus has followed a successive pattern of lumping. Because of the extreme polymorphism of many of the species, several of the phases were originally placed in separate species of *Lactuca* or other genera. These segregate species were later combined to forms or varieties of the same species, and in this study these infraspecific taxa are considered mere morphological phases of highly variable taxa.
CHROMOSOMAL STUDIES

Introduction. The chromosomes of *Lactuca* have been well studied (Babcock et al., 1937; Whitaker and Jagger, 1934; Whitaker and Thompson, 1941), and chromosome numbers of the North American species have been determined by these authors and others (Table 2). The chromosomes of *Lactuca* are large and heteromorphic enough to make a karyotypic study feasible. Consequently, the karyotypic approach has received much emphasis in the present study.

The genus *Lactuca* has three base chromosome numbers, \( n = 9 \), \( n = 8 \), and \( n = 17 \). The \( n = 17 \) species are presumed to be amphidiploids derived from a cross between an \( n = 9 \) species and an \( n = 8 \) species (Babcock et al., 1937; Thompson, et al., 1941). The \( n = 17 \) species studied, the *Canadensis* and *Biennis* groups, are very similar karyotypically and the species cannot be distinguished from one another by their karyotypes. *L. oblongifolia* (\( n = 9 \)) shows some karyotypic relationship to the \( n = 17 \) species but is very distinct from the introduced, \( n = 9 \) species.

Materials and Methods. Bud material for meiotic counts was collected in the field into a modified carnoy’s solution (4 parts chloroform: 3 parts absolute ethanol: 1 part glacial acetic acid). Counts were obtained by the acetocarmine squash technique (Turner and Johnston, 1961). Selected meiotic slides were made semi-permanent by ringing the cover slip with krönig cement. If a permanent slide was desired, the semi-permanent slide was placed on a slab of dry ice for ca. 10 min and the krönig cement and the cover slip were removed. The
slide was then taken through 2 changes of absolute ethanol and one change of xylene. A new coverslip was then mounted in a drop of permount and the slide left to dry. Camera lucida drawings were made of all meiotic counts (Figures 2-9) at magnifications of 1250-2000 x. Voucher specimens have been placed in the Kansas State University Herbarium (KSC).

Mitotic material was used for karyotypic study and additional chromosome counts. The procedure used differs somewhat from most published accounts, so the technique will be reported in detail.

Achenes were placed in petri dishes on moist filter paper at room temperature, and germination usually occurred in a week to 10 days. When the root tips had elongated to about .5 cm, the seedlings were submerged in a .1% aqueous solution of colchicine and kept at ca. 5°C for 3-5 hours. The root tips were then removed from the seedling and placed in a watch glass containing 9 drops of 2% acetic-orcein and 1 drop of 1M HCl (Tijo and Levan, 1950). The watch glass was then heated for 3-4 seconds over a spirit flame (just long enough to cause a small "puff" of vapor to rise from the stain). Root tips were placed on a slide in a small drop of 1% acetic-orcein, and a cover slip was gently lowered onto the root tips. Before squashing, the cover slip was gently tapped over the root tips to help spread the cells. Pressure was then firmly applied to the cover slip. The slides were made semi-permanent and permanent using the same procedure described for meiotic preparations.

Karyotypes were made from metaphase plates in which the chromosomes had reached maximum contraction and which had a minimum of
overlapping chromosomes. The cells were photographed with Panatomic-X film at 1250x on a Zeiss Universal microscope, and the negative was then printed at ca. 4375x. Karyotypes were constructed by cutting the chromosomes out of these pictures and arranging them in putative pairs. Chromosomes were arranged in order of decreasing length with the most metacentric chromosomes first when several pairs of similar length were encountered.

Results. Thirty-six populations of *Lactuca* were examined for chromosome number (Table 1). Karyotypes were obtained from six species (Figures 10-15), and observations were made on the chromosome morphologies from many more populations. The meiotic studies (Figures 2-9) showed normal bivalent pairing in all cells observed.

The karyotypes of *L. canadensis* (Figure 10); *L. ludoviciana* (Figure 11); and *L. biennis* (Figure 12) were identical (Babcock et al., 1937) and showed chromosome pairs 6 and 11 to have satellites on the short arms and chromosome pair 7 was clearly acrocentric.

The karyotype of *L. oblongifolia* (Figure 13) has satellites on the short arms of the 4th largest pair and the 5th largest pair is clearly acrocentric. Based on chromosome size, morphology, and satellite position the chromosomes of *L. oblongifolia* can be matched with 9 pairs in the tetraploids. Chromosome pairs 4 and 5 of *L. oblongifolia* are very distinctive and match pairs 6 and 7 in the tetraploids (Figure 16).

The karyotype of *L. serriola* selected for Figure 14 was not at maximum contraction; however it was chosen to show the two pairs of satellite chromosomes. The karyotype of *L. saligna* (Figure 15) shows
pairs that have the same morphology as those of *L. serriola* except that they are more contracted. Babcock et al., (1937) report that the genomes of *L. serriola* and *L. saligna* are identical. The largest pair of *L. serriola* (Figure 14) has satellites on the short arm and a secondary constriction just below the centromere on the long arm, and pair 5 has satellites on the short arm. The chromosomes of the introduced species tend to be smaller than those of the native species.

**Discussion.** A close relationship among the *n* = 17 species is indicated by the resemblance of their karyotypes. This resemblance was also noted by Babcock et al., (1937).

Karyotypically, *L. oblongifolia* bears a resemblance to the *n* = 17 taxa. Particularly chromosome pairs 4 and 5 of *L. oblongifolia* match pairs 6 and 7 of the tetraploids. This evidence supports the hypothesis that *L. oblongifolia* or a closely related species was the *n* = 9 parent of *n* = 17 North American *Lactucas*. 
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<td>$2n = 18$</td>
<td>Brooks 8264, Monona Co., Iowa (KANU)</td>
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<td></td>
<td>$n = 9$</td>
<td><em>D. 182</em>, Yuma Co., Colorado (KSC)</td>
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<tr>
<td></td>
<td>$n = 9$</td>
<td>D. 187, Goshen Co., Wyoming (KSC)</td>
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<td><em>L. canadensis</em></td>
<td>$2n = 34$</td>
<td>Bare 2649, Greenwood Co.</td>
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* Collections by Dille
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* Collections by Dille
Table 2

PREVIOUS CHROMOSOME COUNTS FOR THE NORTH AMERICAN LACTUCAS

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* The voucher for this plant has not been examined by this author, but it is probably incorrectly determined. The citation locates this plant in Guatemala and L. oblongifolia does not grow south of the U.S.-Mexican border. This plant could possibly be L. graminifolia (2n = 34) since it resembles L. oblongifolia vegetatively, and Guatemala is in the potential distribution of L. graminifolia.
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Figure 2. Camera lucida drawing of the meiotic chromosomes of *L. ludoviciana*, Diakinesis, 1600x, Dille 227, n = 17.

Figure 3. Camera lucida drawing of the meiotic chromosomes of *L. ludoviciana*, Metaphase I, 1600x, Dille 170, n = 17.

Figure 4. Camera lucida drawing of the meiotic chromosomes of *L. ludoviciana*, Diakinesis, 1600x, Dille 190, n = 17.

Figure 5. Camera lucida drawing of the meiotic chromosomes of *L. oblongifolia*, Metaphase I, 1250x, Dille 187, n = 9.

Figure 6. Camera lucida drawing of the meiotic chromosomes of *L. oblongifolia*, Metaphase I, 2000x Dille 182, n = 9.

Figure 7. Camera lucida drawing of the meiotic chromosomes of *L. serriola*, Diakinesis, 2000x, Dille 165, n = 9.

Figure 8. Camera lucida drawing of the meiotic chromosomes of *L. serriola*, Metaphase I, 2000x, Dille 175, n = 9.

Figure 9. Camera lucida drawing of the meiotic chromosomes of *L. serriola*, Diakinesis, 2000x, Dille 150, n = 9.
THIS BOOK CONTAINS NUMEROUS PAGES THAT WERE BOUND WITHOUT PAGE NUMBERS.

THIS IS AS RECEIVED FROM CUSTOMER.
Figure 10. Karyotype of *L. canadensis*, 2200x, Dille 245, 2n = 34.

Figure 11. Karyotype of *L. ludoviciana*, 2200x, Dille 232, 2n = 34.

Figure 12. Karyotype of *L. biennis*, 2200x, Dille 277, 2n = 34.

Line equals 5 microns.
Figure 13. Karyotype of *L. oblongifolia*, 2200x, Tomb 958, 2n = 18.

Figure 14. Karyotype of *L. serriola*, 2200x, Dille 230, 2n = 18.

Figure 15. Karyotype of *L. saligna*, 2200x, Dille 216, 2n = 18.

Figure 16. Marker chromosomes from (A) *L. oblongifolia*, Tomb 958, (B) *L. biennis*, Dille 277, and (C) *L. ludoviciana*, Dille 232, 2200 x.

Line equals 5 microns.
CHROMATOGRAPHIC STUDIES

Introduction. Studies of the chromatographic patterns of phenolic patterns have become a standard technique in systematic botany since the utility of this approach was dramatically demonstrated by Alston and Turner (1959), and since that time chromatographic profiles have been used to elucidate relationships at or below the generic level.

A populational study of the chromatographic patterns of the Great Plains species of Lactuca was undertaken with the goal of elucidating the interspecific relationships within the complex groups, especially within the Canadensis group. It was also hoped that a chromatographic study would help document suspected hybridization. However, the phenolic profiles of the native North American taxa are so similar that the incorporation of UV spectral data may be required before the full potential of this technique can be realized.

Materials and Methods. Bulk material was collected in the field, allowed to air dry, and ground to a fine powder in a blender. The plant material was then extracted in cold 85% methanol, agitated overnight, filtered, and kept at 0°C until use.

The extract was spotted on a 46 x 57 cm sheet of Whatman 3mm chromatography paper. The chromatograms were developed in a scaled cabinet using the standard two-dimensional descending chromatographic techniques (Mabry et al., 1970). The longer dimension was developed in 3 parts tertiary butyl alcohol: 1 part glacial acetic acid: 1 part distilled water (TBA) for 24 hours, dried, turned 90 degrees, and developed along the short dimension in 15% acetic acid (HOAC) for 5 hours. The chromatograms were then dried and examined with ultra-
violet light and with ultraviolet light in the presence of ammonia vapors. The spots were outlined, numbered, the Rf values were calculated in both solvents and the color changes in ammonia were noted (Table 3). Spots having similar Rf values and exhibiting the same color and color changes were co-chromatographed, and all spots appearing interspecifically were co-chromatographed. Co-chromatography was accomplished by cutting similar spots from two chromatograms, cutting them into small pieces, and eluting them in 85% methanol for at least four hours. The resultant extract was concentrated in a rotary evaporator, and spotted on chromatography paper. If the resultant chromatogram showed a single spot with uniform color and color change in ammonia, then the spots were considered to be the same.

