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Cytotaxonomic studies in the Iberian taxa of the genus *Lactuca* (Compositae)

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Abstract

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The 10 taxa representative of the genus *Lactuca* in the Iberian Peninsula have been studied, with the chromosome number for *L. viminea* subsp. *ramosissima* reported for the first time. All the taxa have been found to be diploid: nine of them with chromosome number 2n = 18, and one with 2n = 16. Some differences in chromosome morphology have been detected among diverse populations of some taxa; but in general, the separation of groups according to the karyological characters correlates with the present taxonomic classification of the group. The taxonomic status of *L. livida* is discussed.

Key words: Lactuca, chromosome morphology, Iberian Peninsula

Introduction

The genus *Lactuca* is distributed world wide and can be considered the most evolved and successful from an evolutionary line comprising *Prenanthes*, *Cicerbita*, *Mycelis*, *Lactuca*, *Faberia* and *Cephalorrynchus* (Stebbins 1953). The genus *Cicerbita* is clearly implicated in the origin of *Lactuca*, and in turn may have arisen from *Prenanthes*, probably the most primitive genus of the group. This evolutionary process has involved the conversion of the columnar and beakless cypsela, characteristic of *Prenanthes*, into the compressed fruits of *Lactuca* which bear a beak, very short in their most primitive representatives.

The Mediterranean Region is an important centre of diversification of the genus *Lactuca*, where about 20 taxa can be found (Feráková 1977) from which a total of 10 taxa represent the genus in the Iberian Peninsula: *L. viminea* (L.) J. and C. Presl subsp. *viminea*, *L. viminea* subsp. *chondrilliflora* (Boreau) Bonnier, *L. viminea* subsp. *ramosissima* (All.) Bonnier, *L. serriola* L., *L. saligna* L., *L. virosa* L., *L. livida* Boissier and Reuter in Boissier, *L. perennis* L. subsp. *perennis*, *L. perennis* subsp. *granatensis* Fernández Casas and Charpin, and *L. tenerrima* Pourret; some of these (*L. livida*, *L. perennis* subsp. *granatensis and L. tenerrima*) are considered endemic in the Iberian Peninsula or the West

Mediterranean Basin. *L. sativa* L. has been excluded from this study because of its cultivation in the area.

The karyological studies in *Lactuca* are diverse because of the wide distribution of the genus and its economic interest; but they consist mainly of chromosome counts from some taxa without any particular interest. The most extensive studies are quite old (Babcock et al. 1937 sec. Feráková 1977, Thompson et al. 1941); two general publications on the tribe *Lactuceae* by Stebbins et al. (1953) and Tomb et al. (1978) also ought to be cited, because of some considerations on the taxonomic and chromosomic evolution of the tribe.

The general size and characteristics of the chromosomes in *Lactuca* enable the study of their morphology and the idiogrammatic formulas of the different taxa. Indications have sometimes been given (Stebbins et al. 1953, Feráková 1977) and, there is a very detailed study on *L. serriola* and *L. sativa* (Haque and Godward 1985 a).

This paper reports cytological observations on the representatives of the genus in the Iberian Peninsula. The present investigations were carried out in conjunction with a study of the reproductive biology of *Lactuca* and some related genera with the aim of gaining a deeper biosystematic knowledge of the group.

Material and methods

Mitotic and meiotic observations were made of material from 50 populations. Mitotic studies were done with root tips of plants obtained from seeds collected in the field, or with seedlings obtained by germinating either self-fecundating cypsela or wild seeds. The root tips were treated with 0.002 M 8-hydroxyquinoline for about 3.5 h at room temperature (Tjio and Levan 1950), fixed in Farmer's fluid – ethanol-acetic acid (3:1) (Löve and Löve 1975 a) – and stored at 4 °C in 70% ethanol. At first, material was stained in cold alcoholic-hydrochloric carmine solution; but staining with alcoholic orceine gave better results, so it was used afterwards. For meiotic studies, flower buds were fixed in the field in Carnoy's fluid: ethanol-chloroform-acetic acid (6:3:1) (Löve and Löve 1975 a). They were kept in this for at least 24 h and preserved in 70% ethanol. In this case, staining was always in alcoholic hydrochloric acid-carmine solution.

