Comparison between Two Genera, Species and Cultivars in Lactuceae

I. Karyotype analysis

M. Z. Haque and M. B. E. Godward

School of Biological Sciences, Queen Mary College,
London EI 4NS, Great Britain

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Karyotype analysis was carried out prior to later investigations on dose tolerance, and characters of the pollen grains and carpopodium using the scanning electron microscope. So far as is known, no previous karyotype analysis has been carried out on the three cultivars of *Lactuca sativa*.

Materials and methods

Karyotype analysis was carried out on somatic root tip metaphases of the three cultivars of *Lactuca sativa*, Webb's Wonderful, Lobjoit's Green Cos and Tom Thumb, *Lactuca serriola* collected from Essex, and a cultivar of *Cichorium intybus*, Witloof Chicory.

Seeds were germinated on moist filter paper at 19–22°C. Actively growing root tips of 3–4 mm in length were pretreated with 0.002 M solution of 8-Hydroxyquinoline for 3½ to 4 hours at 14–16°C. After the pretreatment the root tips were thoroughly washed with distilled water and fixed in acetic-alcohol (1: 3).

The root tips were hydrolysed in 1 N Hydrochloric acid at 60°C for 10 minutes and stained in Feulgen's solution for 20 to 40 minutes. Squashes were made in a drop of aceto-carmin. Slides were sealed with rubber solution and examined for suitable metaphases. Fifteen to twenty metaphases with well separated chromosomes were photographed for each cultivar and *L. serriola*. The magnification of the negative was $\times 1760$, and the prints were enlarged $\times 3$, giving a total magnification on the prints of $\times 5280$. Using these prints, chromosomes were cut from single metaphase plates (Figs. 3a, 3b, 4a, 4b, 7a, 7b, 9a, 9b, 11a and 11b) and arranged in pairs, as far as possible according to homology and in order of decreasing length (Figs. 1a, 1b, 2a, 2b, 5a, 5b, 6a, 6b, 10a and 10b.)

Measurements were taken from the prints, in mm, later converted to μm , and the mean lengths, with standard deviations, and ranges, tabulated for each cultivar and species (Table 1). In addition, arm ratios were calculated and similarly tabulated (Table 2). The four N.O. chromosomes of *L. sativa* cultivars and *L. serriola* (see karyotypes and Figs. 1a–9b) could be recognised. The N.O. regions were subject to variable degrees of residual expansion at metaphase (or premetaphase). The data on lengths of N.O. regions and dimensions of the satellites are also tabulated (Table 3).

Figs. 1, 2, 5, 6 and 10. Chromosomes of the karyotypes in order of decreasing length. Each pair of homologues is designated by a letter (A, B etc.). N. O.=nucleolar-organising chromosomes. 1a and 1b, karyotype of *L. sativa* cultivar Lobjoit's Green Cos represented by two metaphases a and b. 2a and 2b, karyotype of *L. sativa* cultivar Webb's Wonderful represented by two metaphases a and b.

Table 1. Chromosome lengths, in μm . Means and range from 5 metaphases of each cultivar and species