Results. In this study only the spots that were purple or yellow under UV light were recorded. Spots appearing blue and green under UV light formed a complex of spots near the solvent front in HOAC that was very difficult to interpret. The composite chromatographic profiles of the populations studied (Table 5) appear in Figures 17-19, Table 3 lists the spots recognized along with their color and Rf values, and Table 4 presents the distribution of those compounds in the populations studied.

*Lactuca canadensis* and *L. ludoviciana* received the most attention in this study in the hope of elucidating the relationship between these two species. Spots 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, and 12 were found in both *L. canadensis* (Figure 18) and *L. ludoviciana*. Spot 9 and 13 were found only in *L. canadensis* and spot 14 was only found in
L. ludoviciana. However, spot 13 was found in only one population of
*L. canadensis* and compound 9 was found in only two populations.
Compound 14 in *L. ludoviciana* was found three of the six populations
studied.

One population each of *L. floridana* and *L. biennis* (Figure 18) were
examined for flavonoid compounds. The population of *L. floridana* had
spots 1, 2, 3, 5, 7, and 12, and the population of *L. biennis* had
spots 1, 2, 3, 5, 7, 8, and 12. All of these spots are found in
common with *L. ludoviciana* and *L. canadensis*, and *L. biennis* and *L.
floridana* differ only in the possession of spot 8 by *L. biennis*.

Two populations of *L. oblongifolia* (Figure 17) were examined and
found to have spots 1, 2, 3, 5, 7, 8, 12, and 15 of which only com-
 pound 15 was not found in common with *L. canadensis*, *L. ludoviciana,*
and *L. biennis*, and only spots 8 and 15 were not in common with *L.
floridana*.

One population each of *L. saligna* and *L. serriola* (Figure 19)
were examined. Both populations had spots 1, 2, 3, and 6 in common
with *L. canadensis*, *L. ludoviciana*, *L. biennis* and *L. floridana*, and
had spot 15 in common with *L. oblongifolia*. *L. saligna* had compound
11 in common with *L. canadensis* and *L. ludoviciana* but not with *L.
serriola*. Compounds 16, 17, 18, 19, 20, 21, and 22 were common to *L.
serriola* and *L. saligna* and to no other taxon examined.

Discussion. Flavonoid chemistry proved ineffective in separating
*L. canadensis* and *L. ludoviciana*. However this approach has confirmed
the close relationships among the native North American lactucas.

One important observation from this study is the resemblance of the
chromatographic pattern of *L. oblongifolia* to those of *L. canadensis*,
L. ludoviciana, L. biennis, and L. floridana. This resemblance supports the hypothesis that L. oblongifolia or a closely related species was the n = 9 parent of the tetraploid species (see section on Chromosomal Studies).

The two introduced species, L. saligna and L. serriola, are chromatographically distinct from the native species by virtue of having 7 spots not found in any of the natives.

The identification of the individual compounds would be a significant addition to this study and may identify species-specific compounds useful in documenting hybridization.
Table 3
Spots Recognized in Species of *Lactuca* Examined for Flavonoids

| Spot | Color U.V. | +NH$_3$ | Rf Values
|------|-----------|--------|-------------
<p>|      |           |        | TBA  | HOAC |
| 1    | y         | y      | .15  | .05  |
| 2    | p         | y      | .24  | .14  |
| 3    | p         | y      | .35  | .12  |
| 4    | y         | y      | .42  | .10  |
| 5    | p         | y      | .70  | .02  |
| 6    | y         | y      | .05  | .20  |
| 7    | p         | y      | .24  | .26  |
| 8    | p         | y      | .36  | .14  |
| 9    | y         | y      | .36  | .41  |
| 10   | p         | y      | .55  | .41  |
| 11   | y         | y      | .49  | .41  |
| 12   | p         | y      | .57  | .27  |
| 13   | y         | y      | .34  | .07  |
| 14   | y         | y      | .29  | .31  |
| 15   | p         | y      | .87  | .07  |
| 16   | y         | y      | .39  | .18  |
| 17   | p         | y      | .45  | .18  |
| 18   | y         | y      | .61  | .13  |
| 19   | y         | y      | .71  | .01  |
| 20   | p         | y      | .45  | .28  |
| 21   | p         | y      | .42  | .43  |
| 22   | p         | y      | .65  | .52  |</p>
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* All collections by Dille
Table 5

Species by *Lactuca* Examined for Flavonoids by Paper Chromatography

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               | *D.* 179, Yuma-Kit Carson Co. Line, Colorado (KSC)       |
| *L. canadensis*  | *D.* 156, Chase Co., Kansas (KSC)                      |
|                | *D.* 204, Osage Co., Kansas (KSC)                      |
|                | *D.* 211, Osage Co., Kansas (KSC)                      |
|                | *D.* 218, Coffey Co., Kansas (KSC)                      |
|                | *D.* 225, Osage Co., Oklahoma (KSC)                     |
|                | *D.* 245, Jackson Co., Kansas (KSC)                      |
|                | *D.* 267, Monona Co., Iowa (KSC)                        |
|                | *D.* 280, Lawrence Co., South Dakota (KSC)              |
| *L. ludoviciana* | *D.* 161, Sedgwick Co., Kansas (KSC)                    |
|                | *D.* 177, Kit Carson Co., Colorado (KSC)                 |
|                | *D.* 181, Yuma Co., Colorado (KSC)                       |
|                | *D.* 196, Stanton Co., Nebraska (KSC)                    |
|                | *D.* 233, Dewey Co., Oklahoma (KSC)                      |
|                | *D.* 235, Ford Co., Kansas (KSC)                         |
| *L. biennis*    | *D.* 275, Lawrence Co., South Dakota (KSC)              |
| *L. floridana*  | *D.* 215, Coffey Co., Kansas (KSC)                      |
| *L. serriola*   | *D.* 174, Powers Co., Colorado (KSC)                     |
| *L. saligna*    | *D.* 153, Chase Co., Kansas (KSC)                        |

* Collections by Dille
Figure 17. Composite chromatogram of *L. oblongifolia*. Stippled spot found in *L. oblongifolia* but in none of the tetraploids.

Figure 18. Composite chromatogram of the tetraploid species, *L. canadensis*, *L. ludoviciana*, *L. biennis*, and *L. floridana*. Spot with vertical lines found only in *L. canadensis*.

Figure 19. Composite chromatogram of *L. saligna* and *L. serriola*. Spots with horizontal lines found only in *L. saligna* and *L. serriola*. 
POLLEN STUDIES

Introduction. Pollen morphology in the tribe Lactuceae has been shown to be a useful character in systematic studies (Stebbins, 1953; Boulos, 1973; Tomb, 1970, 1972; Tomb, Larson & Skvarla, 1974. The present study was initiated to determine the utility of pollen characters in assessing the interspecific relationships among the North American lactucas. This study used Scanning Electron Microscopy (SEM) and Light Microscopy (LM) of specimens collected in the field and from herbarium material.

Wodehouse (1935) did the first modern treatment of the pollen grains within the tribe. Pollen grains of Lactuca are characterized by a distinct and beautiful sculpturing pattern consisting of elaborate systems of spine bearing ridges. This pattern, termed echinolophate by Wodehouse (1935), is found in most of the tribes Lactuceae and Vernoneae. Some of the taxa in the Lactuceae have pollen without elaborate systems of ridges and are simply echinate (as in most of the subtribe Stephanomeriinae (Tomb et al, 1974)). The terminology used to describe the exomorphology of the grains is that of Wodehouse (1935), and the terminology used to describe pollen shape is that of Faegri and Iverson (1964).

Materials and Methods. Mature, unopened heads were obtained from herbarium specimens of Kansas State University (KSC), the University of California, Berkeley (UC), the Missouri Botanical Garden (MO) and from dried material collected in the field (Table 7).

The heads were softened in 10% potassium hydroxide overnight and acetolized in the method described by Erdtman (1960) and modified by
Faegri and Iverson (1964) (Radford et al., 1974 also describe this method). For light microscopic examination, slides with a small amount of glycerin jelly were placed on a slide warmer, a drop of water containing the pollen was mixed with the glycerin jelly, cover slipped, and the cover slip was ringed with clear fingernail polish for permanence. For SEM studies, a drop of water containing pollen was placed on double stick tape on an aluminum specimen stub, allowed to air dry, and coated with a gold-palladium alloy in an evaporator with the specimens rotating at a 45° angle with respect to the vapor source.

Measurements were made in the light microscope at a magnification of 1000x, and the dimensions were measured to the nearest micron. The equatorial diameter is the dimension used as an indicator of the average size of the grains of each taxon. Measurements were obtained from at least four populations in each species and 20 grains were measured per population. The sample, therefore, is based on 80-100 or more individual measurements for each species.

Results. The results of the pollen measurements are presented in Table 6, and the combined results for each taxon are shown in Figure 20. Table 7 lists the material used for pollen measurements and SEM photographs.

An SEM study of pollen exomorphology was done for all native North American taxa, the introduced species L. saligna and L. serriola, and the Asian species L. tatarica. Figures 22-43 are the scanning electron micrographs of these grains. A generic description of Lactuca and descriptions of the species examined follows.
Generic Pollen Description

The pollen grains of the taxa studied are echinolophate, tri- or tetracolporate, oblate in equatorial view and circular to semi-angular in polar view. The spines are restricted to the equatorial and paraporal ridges which define 15 lacunae (6 abporal, 3 poral, and 6 paraporal) in the tricolporate grains and 20 lacunae (8 abporal, 4 poral, and 8 paraporal) in the tetracolporate grains (Figure 21). The pollen of L. canadensis (Figures 22 and 23) is typical of the tetracolporate grains and the pollen of L. oblonifolia (Figures 30 and 31) is typical of the tricolporate grains. The small channels between the abpolar and poral lacunae are called interlacunar gaps. The polar thickenings, the areas at each pole above the paraporal ridges, are large in the native North American taxa or small in the introduced taxa studied. The pollen of L. serriola (Figures 39 and 40) is typical of the type of polar thickening found in the introduced species studied. The spines of both the ridges and polar thickenings have globose, microperforate bases and nonperforate, acute conical apices. The apertures are colporate, annulate with the germ pores taking up most of the poral lacunae, and the colpi extend through the interlacunar gaps into the abporal lacunae.

Species Descriptions

Within each of the species groups, the pollen morphologies are similar enough to warrant description as a group.

Canadensis group (Figures 22-29) and Floridana group (Figures 33-36).

Tetracolporate, oblate in equatorial view and circular to semi-angular or rarely angular in polar view; polar thickening large, spiny
throughout in the canadensis group and mostly spineless and indented in the biennis group.

Oblongifolia group. (Figures 30 and 31)

Tricolporate (occasionally with tetracolporate grains), oblate in equatorial view and circular to semi-angular in polar view; polar thickening large, spiny throughout, and the spines are separate at the base.

Because of the close relationship of the Asian species L. tatarica to L. oblongifolia and the possibility that they may be the same species (Lindberg, 1936; Stebbins, 1939; section on Species Relationships), pollen of L. tatarica was studied to help clarify the relationship.

The pollen morphology of L. tatarica (Figures 41-43) is essentially the same as L. oblongifolia. However, no tetracolpate grains were found and the spines of the polar thickening may or may not be separate at the base. This is only a preliminary survey pending a study of other species which are closely related to L. tatarica.

Serriola group. (Figures 39-42)

Tricolporate, oblate in equatorial view and circular in semi-angular in polar view; polar thickening narrow, consisting of two parallel rows of spines.

Discussion. The native North American species of Lactuca have similar pollen sculpturing patterns yet one can, on a combination of exomorphological characters, separate them into three more or less distinct groups, and the groups are the same as those based on gross morphology (see list on p. 1). The two species of the Serriola group
studied, *L. saligna* and *L. serriola*, are distinct from the native taxa based on the narrow polar thickening of the introduced species as compared the large polar thickening of the indigenous species.

The essentially spineless polar thickening of the *Biennis* group may have some relationship to a polar lacuna as found in *Scorzonera* (Wodehouse, 1935) and some species of *Sonchus* (Boulos, 1973). Transmission electron microscopy of sections of pollen grains of the *Biennis* group needs to be done to help elucidate that possible relationship.

The appearance of tetracolporate pollen grains in *L. oblongifolia* was noted in material from one herbarium specimen (*Fraser 373* (KSC)). The specimen is phenotypically normal, there were many distorted grains noted, and the tetracolporate condition was noted in a very small percentage of the pollen. The occurrence of tri- and tetracolporate pollen in the same plant may be a result of unreduced microgametophytes, hybridization, or other cytological anomalies. However, since no populational and cytological data are available to support any conclusions, one can only state that more populational and cytological study is needed within this and other populations that show this condition.

The North American tetraploid (*n = 17*) taxa have tetracolporate grains almost exclusively. Tricolporate grains occur in small numbers in certain aberrant plants that are possible products of hybridization (see the section on Species Relationships). Polyploidy is generally known to have the effect of increasing mean pollen diameter and the number of apertures, and this phenomenon has been well documented (Lewis, 1964; Chuang and Constance, 1969; Lewis, W.H., 1965). In the
species of *Lactuca* studied, the tetraploid, tetracolporate taxa had larger mean equatorial diameters than the diploid, tricolporate species (Figure 20).

The pollen of the Asian species, *L. tatarica*, is similar to the pollen of *L. oblongifolia* which certainly does not detract from the conclusions of Stebbins (1939) and Lindberg (1936) that the two entities are the same species. However, a more comprehensive study taking in other related species as well as more populations of *L. tatarica* is needed before any conclusions can be drawn from this data.
TABLE 6

POLLEN GRAIN MEASUREMENTS

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<th>Range of Measurements in Microns</th>
<th>Mean Eq. Dia. in Microns</th>
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* Equatorial Diameter

ASH = A.S. Hitchcock (KSC)
FISH = M.C. Fish (KSC)
HAS = H.A. Stevens (KANU)
RB = Ralph Brooks (KANU)
RJL = R.J. Lemaire (KSC)
RKB = R.K. Baumlardi (KSC)
RLM = R.L. McGregor (KANU)
SEN = H.A. Senn (KANU)
WM = W. McMurphy (KSC)

All collections not preceded by initials are those of Dille (KSC).
Figure 20. Graphical representation of pollen size for the Great Plains species of Lactuca (see table 6). Horizontal lines indicate the range of the populational means. Vertical lines indicate the mean of these populational means (grand mean).
TAXON

L. oblongifolia

L. canadensis

L. ludoviciana

L. biennis

L. floridana

L. serriola

L. saligna

FIGURE 20

MEAN EQUATORIAL DIAMETER IN MICRONS

33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52
FIGURE 21

DIAGRAMS OF THE STRUCTURES OF LACTUCA POLLEN

Polar View

Equatorial View

al. abporal lacuna
er. equatorial ridge
gp. germ pore within poral lacuna
ig. interlacunar gap
pl. paraporal lacuna
pr. paraporal ridge
pt. polar thickening

Diagrams and terminology from Wodehouse (1935)
Figure 22. SEM micrograph of a pollen grain of *L. graminifolia*, polar view, 1787x, J. G. Lemmon s.n. (UC).

Figure 23. SEM micrograph of a pollen grain of *L. graminifolia*, equatorial view, 1780x, J. G. Lemmon s.n. (UC).

Figure 24. SEM micrograph of a pollen grain of *L. canadensis*, polar view, 2112x, Gates 15428 (KSC).

Figure 25. SEM micrograph of a pollen grain of *L. canadensis*, equatorial view, 1911x, Gates 15428 (KSC).

Figure 26. SEM micrograph of a pollen grain of *L. ludoviciana*, polar view, 2400x, Weber 401 (KSC).

Figure 27. SEM micrograph of a pollen grain of *L. ludoviciana*, equatorial view, 2400x, Weber 401 (KSC).

Line equals 5 microns.
THIS BOOK CONTAINS SEVERAL DOCUMENTS THAT ARE OF POOR QUALITY DUE TO BEING A PHOTOCOPY OF A PHOTO.

THIS IS AS RECEIVED FROM CUSTOMER.
THIS BOOK CONTAINS NUMEROUS PAGES WITH THE ORIGINAL PRINTING ON THE PAGE BEING CROOKED. THIS IS THE BEST IMAGE AVAILABLE.
Figure 28. SEM micrograph of a pollen grain of *L. hirsuta*, polar view, 1890x, *Lakela 5120* (UC).

Figure 29. SEM micrograph of a pollen grain of *L. hirsuta*, equatorial view, 1800x, *Lakela 5120* (UC).

Figure 30. SEM micrograph of a pollen grain of *L. oblongifolia*, polar view, tricolporate grain, 1584x, *Fraser 373* (KSC).

Figure 31. SEM micrograph of a pollen grain of *L. oblongifolia*, equatorial view, 1584x, *Fraser 373* (KSC).

Figure 32. SEM micrograph of a pollen grain of *L. oblongifolia*, polar view, tetracolporate grain, 1728x, *Fraser 373* (KSC).

Figure 33. SEM micrograph of a pollen grain of *L. floridana*, polar view, 1827x, *Fraser 924* (KSC).

Line equals 5 microns.
Figure 34. SEM micrograph of a pollen grain of *L. floridana*, equatorial view, 1931x, *Fraser 924* (KSC).

Figure 35. SEM micrograph of a pollen grain of *L. biennis*, polar view, 2053x, *Senn 2112* (KANU).

Figure 36. SEM micrograph of a pollen grain of *L. biennis*, equatorial view, 2053x, *Senn 2112* (KANU).

Figure 37. SEM micrograph of a pollen grain of *L. saligna*, polar view, 2600x, *Brooks 7712* (KANU).

Figure 38. SEM micrograph of a pollen grain of *L. saligna*, equatorial view, 2600x, *Brooks 7712* (KANU).

Figure 39. SEM micrograph of a pollen grain of *L. serriola*, polar view, 2426x, *Maus 862* (KSC).

Line equals 5 microns.
Figure 40. SEM micrograph of a pollen grain of *L. serriola*, equatorial view, 2545x, Maus 862 (KSC).

Figure 41. SEM micrograph of a pollen grain of *L. tatarica*, polar view, 1776x, Hohenacker s.n. (MO).

Figure 42. SEM micrograph of a pollen grain of *L. tatarica*, polar view, 2000x, Koelz 6988 (UC).

Figure 43. SEM micrograph of a pollen grain of *L. tatarica*, polar view, 1727x, Chaney 287 (UC).

Line equals 5 microns.
### TABLE 7

**SPECIMENS EXAMINED IN POLLEN STUDY**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. oblongifolia</td>
<td>Frasier 373, Cloud Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>* D. 179, Yuma-Kit Carson Co. Line, Colorado (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 182, Yuma Co., Colorado (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 183, Phillips Co., Colorado (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 185, Banner Co., Nebraska (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 186, Scott's Bluff Co., Nebraska (KSC)</td>
</tr>
<tr>
<td>L. canadensis</td>
<td>D. 156, Chase Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 211, Osage Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 212, Osage Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 214, Coffey Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 246, Jackson Co., Kansas (KSC)</td>
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<td></td>
<td>D. 249, Jackson Co., Kansas (KSC)</td>
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<td></td>
<td>D. 250, Jefferson Co., Kansas (KSC)</td>
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<tr>
<td></td>
<td>D. 253, Atkinson Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 257, Nemaha Co., Nebraska (KSC)</td>
</tr>
<tr>
<td></td>
<td>Gates 15428, Emmet Co., Michigan (KSC)</td>
</tr>
<tr>
<td>L. ludoviciana</td>
<td>A.S. Hitchcock S.N., Ames, Iowa (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 157, Chase Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 161, Sedgwick Co., Kansas (KSC)</td>
</tr>
<tr>
<td></td>
<td>D. 197, Saunders Co., Nebraska (KSC)</td>
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<td></td>
<td>D. 235, Ford Co., Kansas (KSC)</td>
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<td></td>
<td>Weber 401, Sheridan Co., Kansas (KSC)</td>
</tr>
<tr>
<td>L. biennis</td>
<td>Senn 2112, Ottawa District, Quebec, Canada (KANU)</td>
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<td>D. 275, Lawrence Co., South Dakota (KSC)</td>
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<td></td>
<td>D. 277, Lawrence Co., South Dakota (KSC)</td>
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<tr>
<td>L. floridana</td>
<td>McGregor 15973, Anderson Co., Kansas (KANU)</td>
</tr>
<tr>
<td></td>
<td>Fish 871, Pottawatomie Co., Kansas (KSC)</td>
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<td></td>
<td>Frasier 924, Cloud Co., Kansas (KSC)</td>
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<td></td>
<td>D. 255, Doniphan Co., Kansas (KSC)</td>
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<td></td>
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<td>Taxon</td>
<td>Voucher Collection</td>
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<tr>
<td>------------------</td>
<td>-------------------------------------------------------------------------------------</td>
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<tr>
<td>L. serriola</td>
<td>McMurphy S.N., Riley Co., Kansas (KSC)</td>
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<tr>
<td></td>
<td>Baumgardner 175, Stillwater, Oklahoma (KSC)</td>
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<td></td>
<td>Lemaire 1830, Hitchcock Co., Nebraska (KSC)</td>
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<td></td>
<td>D. 174, Powers Co., Colorado (KSC)</td>
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<tr>
<td></td>
<td>Maus 862, Shawnee Co., Kansas (KSC)</td>
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<td>L. saligna</td>
<td>Brooks 7712, Johnson Co., Kansas (KANU)</td>
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<td>McGregor 15972, Anderson Co., Kansas (KANU)</td>
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<td>D. 208, Wabaunsee Co., Kansas (KSC)</td>
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<tr>
<td></td>
<td>D. 216, Coffey Co., Kansas (KSC)</td>
</tr>
<tr>
<td>L. graminifolia</td>
<td>Lemmon S.N., St. Francisco Mts., Arizona (UC)</td>
</tr>
<tr>
<td>L. hirsuta</td>
<td>Lakela 5120, St. Louis Co., Minnesota (UC)</td>
</tr>
<tr>
<td>L. tatarica</td>
<td>Hohenacker S.N., in Arenosis Maritimus</td>
</tr>
<tr>
<td></td>
<td>Prope Lankuran (MO)</td>
</tr>
<tr>
<td></td>
<td>Koelz 6988, N.W. India (UC)</td>
</tr>
<tr>
<td></td>
<td>Chaney 287, Outer Mongolia (UC)</td>
</tr>
</tbody>
</table>