Chromosome	<i>Lactuca sativa</i>			<i>L. serriola</i>	<i>Lactuca</i> overall means	<i>Cichorium</i> <i>intybus</i> Witloof Chicory
	Cos	Webb's	Tom			
A	5.15 $\pm$ 1.06 (3.69 to 6.63)	4.61 $\pm$ 0.66 (3.79 to 5.59)	4.86 $\pm$ 0.71 (4.07 to 6.25)	4.24 $\pm$ 0.44 (3.88 to 4.92)	4.7	3.22 $\pm$ 0.35 (3.13 to 3.79)
B	4.81 $\pm$ 0.98 (3.31 to 6.16)	4.22 $\pm$ 0.66 (3.60 to 5.11)	4.62 $\pm$ 0.61 (4.07 to 5.87)	4.02 $\pm$ 0.47 (3.22 to 4.45)	4.4	3.04 $\pm$ 0.24 (2.75 to 3.31)
C	4.41 $\pm$ 0.38 (3.69 to 4.92)	3.89 $\pm$ 0.51 (3.41 to 4.83)	4.11 $\pm$ 0.54 (3.41 to 5.11)	3.75 $\pm$ 0.25 (3.22 to 4.07)	4.0	2.81 $\pm$ 0.11 (2.65 to 3.03)
D	3.94 $\pm$ 0.65 (2.75 to 4.83)	3.53 $\pm$ 0.54 (3.03 to 4.36)	3.88 $\pm$ 0.37 (3.41 to 4.36)	3.58 $\pm$ 0.43 (3.13 to 4.17)	3.7	2.70 $\pm$ 0.27 (2.08 to 2.94)
E	3.24 $\pm$ 0.53 (2.46 to 4.17)	2.95 $\pm$ 0.38 (2.56 to 3.69)	3.22 $\pm$ 0.38 (2.84 to 3.88)	2.84 $\pm$ 0.25 (2.56 to 3.41)	3.1	2.34 $\pm$ 0.14 (2.08 to 2.56)
F	3.27 $\pm$ 0.59 (2.27 to 3.98)	2.88 $\pm$ 0.45 (2.27 to 3.60)	3.18 $\pm$ 0.39 (2.65 to 3.60)	2.83 $\pm$ 0.22 (2.46 to 3.22)	3.0	2.19 $\pm$ 0.10 (1.99 to 2.37)
G	3.10 $\pm$ 0.51 (2.37 to 3.98)	2.76 $\pm$ 0.34 (2.27 to 3.22)	3.01 $\pm$ 0.42 (2.46 to 3.79)	2.79 $\pm$ 0.26 (2.27 to 3.03)	2.9	2.08 $\pm$ 0.09 (1.89 to 2.18)
H	2.83 $\pm$ 0.59 (1.70 to 3.60)	2.67 $\pm$ 0.42 (2.18 to 3.22)	2.65 $\pm$ 0.40 (1.99 to 3.31)	2.52 $\pm$ 0.33 (2.27 to 3.22)	2.7	2.05 $\pm$ 0.17 (1.80 to 2.37)
I	2.86 $\pm$ 0.44 (2.18 to 3.22)	2.59 $\pm$ 0.38 (2.27 to 3.22)	2.66 $\pm$ 0.38 (2.08 to 3.31)	2.39 $\pm$ 0.19 (2.08 to 2.65)	2.6	1.85 $\pm$ 0.19 (1.61 to 2.27)
Total length (n)	33.61	30.10	32.19	28.96		22.28

Mainly in order of
decreasing length

Table 2. Arm ratios. Means and range from 5 metaphases of each cultivar and species

Chromosome	<i>Lactuca sativa</i>			<i>L. serriola</i>	<i>Lactuca</i> overall mean arm ratios	<i>Cichorium intybus</i>
	Cos	Webb's	Tom			
A	1:2.4 ± 0.60 (1:2.14 to 1:2.38)	1:2.1 ± 0.16 (1:1.8 to 1:2.4)	1:2.1 ± 0.34 (1:1.70 to 1:2.8)	1:2.1 ± 0.15 (1:1.9 to 1:2.3)	1:2+	1:1.5 ± 0.21 (1:1.27 to 1:1.83)
B	1:2.2 ± 0.33 (1:1.68 to 1:2.71)	1:2.1 ± 0.08 (1:2.0 to 1:2.2)	1:2.2 ± 0.18 (1:2.07 to 1:2.5)	1:2.5 ± 0.18 (1:2.1 to 1:2.7)	1:2+	1:1.43 ± 0.36 (1:1.9 to 1:1.47)
C	1:3.0 ± 0.63 (1:2.07 to 1:4.00)	1:3.0 ± 0.58 (1:2.13 to 1:3.9)	1:3.1 ± 0.32 (1:2.62 to 1:3.6)	1:3.4 ± 0.24 (1:3.1 to 1:3.8)	1:3	1:1.72 ± 0.26 (1:1.23 to 1:1.80)
D	1:2.2 ± 0.3 (1:1.5 to 1:2.57)	1:2.2 ± 0.31 (1:1.67 to 1:2.33)	1:2.1 ± 0.17 (1:1.86 to 1:2.38)	1:2.2 ± 0.15 (1:2.0 to 1:2.42)	1:2+	1:1.51 ± 0.23 (1:1.20 to 1:1.80)
E	1:2.5 ± 0.5 (1:1.6 to 1:3.38)	1:2.3 ± 0.25 (1:2.0 to 1:2.6)	1:2.3 ± 0.27 (1:1.92 to 1:2.6)	1:2.1 ± 0.28 (1:1.6 to 1:2.6)	1:2+	1:1.76 ± 0.47 (1:1.8 to 1:2.86)
F	1:1.9 ± 0.21 (1:1.46 to 1:2.23)	1:1.5 ± 0.23 (1:1.17 to 1:1.8)	1:1.6 ± 0.16 (1:1.38 to 1:1.90)	1:1.7 ± 0.17 (1:1.43 to 1:2.00)	1:1.6+	1:1.6 ± 0.27 (1:1.27 to 1:2.0)
G	1:1.6 ± 0.3 (1:1.33 to 1:2.40)	1:1.6 ± 0.25 (1:1.33 to 1:2.20)	1:1.5 ± 0.10 (1:1.36 to 1:1.67)	1:1.6 ± 0.47 (1:1.15 to 1:2.40)	1:1.6	1:1.41 ± 0.21 (1:1.20 to 1:1.86)
H	1:1.4 ± 0.2 (1:1.2 to 1:1.17)	1:1.2 ± 0.1 (1:1.09 to 1:1.27)	1:1.3 ± 0.12 (1:1.07 to 1:1.50)	1:1.2 ± 0.1 (1:1.13 to 1:1.40)	1:1.3+	1:1.42 ± 0.19 (1:1.2 to 1:1.75)
I	1:1.1 ± 0.07 (1:0.9 to 1:1.3)	1:1.06 ± 0.1 (1:1.0 to 1:1.29)	1:1.08 ± 0.1 (1:1.0 to 1:1.29)	1:1.08 ± 0.12 (1:1.0 to 1:1.3)	1:1.1	1:1.51 ± 0.31 (1:1.0 to 1:2.0)