* refers to collections by Dille
MORPHOLOGY STUDIES

Introduction. This section deals primarily with the morphology of the achene because historically the members of the tribe Lactuceae have been finely divided on the basis of achene shape and the nature of the pappus. At times, however, these characters have been relied upon much too heavily in making taxonomic decisions, and *Lactuca* is no exception (Stebbins, 1937a). Stebbins (1937a) cites the following series of morphological criteria that separate *Lactuca* from related genera: (1) the corolla tube is more than half as long as the ligule or may equal the ligule, (2) the pappus bristles are relatively weak and at least some of the bristles are not more than four cells in thickness, (3) the achene is definitely flattened and has two prominent lateral ridges or wings, and (4) the achene may or may not be beaked, but the pappus is borne on a strongly expanded pappus disk. Anatomical data cited by Stebbins states that the ovaries of *Lactuca* usually have two or three (sometimes four) vascular bundles while *Crepis* usually has five and *Prenanthes* usually has between five and 18. Jeffrey (1966) cites additional characters that separate *Lactuca* and *Prenanthes* from the rest of the Lactuceae. These characters are long style arms with long, prominent collecting hairs, corolla tube glabrous or with crisped hairs in the upper part, and achenes smooth or hairy on the ribs.

Materials and Methods. An SEM study of the species of mature achenes was accomplished by removing the pappus bristles from the achene, separating the beak from the achene body, and mounting the beak in a drop of silver paste on an SEM specimen stub. The specimens
were then coated with a gold-palladium alloy in an evaporator with the
specimens rotating at a 45° angle with respect to the vapor source.

Studies of flower morphology were accomplished by making whole
mounts. Flowering heads were removed from material collected in the
field by this author, soaked in Pohl's solution (1 part aerosol: 25
parts methanol: 75 parts water) for ca. 15 min, and individual
florets were removed and mounted in Hoyer's solution. ¹

Results. Morphological characters associated with leaf shape,
flower color, and floral morphology proved to be of little taxonomic
significance, and these results are reported in each species description.

A photograph of the achenes of the species of *Lactuca* in the
Great Plains is presented in Figure 44. Figures 45 and 46 are photo-
graphs of the ranges of variation found in the size of the achenes of
the *Canadensis* and *Biennis* groups. Figures 47 and 48 are photographs
of achenes from each species of the *Canadensis* and *Serriola* groups in
North America.

The morphology of the fruit apicies was examined with SEM, and
the nature of the insertion of the pappus bristles into this area is
of particular interest. The results of this study for each species
will be discussed in the following paragraphs.

*L. canadensis* and *L. judoviciana* (Figures 49 and 50) have pappus
bristles that are 3–4 cells in thickness and occur in 2–3 series. The
bristles are inserted laterally near the apex of the fruit.

*L. oblongifolia* (Figures 51 and 52) has pappus bristles that are
5–9 cells in thickness. This observation is an exception to Stebbins' ¹

¹ 30 gm. gum arabic, 50 ml. water, 200 gm. chloral hydrate, and
20 ml. glycerine.
(1937a) statement that at least some of the bristles are four cells or fewer in thickness. The bristles occur in 3-4 series and are inserted laterally at the apex of the fruit.

*L. serriola* and *L. saligna* (Figures 53 and 54) have pappus bristles that are mostly two cells in thickness and occur in 2-3 series. The pappus bristles appear to be inserted distally into the fruit apex.

*L. biennis* and *L. floridana* (Figures 55-59) have heteromorphic bristles. The innermost bristles are mostly four cells in thickness and occur in 2-3 series, and the outermost bristles are much shorter and one cell in thickness (Figure 59). The pappus bristles of *L. biennis* (Figures 55 and 56) are inserted laterally slightly below the apex of the fruit, and the pappus bristles of *L. floridana* (Figures 57 and 58) are inserted laterally near the apex of the fruit.

Discussion. The characters observed in the SEM study of the fruit apicies support the separation of these species into four species groups. This type of study could provide valuable new characters for making systematic decisions within the tribe Lactuceae, but the total significance of these characters will not be known until this study is broadened to include several other genera and until anatomical evidence is included to help determine the nature of this area.
Figure 44. Photographs of achenes of the species of Lactuca in the Great Plains. L. to R., L. oblongifolia, Tomb 958; L. canadensis, Dille 266; L. ludoviciana, Dille 231; L. biennis, Dille 277; L. floridana, Stephens 63694 (KANU); L. serriola, Dille 230; L. saligna, Dille 216.

Figure 45. Photographs of achenes of L. canadensis and L. ludoviciana showing size variation. L. to R., L. canadensis, Dille 254, 281, 211, 250; L. ludoviciana, Dille 273, 269, 234, 233.

Figure 46. Photographs of achenes of L. biennis and L. floridana showing size variation. L. to R., L. biennis, Hitchcock s.n. (MO), Dille 277; L. floridana, Wagenknecht 3370 (KANU), Ross 245 (KSC), Stephens 83430 (KANU), Gates 18887 (KSC).

Figure 47. Photographs of achenes of the species of the canadensis group in North America. L. to R., L. canadensis, Dille 266; L. graminifolia, Genelle and Flemming 772 (MO); L. hirsuta, Jermy s.n. (MO); L. ludoviciana, Dille 231.

Figure 48. Photographs of achenes of the species of the serriola group in North America. L. to R., L. saligna, Dille 216; L. sativa, Marlat s.n. (KSC); L. serriola, Dille 230; L. virosa, Howell 19310 (MO).

Bottom line is millimeter scale.
Figure 49. SEM micrograph of a fruit apex of *L. canadensis*, top view, 150x, *Dille 214* (KSC).

Figure 50. SEM micrograph of a fruit apex of *L. canadensis*, side view, 150x, *Dille 214* (KSC).

Figure 51. SEM micrograph of a fruit apex of *L. oblongifolia*, top view, 130x, *Tomb 958* (KSC).

Figure 52. SEM micrograph of a fruit apex of *L. oblongifolia*, side view, 130x, *Tomb 958* (KSC).

Figure 53. SEM micrograph of a fruit apex of *L. serriola*, top view, 200x, *Dille 165* (KSC).

Figure 54. SEM micrograph of a fruit apex of *L. serriola*, side view, 200x, *Dille 165* (KSC).

Line equals .1 millimeter.
Figure 55. SEM micrograph of a fruit apex of L. biennis, top view, 120x, Dille 277 (KSC).

Figure 56. SEM micrograph of a fruit apex of L. biennis, side view, 120x, Dille 277 (KSC).

Figure 57. SEM micrograph of a fruit apex of L. floridana, top view, 120x, McGregor 15079 (KANU).

Figure 58. SEM micrograph of a fruit apex of L. floridana, side view, 120x, McGregor 15079 (KANU).

Figure 59. SEM micrograph of a fruit apex of L. floridana, side view showing short outer pappus and main pappus, 74x, Stephens 83430 (KANU).

Line equals .1 millimeter.
SPECIES RELATIONSHIPS

The North American species of Lactuca considered in this study comprise four species groups. These groups are the Canadensis group (L. canadensis*, L. ludoviciana*, L. graminifolia and L. hirsuta), the Biennis Group (L. biennis* and L. floridana*), the Oblongifolia group (L. oblongifolia*) and the Serriola Group (L. serriola*, L. saligna*, L. virosa and L. sativa). The basis for the recognition of these species groups is presented in Table 8.

The Canadensis group comprises several very closely related autogamous species all of which have a chromosome number of \( n = 17 \). These species are probably very interfertile as Whitaker (1944) obtained a highly fertile \( F_3 \) generation from a cross between L. canadensis and L. graminifolia. Natural hybrids are believed to occur between members of this group in areas of sympatry. J.B. Norton (in Whitaker, 1944) reports the observation of populations with plants intermediate between L. canadensis and L. graminifolia in South Carolina. These two species are temporally isolated (Thompson in Whitaker, 1944) with L. graminifolia flowering well in advance of L. canadensis so the opportunity for hybridization is kept to a minimum.

L. ludoviciana and L. canadensis are sympatric in the eastern Great Plains and hybridization between these two species is suspected. Correll and Johnston (1970) note that the two taxa intergrade or have merely contaminated each other through introgression, and two populations of apparent hybrid origin (Dille 209 and 245; Figure 60 and 61) were collected in the field. This hybridization proved very difficult to document because the two suspected parents are so close in every

* Taxa present in the Great Plains.
respect. These two unusual populations are similar and a brief description of them will be presented. However, more field study of these populations needs to be done before their nature is fully understood. These populations had plants that were "typical" L. canadensis with large dark green leaves and dense inflorescences, and other plants that were smaller, had narrow, light green leaves, and sparse inflorescences. This phase was observed to segregate out in crossing experiments by Whitaker et al., (1941). These two extremes appeared to grade into each other judging by the plants collected (Figures 60 and 61). The effect of cross-pollination on autogamous plants was noted by Stebbins (1950). He states that the progeny of such a cross, being highly heterozygous, would segregate extensively producing an explosion of variation for six to eight generations. The populations collected may represent this explosion several generations after the original hybridization. If this is the case, natural selection and inbreeding will serve to stabilize the populations, and field observations in future seasons will help elucidate the nature of these populations. It should be noted that the opportunity for hybridization between these two species is reduced because L. ludovicaea flowers two to four weeks before L. canadensis (R.L. McGregor, in verb; Johnson and Iltis, 1963).

The two species of the biennis group (n = 17), L. biennis and L. floridana, are autogamous, very similar morphologically and their sympatric in the eastern United States, but no hybridization has been reported between them. L. terra-nove Fern (Fernald, 1927) received no attention in this study, but according to Fernald (1927) it is allied very closely with L. biennis. Fernald described this species from one
plant he had collected in Newfoundland among a population of L. biennis, so further investigation is indicated to uncover the nature of this entity.

An intergroup hybrid between L. biennis and L. canadensis has been observed in the eastern United States and named L. morssii Robins (Robinson, 1899). This plant was not examined in this study, and a biosystematic study of this problem is indicated to fully document this hybrid. Whitaker et al. (1941) obtained hybrid plants by crossing L. canadensis with L. biennis and L. floridana, and by crossing L. graminifolia with L. floridana and L. biennis. Cytological observations of meiosis in pollen mother cells (Whitaker and Thompson, 1941) from the above hybrids showed the L. canadensis x L. biennis, L. canadensis x L. floridana, and L. graminifolia x L. floridana F₁'s to have normal pairing of 17 bivalents in almost all cells observed. The L. biennis x L. graminifolia cross produced a sterile hybrid.

The close relationships among the n = 17 taxa as indicated by the results of the crossing experiments and the biosystematic data presented in this study give strong evidence that the separation of the Biennis and Canadensis groups into different subgenera is not warranted. A tentative reclassification of the species examined is discussed in Appendix I.

L. oblongifolia is the only diploid, perennial and obligate outcrossing Lactuca native to North America. This species is very closely allied to the Asian species L. tatarica and has been considered a subspecies of it (Lindberg, 1936; Stebbins, 1939); however, the name L. oblongifolia is retained in this study until more biosystematic data can be gathered on this problem.
L. tatarica was used in crossing experiments by Whitaker et al. (1941) and Whitaker and Thompson (1941). The L. tatarica (n = 9) x L. floridana (n = 17) mating produced hybrids that had between 9 and 11 bivalents and 8 and 4 univalents upon cytological examination of pollen mother cells, and the L. graminifolia (n = 17) x L. tatarica (n = 9) mating produced hybrid plants that had 8 bivalents and 10 univalents.

The results of the crossing experiments and the biosystematic data presented in this study show a close relationship between L. tatarica - L. oblongifolia and the tetraploid North American taxa. This relationship gives evidence to support the hypothesis that L. oblongifolia or a closely related species was the n = 9 parent of the tetraploids. The possibilities for the origin of the n = 17 North American species will be outlined in the phylogeny section.

In North America, the Serriola group is represented by introduced species only. Lindquist (1956, 1958, 1960, a, b, c) has done extensive work on these plants because they are closely related to the cultivated lettuce, L. sativa. These taxa have a chromosome number of n = 9 and are distinct from L. oblongifolia and its relatives which are also n = 9 (Whitaker and Thompson, 1941; Whitaker et al., 1941).
<table>
<thead>
<tr>
<th>Oblongifolia group</th>
<th>Canadensis group</th>
<th>Biennis group</th>
<th>Serriola group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achenes flattened with 5-6 ridges on each face; unwinged; beak short, stubby and white.</td>
<td>Achenes severely flattened; 1 ridge on each face; 2 lateral wings; beak filiform.</td>
<td>Achenes flattened with 4-5 ridges on each face; unwinged; beak absent or very short and stubby; short outer pappus present.</td>
<td>Achenes flattened with 5-6 ridges on each face; unwinged (winged in <em>L. virosa</em>); beak very long and filiform.</td>
</tr>
<tr>
<td>Pollen grains usually tricolporate; polar thickening large, spint throughout, spines separate at the base.</td>
<td>Pollen grains tetracolporate; polar thickening large, spiny throughout.</td>
<td>Pollen grains tetracolporate; polar thickening large, indented, essentially spineless.</td>
<td>Pollen grains tricolporate; polar thickening small.</td>
</tr>
<tr>
<td>Distribution: 1 sp. native to North America; most taxa are Asian.</td>
<td>Distribution: 4 spp. endemic to North America.</td>
<td>Distribution: 2 spp. endemic to North America.</td>
<td>Distribution: 4 spp. introduced to North America; these and related species European.</td>
</tr>
</tbody>
</table>
Figure 60. Population of *L. canadensis* of apparent hybrid origin. *Dille 245*.

Figure 61. A close-up of the two extremes of the above population.
PHYLOGENY

This section is devoted to outlining several possible routes of evolution of the native North American species of Lactuca. A major problem in elucidating the phylogeny of the North American lactucas is the determination of the origin of the \( n = 17 \) taxa. Determination of the progenitors of the \( n = 17 \) taxa is also important in understanding how the North American lactucas related to the rest of the genus on a worldwide scale.

The biosystematic evidence presented in this study and the results of crossing experiments from other studies have led to the following conclusions: (1) the \( n = 17 \) North American species are of amphidiploid origin most probably from a hybridization between an \( n = 9 \) and an \( n = 8 \) species, (2) the \( n = 17 \) taxa are very closely related to each other, and (3) L. oblongifolia is closely related to the \( n = 17 \) taxa, and L. oblongifolia or a closely related species was probably the \( n = 9 \) parent of the amphiploids. Stebbins (1939) points out that the ancestors of L. oblongifolia probably migrated across the Siberian-Alaskan land bridge in late Pliocene or Pleistocene time. The possibility of long distance dispersal of the ancestors of L. oblongifolia from Asia is also possible, but this route would have to involve two separate dispersal events because L. oblongifolia is self compatible and is not very probable. There are no \( n = 17 \) species of Lactuca in Asia so the assumption is made that the hybridization between the \( n = 9 \) and \( n = 8 \) species and consequent speciation of the \( n = 17 \) taxa occurred in North America. At the present time there are no \( n = 8 \) lactucas in North America. The lactucas with chromosome numbers of
"n = 8 are all old world species and do not appear to be closely related to the new world n = 17 species. Consequently, the n = 8 probably had to come from either an extinct n = 8 Lactuca or from a closely related genus such as Prenanthes.

The North American members of the genus Prenanthes (base chromosome number, x = 8) are also believed to have migrated across the Siberian-Alaskan land bridge (Milstead, 1964). Several members of this genus would have been in an excellent geographical position to be the n = 8 parent of the n = 17 taxa. Prenanthes is considered to be in the same evolutionary line as Lactuca and closely related to it (Babcock et al., 1937; Jeffrey, 1956).

Accounting for two rather distinct yet closely related amphiploid groups presents another problem. The hybridization could have happened between the ancestral L. oblongifolia and two closely related ancestral species of Prenanthes thus starting two lines, the Canadensis group and the Biennis group, or the hybridization could have happened with one ancestral species of Prenanthes and two different segregates could have started the two lines.

A hypothetical karyotype of the n = 8 taxa involved in the hybridization was constructed by removing chromosome pairs from the karyotype of L. canadensis that match pairs from the karyotype of L. oblongifolia (Figure 62). Chromosome pairs 1, 3, 4, 6, 7, 8, 9, 12, and 14 of L. canadensis match pairs 1–9 of L. oblongifolia. Chromosome pairs 2, 5, 10, 11, 13, 15, 16, and 17 of L. canadensis, therefore, remain as the hypothetical 2n = 16 karyotype. Chromosome pair 11 of this hypothetical karyotype has satellites on the short arms. This hypothesis is speculative and detailed biochemical, morphological, and karyotypic data need to be gathered before it can be vigorously supported.
Figure 62. The derivation of a hypothetical karyotype of the $2n = 16$ species involved in the amphiploid origin of the $2n = 34$ Lactuca. Top, karyotype of the L. oblongifolia matched with similar pairs in L. canadensis, middle. Bottom, hypothetical $2n = 16$ karyotype, 1800x.

Line equals 5 microns.
L. bilineololia
Tomb 958

L. camadensis
Dille 745

Hypothetical
2n 16
Karyotype
SPECIES CONCEPT

Species based on morphological criteria best represent the populations encountered in the North American luctucas. Many of the taxa have been successfully crossed under artificial conditions, and intermediate populations have been found in areas of sympathy. In nature, though, the species generally remain distinct through a combination of temporal isolation and autogamy (most of the species are antogamous and predominantly selfing. The exception is L. oblongifolia which is self incompatible).

Adherence to a strict biological species concept (Grant, 1963) would force the lumping of entities with distinct distributions and combinations of characters. Therefore, the species recognized represent the geographical modes of morphological variation. The species of Lactuca recognized in this study are the same as those of most modern authors (Gleason and Cronquist, 1963; Steyermark, 1963; Correll and Johnston, 1970).

No infraspecific taxa are recognized in this study, and in this way the present study departs from most of the previous treatments of Lactuca. Numerous infraspecific taxa have been proposed in each of the species of Lactuca in North America, especially in L. canadensis. In this taxon Fernald (1950) and Steyermark (1963) recognize nine forms distributed in four varieties and Radlof (1961) recognizes 15 forms. These taxa are based totally on variations in leaf morphology and the amount of hair on the midrib of the lower leaves and lower stem. These characters have been shown by Thompson et al., (1941) and Whitaker (1944) to be based on single gene differences in the presence
of modifiers, and these characters segregate to the point that several of the forms recognized by Radloff (1961), Fernald (1950) or Steyermark (1963) may be found on the same plant. Infraspecific taxa must be based on distinct morphological, distributional or ecological differences (Lewis, 1963; Davis and Heywood, 1965), and although a few variations in *Lactuca* may approach the necessary criteria for recognition as infraspecific taxa, none are recognized in this treatment pending a more comprehensive populational study.
TAXONOMIC TREATMENT OF LACTUCA IN THE GREAT PLAINS


*Agathyrsus* D. Don, Edin. N. Phil. Jour. 6:310. 1828.


Herbaceous annuals, biennials or perennials; stems erect, arising singly or rarely loosely clustered in *L. oblongifolia*, branching only in upper third or occasionally branched from base, glabrous, hirsute or with stiff bristles; taprooted but may become fibrous at maturity; latex white or brown. Basal leaves early deciduous; lowermost cauline leaves sessile, linear-ovate to obovate or lanceolate, variously dentate or pinnatifid to deeply pinnate-lobed or runcinate; middle and upper cauline leaves about equalling the lower cauline leaves in size but frequently differing in shape; uppermost leaves reduced to bracts. Inflorescence a diffuse conical panicle, corymbose in *L. oblongifolia* or virgate in *L. saligna*. Heads few to many; cylindrical at anthesis, becoming urceolate at maturity; involucral bracts imbricate in 3-4 series, progressively longer inward; outer bracts ovate, inner bracts lanceolate, apex dark, tomentose, margin scarious; receptacle flat, naked; florets 9-45; ligule yellow, blue, violet, reddish or rarely white; corolla tube over half as long as ligule, with or without ring of hairs at summit; anther bases sagittate; pappus of capillary bristles, white or brown; beak filiform and prominent to stubby or absent;
achene body dorsiventrally compressed with prominent lateral ridges or wings. Pollen echinolophe, tricolporate or tetracolporate. \( n = 9 \) or \( n = 17 \).