Results

In *Lactuca*, no pronounced difference appears at first glance between the three cultivars and *L. serriola*, in the morphology of the somatic chromosomes of the root tip (Figs. 1a, 1b, 2a, 2b, 5a, 5b, 6a and 6b and Tables 1–3). The chromosomes of Cos are however the longest (Table 1) followed by Tom, Webb's and *L. serriola*.

Figs. 3–4. 3a and 3b, somatic metaphases of Cos with $2n=18$, showing all 4 satellited chromosomes (Lettered as in karyotype, Figs. 1a and 1b). Bar representing $10\ \mu\text{m}$ applies to Figs. 3a, 3b, 4a and 4b. $\times 2700$. 4a and 4b, somatic metaphases of Webb's with $2n=18$, showing 3 of the 4 satellited chromosomes (Lettered as in karyotype, Figs. 2a and 2b). $\times 2700$.

The $2n=18$ chromosomes can be identified and grouped on the basis of length (Table 1), arm ratios (Table 2) and presence or absence of a secondary constriction (Table 3) as follows:

- A. Long chromosome with submedian centromere.
- B. " " " " "
- C. " " but not as long as A and B, with subterminal centromere. Its short arm is notably short and carries a satellite with the intervening N.O. region much or little contracted.
- D. Fairly long but not as long as A, B or C, with submedian centromere.
- E. Chromosome of medium length, with submedian centromere. The short arm carries a satellite. The N.O. region is again variable in degree of contraction.
- F. Fairly short chromosome, with submedian centromere.
- G. Fairly short chromosome, " " "
- H. Short chromosome, arms not quite the same length, centromere just submedian.
- I. Short chromosome, with almost median centromere.

The complement of *L. sativa* cultivars and that of *L. serriola* may therefore be represented by the idiogram $4L+3M+2S$ (Table 1, Figs. 1a, 1b, 2a, 2b, 5a, 5b, 6a and 6b).

The ($2n=18$) chromosomes of *C. intybus* can be classified as follows on the basis of length and arm ratios:

1. Four pairs of chromosomes are long with submedian centromeres.
2. Three pairs of chromosomes are of median length with submedian centromeres.
3. Two pairs of chromosomes are small and have submedian centromeres.

The complement of *C. intybus* cult. Witloof Chicory may therefore be represented by the idogram $4L+3M+2S$ (Table 1 and Figs. 10a and 10b).

In the present work the N.O. chromosomes of Witloof Chicory were recognized for the first time, having not previously been reported in *Cichorium* by any author.

In three prometaphases one or more chromosomes were seen to be closely accompanied by a satellite in line with the long axis of the chromosome (Fig. 12, arrow).

This finding was further confirmed by examining PMCs and observing two bivalents attached to, or probably attached, to the nucleolus. This would imply the presence of four N.O. chromosomes (two pairs) in the somatic prometaphase.

The karyotypes of the three cultivars of *L. sativa* (Figs. 1a, 1b, 2a, 2b, 5a and 5b), *L. serriola* (Figs. 6a and 6b) and *C. intybus* (Figs. 10a and 10b) are illustrated in the following pages. Each is represented by two metaphases. Chromosomes are in order of decreasing length. Each pair of homologues is designated by a letter (A to I) and the nucleolar-organising chromosomes also marked N.O. The metaphases from which the karyotypes are assembled are also shown (Figs. 11a and 11b).