Lactuca is the ancient name of lettuce, *L. sativa*. The name is derived from *Lac*, milk, in reference to the milky juice (Fernald, 1950).

Key to the Great Plains Species

1. Achene beak distinctly filiform, at least 2 mm long.

2. Achene at least 2 mm wide; beak no longer than achene body; latex brown.

3. Achene and beak 5-6 mm long; involucral bracts 8-12 mm long; pappus bristles 5-6 mm long . . . 1. *L. canadensis*

3. Achene and beak 7-9 mm long; involucral bracts 13-20 mm long; pappus bristles 8-9 mm long . . . 2. *L. ludoviciana*

2. Achene about 1 mm wide; beak conspicuously longer than achene body; latex white.

4. Achene body with conspicuous bristles at base of beak; stiff bristles present on lower stem and abaxial midrib of most leaves . . . . . . .3. *L. serriola*

4. Achene body without conspicuous bristles at base of beak; stem glabrous and abaxial midrib of leaves glabrous or merely hirsute . . . .4. *L. saligna*

1. Achene beak stubby, less than 2 mm long or absent.

5. Beak whitish; involucral bracts 12-17 mm long;

   plants 1 m tall or less at maturity . . . . . . .5. *L. oblongifolia*
5. Beak brown or absent; involucral bracts 8-11 mm
tall; plants 1.5-2(+) m tall at maturity.

6. Pappus white; involucre of 14-17 bracts . . . 6. L. floridana
6. Pappus brown; involucre of 23-25 bracts . . . 7. L. biennis

1. Lactuca canadensis Linn.

Lactuca canadensis Linn., Sp. Pl. 799. 1753. Cicerbita canadensis
4:154. 1841. Lactuca canadensis Linn. var. typica Wieg., Rhodora
seen).

Lactuca longifolia Michx., Fl. Bor. Am. 2:85. 1803. Lactuca elongata
Lactuca canadensis Linn. var. longifolia (Michx.) Farwell, Mich.
Acad. Sci. 2:45. 1923. Type locality: "Hab in Carolina Superiore."
(not seen).


Galathenium elongatum (Muhl.) Nutt., Trans. Am. Phil. Soc.,
N.S., 7:430. 1841. Lactuca canadensis Linn. var. elongata
(Muhl.) Farwell, Mich. Acad. Sci. 2:45. 1923. Type locality:
"Habitat in Pennsylvania." (not seen).

Lactuca sagittifolia Elliot, Sketch 2:253. 1823.

Lactuca integrifolia Bigelow, Fl. Bost. ed. 2. 287. 1824. Galathenium
integrifolium (Bigel.) Nutt., Trans. Am. Phil. Soc., N.S.,
7:430. 1841. Lactuca elongata Muhl. var. integrifolia (Bigel.)
integrifolia (Bigel.) Gray, Gray Man. ed. 5. 281. 1896. Not

Lactuca canadensis Linn. var. latifolia O. Ktze., Rev. Gen. 1:349.
1891.

Lactuca canadensis Linn. var. angustifolia O. Ktze., Rev. Gen. 1:349.
1891.

Lactuca canadensis Linn. var. montana Britton, Brit. & Brn. Illus. Fl.
3:274. 1898. Type Localities: "Pocono Mt., Penn. and Catskill
Mts. N.Y." (not seen).


Herbaceous biennial (.5) 1-2 (3) m tall; stem glabrous or rarely hirsute; latex brown. Basal and lower cauline leaves highly variable, sessile, often falcate, linear-ovate, obovate to ovate, variously weakly dentate or pinnatifid to deeply pinnate-lobed, margins ciliolate, base sagittate to cuneate, 20-30 cm long, 5-15 cm wide, abaxial midrib often hirsute; middle and upper cauline leaves linear-ovate, obovate
to ovate or lanceolate, variously subentire to pinnate-lobed, margin
ciliolate or rarely glabrous, base sagittate to cuneate, abaxial
midrib glabrous. Inflorescence a diffuse, conical panicle of 50-
100(+) heads. Heads cylindric, involucral bracts 17, 8-9 mm long at
anthesis, 11-12 mm long in fruit; florets 17-22; ligule reddish at the
apex becoming yellow at the base or entirely yellow in the eastern
portion of the range, 3.5-4 mm long; corolla tube 4-4.5 mm long with a
ring of hairs at the summit; anthers yellow, exerted ca. 2 mm; style
branches reddish, exerted ca. 1 mm beyond anther tube; pappus white,
in 3-4 series, each bristle 5-6 mm long, 3-4 cells thick; beak fili-
form, 2-2.5 mm long; achene body dk. brown, 3(4) mm long, ca. 2 mm
wide, dorsiventrally compressed with prominent lateral wings and a
conspicuous ridge on the abaxial and adaxial surfaces. Pollen tetra-
colporate. n = 17.

Common in forest clearings and margins from Manitoba and e. Texas
east to Nova Scotia and n. Florida. It flowers in July and August.

REPRESENTATIVE SPECIMENS

IOWA: Burden Co.: 1 mi. W. Hillsboro, 1 Sep 1952, Davidson 118
(SMU). Clinton Co.: near Toronto, 18 June 1956, Cooperrider 2088
(SMU). Harrison Co.: Iowa 183 2 mi N. Pisqa, 18 Aug 1975, Dille 264
(KSC). Keokuk Co.: 8 June 1953, Davidson 262 (SMU). Louisa Co.: 13
Sep 1953, Davidson 1320 (SMU). Monona Co.: Iowa 183 1 mi S. Soldier,
18 Aug 1975 Dille 267 (KSC). Warren Co.: Lake Ahquabi State Park, 4
July 1957, VanBruggen 2627 (SD).

KANSAS: Allen Co.: 17 July 1896 Hitchcock s.n. (KSC). Anderson Co.: 3
Aug 1975, Clothier & Whitford s.n. (KSC). Bourbon Co.: Brown Co.: Aug 1925,
Garner s.n. (KSC). Butler Co.: July 1893, Eggert s.n. (MO). Chase
Co.: 1.7 mi W. Cottonwood, 7 July 1975, Dille 156 (KSC). Chautauqua
Co.: 4.5 mi W. Peru, 21 Sep 1974, Stephens 83195 (KANU). Cherokee
Co.: 23 July 1937, Jacobs 41 (KSC); 3 mi. N. Galena, 10 Aug 1964


L. canadensis is by far the most variable of the North American lactuca species, and many infraspecific taxa have been described on the basis of variation in leaf morphology. There are four phases with perhaps as many intermediate individuals as there are 'distinct' members of each phase. Little distributional data are available for these phases and they often grow in mixed populations.

The phase with lanceolate upper cauline leaves and unlobed lower cauline leaves is probably the phase upon which Linnaeus based the species (Farwell, 1923). Linnaeus (1753) described L. canadensis as
follows: "Foliis lanceolato-ensiformibus dentatis intermissis." The names *L. integrifolia* and *L. sagittifolia* are based on this phase.

The phase with obovate upper cauline leaves and unlobed lower cauline leaves has been recognized as var. *obovata*. This phase grades completely into the preceding one with no distinct break.

The phase with lobed lower cauline leaves having linear-falcate lobes is the basis for the names var. *typica* and *L. longifolia*. The upper cauline leaves of this phase may be pinnatifid, lanceolate, or obovate.

The fourth phase with lobed lower cauline leaves having broad triangular lobes has been recognized as var. *latifolia* and *L. elongata*. The upper cauline leaves of this phase may be ovate, obovate or lanceolate, and the very lowermost cauline leaves may be pinnatifid. These lowermost leaves, on the bottom 3-4 inches of the stem, are deciduous early in the season.

Two geographically distinct phases based on flower color also exist in this species. In the Great Plains and as far east as St. Louis the flower color is always reddish or orange, and farther east, the flower color is brilliant yellow. The areas of sympathy of these two phases have not been determined.

2. *Lactuca ludoviciana* (Nutt.) Riddell


Herbaceous biennial 1-2 m tall; stem glabrous; latex brown.

Basal and lowermost cauline leaves sessile, ovate to obovate, variously dentate or pinnatifid to deeply pinnate-lobed or lyrate, margins glabrous or rarely ciliate, base sagittate to clasping, 20-30 cm long, 5-10 cm wide, abaxial midrib often hirsute; middle and upper cauline leaves ovate to obovate, variously dentate or pinnate-lobed to sinuate, margin glabrous, base sagittate to clasping, abaxial midrib glabrous.

Inflorescence a diffuse, conical panicle of 50-100(+) heads. Heads cylindric, involucral bracts 17, 13-15(17) mm long at anthesis, 18-20 mm long in fruit; florets 20-30; ligule blue, blue with yellow apex or yellow, 5-5.5 mm long; corolla tube 7-7.5 mm long with a ring of hairs at the summit; anthers white, exerted ca. 3 mm; style branches white, exerted ca. 1 mm beyond anther tube; pappus white, in 3-4 series, each bristle 8-9 mm long, 3-4 cells thick; beak filiform 3-4 mm long;

achene body dk. brown 4-5 mm long, 2-3 mm wide, dorsventrally compressed with strong lateral wings and a conspicuous ridge on the abaxial and adaxial surfaces. Pollen tetracolporate. n = 17.

Common in prairies and open places from central Saskatchewan and w. central Texas east to central Ontario and Mississippi. It flowers in June, July, and August.

REPRESENTATIVE SPECIMENS:

COLORADO: Kit Carson Co.: ½ mi S Bethune, 10 July 1975, Dille 177 (KSC). Yuma Co.: 1.8 mi S US 385/US 36, 10 July 1975, Dille 181 (ISC).


This taxon has several phases defined by variations in flower color and leaf morphology. The phases based on leaf shape often grow in mixed populations, but little data have been gathered on flower color distribution.

The phase with all leaves obovate and unlobed is relatively uncommon as is the phase with all leaves pinnatifid. The phase most commonly observed has the lower cauline leaves pinnate-lobed to sinuate and the upper cauline leaves ovate and unlobed to sinuate. This last phase is probably an intermediate between the two more 'distinct' phases.

The ligule color may be yellow, blue, or blue with a yellow apex. The blue phase is the basis for the name L. campestris.

3. Lactuca serriola Linnaeus


Lactuca virosa sensu Small, Man. Se. Fl. 1497. 1933. Not Lactuca
Herbaceous winter annual 0.5-1.5 m tall; stem with stiff bristles on lower third; latex white. Basal and lower cauline leaves sessile, obovate to ovate, variously dentate to deeply pinnate-lobed, base sagittate, 15(20) cm long, 5(8) cm wide, abaxial midrib with stiff bristles; middle and upper cauline leaves lanceolate to lance-ovate, variously dentate to pinnate-lobed; abaxial midrib glabrous or rarely with stiff bristles. Inflorescence a diffuse. Conical panicle of 50-100(+) heads. Heads cylindric; Involucral bracts 17, 7-8 mm long at anthesis, 11-12 mm long in fruit; florets 18-25; ligule yellow with dark blue stripe on abaxial side, 4.5-5 mm long; corolla tube 3-3.5 mm long with a ring of hairs at the summit; anthers yellow, exerted ca 2-2.5 mm; style branches yellow, exerted ca. 1 mm beyond anther tube; pappus white, in 2-3 series, each bristle 4 mm long, 2 cells thick; beak filiform 4 mm long; achene body lt. brown, 3 mm long, 1 mm wide, dorsiventrally compressed with prominent lateral ridges, 5-7 conspicuous ridges on the abaxial and axaxial surfaces, and conspicuous bristles at base of beak. Pollen tricolporate. n = 9.

Common in disturbed habitats and waste areas throughout the continental United States. Flowers in June, July, and August.

REPRESENTATIVE SPECIMENS:


The first North American collections of this European native were made near Cambridge, Mass. in 1863, and it quickly spread throughout North America (Dewey, 1905). This plant is by far the most 'weedy' of the North American lactucas.

Three phases of L. serriola based solely on variations in leaf morphology occur throughout the range and in mixed populations. The phase with unlobed obovate leaves does not appear to be as common as the phase with deeply pinnate-lobed leaves. The third very common phase has the lower cauline leaves variously sinuate to deeply pinnate-lobed and the upper cauline leaves variously unlobed to sinuate. This last phase may be an intermediate between the two more 'distinct' phases. The totally unlobed phase is the basis for the names var. integrata and var. integrifolia.

The leaves of this plant will often rotate 90° on their longitudinal axis when exposed to full sunlight throughout the day. The margins of the leaves will then be vertical instead of horizontal. This characteristic has earned the name 'compass plant' for this species as the leaf apicies were believed to point north and south.
L. serriola or a closely related species is believed to have been the ancient progenitor of the cultivated lettuce, L. sativa (Lindquist, 1960), and those two species hybridize under artificial and natural conditions (Thompson et al., 1941; Anderson, 1949).

4. Lactuca saligna Linnaeus

Lactuca saligna Linn., Sp. Pl. 796. 1753. Type locality: "Habitat in Gallia, Lipsiae." (not seen).

Lactuca saligna Linn. f. ruppiana (Wallr.) G. Beck.

Herbaceous winter annual .5-1 m tall; stem whitish, glabrous; latex white. Basal and lower cauline leaves sessile, linear, entire to pinnate-lobed with 1-2 pair of linear lobes near base or pinnatifid, base sagittate, 15-25 cm long, .5-4 cm wide, abaxial midrib often hirsute; middle and upper cauline leaves linear, entire or pinnate-lobed with 1-2 pair of linear lobes. Inflorescence a virgate panicle of 50-100 heads. Heads cylindric; involucral bracts 17, 7 mm long at anthesis, 12 mm long in fruit; florets 10-15; ligule yellow with a dark blue stripe on the abaxial side, 4.5-5 mm long; corolla tube yellow, 3-3.5 mm long with a ring of hairs at the summit; anthers yellow, exerted 2-2.5 mm; style branches yellow, exerted ca. 1 mm beyond anther tube; pappus white, in 2-3 series, each bristle 4 mm long, 2 cells thick; beak filiform 4-4.5 mm long; achene body lt. brown, 3 mm long, 1 mm wide, dorsiventrally compressed with prominent lateral ridges and 5-7 conspicuous ridges on the abaxial and adaxial surfaces. Pollen tricolporate. n = 9.

Infrequent in disturbed habitats and waste areas from e. central Kansas to Ohio. It has also become established in central California. It flowers in July and August.
REPRESENTATIVE SPECIMENS:


The first collections of this European native were made in Ohio in the 1870's (Radloff, 1961). It has spread very slowly and localized in the Midwest and California.

Three phases of L. saligna based totally on leaf morphology occur through its range and in mixed populations. The phase with all leaves linear and entire will often occur in the same population with the phase that has all leaves pinnatifid. The phase with lower cauline leaves pinnatifid and upper cauline leaves linear and entire may be found with one or both of the previous phases. The name f. rupplana is based on the totally pinnatifid phase.
5. *Lactuca oblongifolia* Nuttall

*Lactuca oblongifolia* Nutt., A Cat. of New and Interesting Plants...
For Sale at Messrs. Fraser's Nursery (Reprinted by Greene,
2. 287. 1824. Type Locality: "Missouri" (not seen).

*Lactuca pulchella* (Pursh) DC. Prod. 7:134. 1838. *Mulgedium
pulchellum* (Pursh) G. Don, Sweet's Hort. Brit. 418. 1839.
*Lactuca tatarica* (Linn.) C.A. Mey. subsp. *pulchella* (Pursh)
Stebbins, Madrno 5:123. 1939. *Lactuca tatarica* (Linn.)
71:70. 1957. Type Locality: "On the Banks of the Missouri."
(not seen).

*Lactuca pulchella* (Pursh) DC. var. *heterophyllum* (Nutt.) Farwell,
Mich. Acad. Sci. 6:214. 1904. Type Locality: "Hab. Lake Huron,
and Canada, to Latitude 66°." (not seen).

Herbaceous perennial, .3-1 m tall; stem glabrous, arising singly
or rarely loosely clustered from a deeply taprooted rhizomatous caudex;
latex white. Lower cauline leaves sessile linear-ovate to oblong,
variously pinnate-lobed to runcinate or entire, base sagittate to
cuneate, 9-13 cm long, 1-3 cm wide, abaxial midrib glabrous; middle
and upper cauline leaves linear or lanceolate to oblong, pinnate-lobed
or entire. Inflorescence a corymbose panicle of 20-50 heads; involucral
bracts 18, 12-13 (15) mm long at anthesis, 15-17 mm long in fruit; florets
19-21; ligule blue to violet (white), 9-10 mm long; corolla tube 6 mm
long with a ring of hairs at the summit; anthers white, exerted ca. 5 mm;
style branches blue, exerted ca. 2 mm beyond anther tube; pappus white,
in 3-4 series, each bristle 8-10 mm long, 5-9 cells thick; beak whitish,
stout, 1.5 mm long; achene body reddish 4 mm long, 1-1.5 mm wide, dorsi-
ventrally compressed with prominent lateral ridges and 4-6 conspicuous ridges on the abaxial and adaxial surfaces. Pollen tricolporate or occasionally with tetracolporate grains. n = 9.

Locally common in low, moist open meadows from s. central Alaska and s. central California east to w. Ontario, e. central Kansas and w. Texas. It flowers in July and August.

REPRESENTATIVE SPECIMENS:


MISSOURI: Atchison Co.: 3 mi. E Tarkio, 9 July 1940, Gleason 9272 (SMU).


OKLAHOMA: Washita Co.: 17 June 1913, G.W. Stevens 979 (OKL, MO).

1971, Stephens 48918 (KANU). Gregory Co.: 2 mi. W Picktown, 1 mi. S
on Access Rd., 30 July 1965, Harms 3078 (KANU). Hanson Co.: Edge
SE Pierre, 2 July 1969, Stephens 33012 (KANU). Hutchinson Co.: 29 June
15306 (KANU). Jackson Co.: Cedar Pass, 24 July 1913, Over 6194 (SD).
Jerauld Co.: 2 mi. E Lane, 11 Sept 1972, Stephens 61180 (KANU). Jones
Kingsbury Co.: 2 mi. E Desmet, 21 July 1967, Stephens 14268 (KANU). Lake
Co.: 3 mi. SE Madison, 29 June 1966, Crow 2176 (KANU). Lawrence Co.: N
Black Hills, 26 July 1947, Bennett 646 (SD); 2 mi. S Cheyenne Crossing,
26 July 1966, Stephens 7501 (KANU); Spearfish Canyon, 19 Aug 1975, Dille
276 (KSC). Lincoln Co.: 29 June 1958, Messerli 168 (SD). Lyman Co.: 8 mi.
1959, Ailts 214 (SD). McPherson Co.: 4.5 mi. N Eureka, 29 July
1967, Stephens 15174 (KANU). Minnehaha Co.: Rapid City, 13 July
1959, Messerli 718 (SD). Pennington Co.: Rapid City, 19 July
1922, Lee E-191 (SD); 29 July 1957, Lindstrom 323 (SD); Badlands, 19 Aug
1967, Stockert 166-67 (SD). Perkins Co.: 7 mi. E Lemmon, 18 July 1971,
Stephens 49549 (KANU). Potter Co.: 16 mi. W, 7 mi. S Gettysburg, 3 July
1969, Stephens 33098 (KANU). Roberts Co.: White Rock, 15 July 1897,
Powell s.n. (SD); 14 mi. SE Wilmot, 22 July 1967, Stephens 14403 (KANU).
Sanborn Co.: 13 July 1910, Vischer 4416 (MO). Stanley Co.: 13 mi. SE
Mission, 5 July 1973, Stephens 66832 (KANU). Tripp Co.: 2 mi. E Colome,
Berensford, 1 July 1959, Messerli 529 (SD); 10 mi. S, 4 mi. W Marion,
(SD). Walworth Co.: Selby, 22 Aug 1950, Paul s.n. (SD). Wasabaugh Co.: 7
Harms 2507 (KANU). Ziebach Co.: 2 mi. W, 5 mi. S Eagle Butte, 12 July
1969, Stephens 33855 (KANU).

WYOMING: Albany Co.: 28 July 1943, Porter 3301 (MO). Campbell Co.: 23
mi. NW Gillette, 2 Aug 1573, Stephens 69806 (KANU). Carbon Co.: .5
mi. S Meriden, 12 Aug 1973, Stephens 71002 (KANU). Lincoln Co.: 1

This plant was known as L. pulchella (Pursh) DC. until Reveal (1968)
pointed out that the name L. oblongifolia Nutt. has one year priority
over Sonchus pulchellus Pursh (see synonymy). However, this plant may be
a subspecies of the Asian taxon L. tatarica as proposed by Stebbins (1939). The name L. oblongifolia is retained in this treatment until more biosystematic data can be gathered on this problem.