Figs. 5-6. 5a and 5b, karyotype of *L. sativa* cultivar Tom Thumb represented by two metaphases a and b. 6a and 6b, karyotype of *Lactuca serriola* represented by two metaphases a and b.

Discussion

i. Length and arm ratios

The chromosomes of *C. intybus* are shorter than those of *Lactuca*.

When the chromosomes of the four representatives of *Lactuca*, *L. sativa* cultivars and *L. serriola* are compared, the remarkable similarity between the cultivars

Figs. 7-8. 7a, somatic metaphase of Tom Thumb with $2n=18$, showing 3 of the 4 satellited chromosome (Lettered as in karyotype Figs. 5a and 5b). Bar representing $10\ \mu\text{m}$ applies to Figs. 7a, 7b and 8. $\times 2700$, 7b and 8, somatic metaphase of Tom Thumb with $2n=18$, showing all the 4 satellited chromosomes (Lettered in 7b as in karyotype Figs. 5a and 5b). $\times 2700$.

Figs. 9a and 9b. Somatic metaphase of *L. serriola*, showing at least 3 perhaps all 4 of the satellited chromosomes (Lettered as in karyotype Figs. 6a and 6b). Bar representing $10\ \mu\text{m}$ applies to both Figs. 9a and 9b.

and *L. serriola*, both as to length (Table 1) and arm ratios (Table 2) as well as the characteristics of the N.O. chromosomes, is seen to be such that no numerical distinction can be made between their chromosome complements. On the graph (Fig. 13) the standard deviations of lengths are shown overlapping, only those of *Cichorium* remaining distinct. The standard deviations of *L. serriola* occupy a position near the bottom of the total *Lactuca* range, although entirely within it; *L. serriola* is characterised by less variability than the cultivars. The idiogram $4L+3M+2S$ found in the present work is therefore common to the cultivars and *L. serriola*.

Rather different results are reported from studies in America (Whitaker and Jagger 1939) where *L. sativa* cultivars Imperial D, Chinese stem, Bavarian Brown are reported with $3L+3M+3S$; the same authors also differ from the writer in finding $4L+2M+3S$ in *L. serriola* var. *integrata* from California and in *L. serriola* material from the U.S.S.R. No detailed measurements are given, and no arm ratios, so that the significance of their L, M and S is difficult to compare with that in present work. Curiously, using material of *L. serriola* from the same American source, other authors (Chatterjee and Sharma 1969), have not apparently confirmed the above idiogram but have found $2L+4M+3S$. On the other hand, there are reports of $4L+2M+3S$ (McCollum 1953). The detailed account of Lindqvist (Lindqvist 1960) shows idiograms of *L. sativa* which would be interpreted as $4L+2M+3S$, while the same two chromosomes (*i.e.* third and fifth in order of length, corresponding to

Figs. 10a and 10b. Karyotype of *Cichorium intybus* cultivar Witloof Chicory represented by two metaphases a and b. $\times 2700$.

C and E of the present work), are satellited and have submedian centromeres (Lindqvist 1960, pp 83 and 84).

The work of the present writers indicates the essential similarity between the chromosomes of *L. sativa* cultivars and those of *L. serriola* in the U.K., but the reports on material studied in other parts of the world indicate some variability in chromosome lengths, particularly as regards the long and medium length chromosomes.

Table 3. Expansion of N.O. region and satellite diameters in μm

Chromosome	<i>Lactuca sativa</i> cultivars				<i>L. serriola</i>
		Cos	Webb's	Tom	
N. O. region:					
C					
Homologue	1	0.09–2.08	0.09–0.47	0.09–1.14	0.09–0.28
"	2	0.09–1.70*	0.09–	0.09–0.76*	0.15–0.28
E					
Homologue	1	0.09–1.04	0.06–0.66	0.09–0.09	0.04–0.28
"	2	0.09–0.85	0.09–0.38	0.13–0.57	0.04–0.28
Satellites diameters separately measured	C1	0.47–	0.38–0.47	0.38–	0.39–0.47
	2	0.47–		0.38–0.47	0.44
Diameter of fused satellites	1	0.57–0.85	0.57–0.66	0.66–0.76	0.57–0.76
	2	0.76–0.85	0.57–0.76	0.57–0.76	0.66–
Satellites diameters separately measured	E1	0.38–0.47	0.47–	0.38–0.57	0.38–0.47
	2	0.47–	0.38–	0.47–	0.38–0.47
Diameter of fused satellites	1	0.66–0.76	0.57–0.76	0.57–0.76	0.57–0.66
	2	0.57–0.76	0.66–0.76	0.57–0.76	0.76–

* indicates very wide range.

ii. *N.O. chromosomes*

In the present work, the difference between varieties in respect of their N.O. chromosomes (Table 3) are only that the N.O. region of chromosome C is seen more expanded in Cos and Tom than in Webbs and *L. serriola*. The diameters of the satellites are identical throughout the three cultivars and *L. serriola*, although they are sometimes seen separately as one on each chromatid (Fig. 6a) and sometimes these are so close as to appear fused (Fig. 8). This may be the basis of size differences in different cultivars and species found by a previous author (Lindqvist 1960, p. 84).