The populations of L. oblongifolia are usually very uniform because of the rhisominous nature of this species. The flower color is almost always blue or lavender, but specimens have been collected from a population that had pure white flowers.

Three phases based on the leaf morphology have been identified, but little data on the distribution of them are available. The most common phase has oblong leaves with the lower cauline leaves possessing 1-3 pair of linear lobes close to the leaf base. Of the two less common phases, one has totally linear leaves and the other has ovate-runcinate leaves.

6. Lactuca floridana (Linn.) Gaertner


Type Locality: "Habitat Louisiana." (not seen).

Lactuca florigata (Linn.) Gaertn. f. leucantha Fern., Rhodora 42:498.  
1940. Type Coll.: Ferald and Long 11,484, Sussex Co., Virginia  
(CH,-Holotype, PH, not seen).

Herbaceous biennial 1.5-2 (3) m tall; stem glabrous; latex white.  
Basal and lower cauline leaves sessile, ovate, variously dentate to  
deployed pinnate-lobed, apex broadly triangular, base attenuate and  
sagittate, 17 (+) cm long, 9 (+) cm wide, abaxial veins hirsute; middle  
and upper cauline leaves ovate to lanceolate, variously dentate to  
pinnately lobed, apex broadly triangular to acute, base attenuate,  
sagittate, glabrous throughout. Inflorescence a diffuse panicle of  
50-100+ heads. Heads cylindric; involucral bracts 14-17, 8-9 mm long  
at anthesis, 8-11 mm long in fruit; florets 11-16; ligule light blue  
or rarely white, 5.5-6 mm long; corolla tube 5 mm long with a ring of  
hairs at the summit; anthers dark blue exerted ca. 3 mm; style branches  
light blue exerted ca. 1 mm beyond anther tube; pappus white, in 3-4  
series, each bristle 5-6 mm long, 3-4 cells thick, short outer pappus  
present; beak brown, stout or absent, 1 mm long if present; achene body  
dark brown, 4-5 mm long, 1.5-2 mm wide, dorsiventrally compressed with  
prominent lateral ridges and 4-5 conspicuous ridges on the abaxial and  
adaxial surfaces. Pollen tetracolporate. n = 17.

Common in forest clearings and along streams and lakes in rich  
moist soil from e. North Dakota and e. Texas east to Maine and southern  
Florida. It flowers from July to August.
REPRESENTATIVE SPECIMENS:


This species has several phases based on variations in leaf morphology and flower color. The flower color is usually light blue, but occasionally the flowers are white. This latter phase has been referred to as f. leucantha. The lower leaves always have the broadly triangular apex but may either be pinnate-lobed below the apex or unlobed below the apex. The phase with the unlobed leaves is the basis for the name L. villosa.

7. *Lactuca biennis* (Moench) Fernald


Herbaceous biennial 1.5–2 m tall; stem glabrous; latex white.

Basal and lower cauline leaves sessile, variously pinnatifid to deeply pinnate-lobed with a broadly triangular apex, dentate, base atenuate, sagittate, often with trichomes on abaxial and adaxial surfaces; middle and upper cauline leaves lanceolate, pinnate-lobed to entire, base atenuate, sagittate, glabrous throughout. Inflorescence a diffuse conical panicle of 50–100+ heads. Heads cylindric; involucral bracts ca. 24, 8 mm long at anthesis, 11 mm long in fruit; florets 25–40; ligule light blue with purple apex, 4 mm long; corolla tube 3 mm long without a ring of hairs at the summit; anthers blue, exerted ca. 1 mm beyond anther tube; pappus brown, in 3–4 series, each bristle 5–6 mm long, 3–4 cells thick, short outer pappus present; beak brown, stout or absent, 1 mm long if present; achene body light brown, 4–5 mm long, 1.5–2 mm wide, dorsiventrally compressed with prominent lateral ridges and 4–5 conspicuous ridges on the abaxial and adaxial surfaces. Pollen tetracolporate. n = 17.

Found in forest clearings and along streams and lakes in rich, moist soil from central British Columbia and northern California, east to Newfoundland and North Carolina, and south to Wyoming, South Dakota, and Iowa. It is rare in the Great Plains as it is found principally in the northern portion of the Black Hills of South Dakota.
REPRESENTATIVE SPECIMENS:


NORTH DAKOTA: Benson Co.: Lake Ibsen, 7 July 1909, Linnell s.n. (SD).


The flower color is blue with purple tips, but a yellow phase is found in western Pennsylvania. Two phases may be defined based on variation in leaf morphology. One phase has pinnatifid leaves and the other phase has leaves with a broadly triangular apex and pinnate-lobed below the apex. No data have been gathered by this author on the distribution of these phases as the plant is rare in the Great Plains.

Doubtful and Excluded Names


Sonchus acuminatus Bigel. Fl. Bost. ed 2. 290. 1824. This may be L. biennis upon examination of the type.

Agathyrsus macrophyllus (Willd.) L. Beck, Bot. 170. 1833.
Mulgedium macrophyllum (Willd.) DC. Prod. 7:248. 1838.
N.S. 7:441. 1841. This may be either L. biennis or L. floridana
upon examination of the type.
Figure 63. Distribution of *L. canadensis*.

Figure 64. Specimen of *L. canadensis*, Stephens 59018 (KANU).

Figure 65. Specimen of *L. canadensis*, T.B. Croat 2487 (KANU).

Figure 66. Specimen of *L. canadensis*, C.S. Wallis 7649-1 (KANU).

Magnification of herbarium specimens is .26x.
Figure 67. Specimen of *L. canadensis*, Stephens 60735 (KANU).

Figure 68. Distribution of *L. ludoviciana*.

Figure 69. Specimen of *L. ludoviciana*, Stephens 83026 (KANU).

Figure 70. Specimen of *L. ludoviciana*, Stephens 59162 (KANU).

Magnification of herbarium specimens is .26x.
Figure 71. Distribution of *L. serriola*.

Figure 72. Specimen of *L. serriola*, Stephens 43421 (KANU).

Figure 73. Specimen of *L. serriola*, Stephens 44937 (KANU).

Figure 74. Distribution of *L. saligna*.

Magnification of herbarium specimens is .26x.
Figure 75. Specimen of *L. saligna*, Richards 3425 (KANU).

Figure 76. Specimen of *L. saligna*, Stephens 82814 (KANU).

Figure 77. Distribution of *L. oblongifolia*.

Figure 78. Specimen of *L. oblongifolia*, Stephens 55860 (KANU).

Magnification of herbarium specimens is .26x.
Figure 79. Specimen of L. oblongifolia, Stephens 33030 (KANU).

Figure 80. Distribution of L. floridana.

Figure 81. Specimen of L. floridana, Stephens 18731 (KANU).

Figure 82. Specimen of L. floridana, Stephens 17715 (KANU).

Magnification of herbarium specimens is .26x.
Figure 83. Distribution of *L. biennis*.

Figure 84. Specimen of *L. biennis*, *Stephens 7215* (KANU).

Figure 85. Specimen of *L. biennis*, *J.R. Churchill s.n.* (MO).

Figure 86. Specimen of *L. sativa*, *N.B. Jacobs s.n.* (KSC).

Magnification of herbarium specimens is .26x.
Figure 87. Specimen of L. virosa, J.T. Howell 19310 (MO).

Figure 88. Specimen of L. graminifolia, A.H. Curtiss 4504 (UC).

Figure 89. Specimen of L. hirsuta, O. Lakella 5120 (UC).

Figure 90. Specimen of L. tatarica, I. Schiraevsky s.n. (MO).

Magnification of herbarium specimens is .26x.
APPENDIX I

A TENTATIVE INFRAGENERIC RECLASSIFICATION OF THE NORTH AMERICAN LACTUCAS AND RELATED SPECIES

This proposed infrageneric reclassification is only tentative and no formal changes are intended at this time. The formal reclassification must await a comprehensive study of the genus.

Present Classification:

<table>
<thead>
<tr>
<th>Lactuca subg. Lactuca</th>
<th>Lactuca subg. Mulgedium</th>
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<tr>
<td>L. sativa</td>
<td>L. floridana</td>
</tr>
<tr>
<td>L. serriola</td>
<td>L. biennis</td>
</tr>
<tr>
<td>L. saligna</td>
<td>L. oblongifolia</td>
</tr>
<tr>
<td>L. virosa</td>
<td>L. tatarica</td>
</tr>
<tr>
<td>L. canadensis</td>
<td></td>
</tr>
<tr>
<td>L. ludoviciana</td>
<td></td>
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<tr>
<td>L. hirsuta</td>
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<tr>
<td>L. graminifolia</td>
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</tbody>
</table>

Proposed Reclassification:

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<th>Lactuca subg. Mulgedium</th>
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</thead>
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<td>sect. Mulgedium</td>
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<td>L. serriola</td>
<td>L. tatarica</td>
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<tr>
<td>L. saligna</td>
<td>L. oblongifolia</td>
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<td>L. virosa</td>
<td>sect. Cicerbita</td>
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<td>L. canadensis</td>
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<td>L. floridana</td>
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</table>
REFERENCES


. 1969. in IOPB Chromosome Number Reports XX. Taxon 18:213-221.


A REVISION OF THE GENUS LACTUCA
(COMPOSITAE: LACTUCEAE) IN THE GREAT PLAINS

by

DAVID P. DILLE

B. S., Kansas State University, 1974

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1976
A REVISION OF THE GENUS LACTUCA  
(COMPOSITAE: LACTUCEAE) IN THE GREAT PLAINS

ABSTRACT

Seven species of Lactuca occurring in the Great Plains were revised using modern biosystematic techniques. These species are L. serriola and L. saligna (introduced) and L. canadensis, L. ludoviciana, L. biennis, and L. floridana (native).

Chromosome numbers of L. serriola, L. saligna, and L. oblongifolia are \(n = 9\) and L. canadensis, L. ludoviciana, L. floridana, and L. biennis are \(n = 17\). The \(n = 17\) species are believed to be amphidiploids derived from a cross between an \(n = 9\) species (L. oblongifolia or a closely related species) and an undetermined \(n = 8\) species. Karyotypic studies, chromatographic studies, and pollen studies show close relationships among the \(n = 17\) species and a close relationship between L. oblongifolia (\(n = 9\)) and the \(n = 17\) species. L. serriola and L. saligna are distinct from the native species. SEM micrographs are provided for pollen and achene morphology.

A key is provided, and synonymies, descriptions, and distribution maps are presented for each species. No infraspecific taxa are recognized. The infraspecific variation is thought to be best treated as simple phases of highly polymorphic species.