It is of interest that both *Lactuca* and *Cichorium* have two pairs of N.O. chromosomes, of which one pair is long and the other is short.

Chicory

The present work claims only that there are 18 chromosomes, on the basis of formation of 9 bivalents as well as presence of 18 chromosomes in somatic mitosis in the root tip. Other authors have claimed the presence of B chromosomes, and a diploid chromosome number of 20 (Javorciková 1970, Feráková and Javorciková

1970). In the opinion of the writers the chromosomes of *Cichorium* are liable to break through the centromere during preparation of the slide by the squash technique; a short arm broken off will convey the impression of a B chromosome and also increased chromosome number. This occurrence has been found several times in the writers' material (Fig. 11a).

Figs. 11–12. 11a and 11b, somatic metaphases of *C. intybus* with $2n=18$ chromosomes (Lettered as in karyotype Figs. 10a and 10b). Bar representing $10\ \mu\text{m}$ applies to Figs. 11a, 11b and 12. $\times 2700$. 12, somatic prometaphase of *C. intybus* clearly showing one of the satellited chromosomes (arrow). $\times 2700$.

The number of N.O. chromosomes present in *Cichorium* has been established as four by the present authors, on the evidence that two bivalents are attached to the nucleolus at diakinesis.

A reliable count of four N.O. chromosomes in somatic mitosis has not however been possible. It may be that the tendency for the satellite to become detached, as sometimes happens in *Lactuca*, is even more marked in *Cichorium* and this is

responsible for the difficulties of finding all four N.O. chromosomes. The non-recognition of any N.O. chromosomes by previous workers may be due to the same cause.

All the chromosomes of *Cichorium* were found in the present work to have submedian centromeres, and this is confirmed by the idiograms (Figs. 2 and 3 Dujardin *et al.* 1979) in a recent publication (although the authors state that 5 are median!). Another account (Ricci 1964) refers to the centromeres as submedian or subterminal except for one pair with median centromeres in the "typical form" of *C. intybus*, and two pairs with median centromeres in a sub-species.

Fig. 13. Means and standard deviations of chromosome lengths in *L. sativa* cultivars, *L. serriola* and *C. intybus*. For identification of individual chromosomes see Figs. 1, 2, 5, 6 and 10.

On balance it does not seem likely that much chromosomal variation in *C. intybus* has been found.

iii. Chromosome number

Chromosome counts of $2n=18$ were observed in all three cultivars of *L. sativa* and *L. serriola*. This is the first determination for the cultivars Cos, Tom and Webb's. However the chromosome number ($2n=18$) of *L. serriola* has been frequently reported (Löve and Löve 1961, Moore 1973, 1974, 1977, Tomb *et al.* 1978).

The most detailed study is that of Lindqvist (1960), which will be discussed later (Haque and Godward 1984) in relation to meiosis.

Chromosome counts of $2n=18$ for *L. sativa* and *C. intybus* have been reported by several authors (Löve and Löve 1961, Moore 1973, 1974, 1977, Tomb *et al.* 1978).

Summary

Karyotypes of three cultivars of *Lactuca sativa* (Webb's Wonderful, Lobjoit's Green Cos and Tom Thumb), *Lactuca serriola* collected from the field in the county of Essex, U.K. and a cultivar of *Cichorium intybus* (Witloof Chicory), were analysed in detail so that essential comparative information was available for use in later studies (Haque and Godward, Papers II, III and IV). Statistical data on chromosome lengths and centromere positions, together with the recognition of the nucleolar-organising chromosomes, enabled the nine chromosomes of the haploid sets to be recognised individually, and these were designated A, B, C, D, E, F, G, H and I, C and E being the nucleolar organising chromosomes, these being recognised in *C. intybus* for the first time. There were slight differences in chromosome lengths, the *Lactuca sativa* cultivars and *L. serriola* being distinguishable by their mean lengths, but only those of *C. intybus* were significantly smaller. Comparisons with the previously published data on *Lactuca* and *Cichorium* are made.

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