Whenever possible, the idiogrammatic formula for the population has been indicated. The terminology of Levan et al. (1965) modified by Küpfer (1974) has been used for describing the morphology of chromosomes and the pairs established. These authors classified the chromosomes in six classes, depending on the rate r = long arm length/short arm length: metacentric (M) with the centromere in the median point ($r = 1$); metacentric (m) with the centromere in the median region ($1 < r < 1.7$); submetacentric (sm) with the centromere in the submedian region ($1.7 \leqslant r < 3.0$); subtelocentric (st) with the centromere in the subterminal region ($3.0 \leqslant r < 7.0$); telocentric (t) with the centromere in the terminal region ($7.0 \leqslant r < 39$), and telocentric (T) with the centromere in the terminal point ($39 \leqslant r \leqslant \infty$). The terminology of Stebbins (1938, 1971) has been used for apparent size of chromosomes and karyotype asymmetry. Coefficients A_1 and A_2 proposed by Romero (1986) have also been used for a more accurate estimation of karyotype asymmetry. If two chromosomes, assumed homologues, had to be included in different classes, an intermediate class for the pair was considered (e.g., m-sm for pairs comprising a metacentric chromosome and a submetacentric chromosome).

An average of three plants from each population was studied for meiosis and four for mitosis. Voucher specimens are conserved in the Herbarium of the Department of Botany, Faculty of Biology (see Appendix).

Results

Chromosome numbers

The chromosome numbers of the populations studied are given in Table 1. It can be seen that among the Iberian representatives the somatic number 2n = 18 is the most common, being reported in 9 of a total of 10 taxa: *Lactuca viminea* subsp. *viminea*, *L. viminea* subsp. *chondrilliflora*, *L. viminea* subsp. *ramosissima*, *L. serriola*, *L. saligna*, *L. virosa*, *L. livida*, *L. perennis* subsp. *perennis* and *L. perennis* subsp. *granatensis*. Only one other taxon, *L. tenerrima*, shows a different number, 2n = 16. These chromosomes were always observed to go through regular meiosis, so the gametic numbers n = 9 and n = 8 have been reported, respectively.

Chromosome morphology

In the present investigation, chromosome morphology was found to vary, in general between the classes metacentric (M and m) and telocentric (t), the class of submetacentric chromosomes (sm) being the most common overall and in every species, except for the representatives of the sect. *Lactuca* subsect. *Cyaniceae: L. perennis* and *L. tenerrima*. In these, metacentric chromosomes (M and m) prevailed, a class also frequent in the rest of the taxa. Some subtelocentric chromosomes (st) were also found, and a telocentric pair (t) was always observed in *L. virosa* and *L. livida*. This situation is reflected by the A_1 coefficient that denotes *L. perennis* and *L. tenerrima* as the species with the morphologically most symmetrical chromosomes, whereas *L. serriola*, *L. saligna* and specially *L. virosa* and *L. livida* exhibit the most asymmetrical karyotypes. 1 or 2 satellite pairs of chromosomes are present in each karyotype.

The idiogrammatic formulas established from the study of the chromosome morphology are shown in Table 1. There is some degree of variation in arm ratios among the populations studied for a single taxa that is reflected in differences in the number of pairs included in each morphological class, and A_1 coefficient values. Sometimes, these differences could have been increased by the antimitotic treatment, although special care was taken to homogenize the period of treatment. The most variable group in this sense is *L. viminea*, whose karyotype has been found to be composed mainly of metacentric and submetacentric chromosomes in variable ratios, regardless of the subspecies. Notable differences have been found in *L. perennis* and *L. tenerrima*, not attributable to antimitotic treatment. In the plants from Puerto de la Bonaigüa a regular karyotype comprising 9 homomorphic pairs of chromosomes has always been found, but among three plants studied from a population collected between Rosas and Cadaqués, two individuals with a heteromorphic pair of chromosomes were detected (Table 1, Figure 9), the remaining individual showing the same idiogrammatic formula indicated for Puerto de la Bonaigüa. It has not been possible to study the meiotic behaviour in the plants with the heteromorphic pair of chromosomes because of the lack of flower production in the experimental ground; in any case, they showed well-developed vegetative characters. Chromosome morphology in *L. tenerrima* was studied in material from two populations, those from Valle de Añísclo and Sierra de Cazorla (Table 1). Although the idiogrammatic formulas obtained are very similar, both karyotypes can be recognized by the position of the satellites, which are borne in the long arm of a pair of chromosomes in the plants from Sierra de Cazorla (Figure 12) and in a short arm in the plants from Valle de Añísclo (Figure 13), and in the remaining populations studied. The presence of conspicuous

Tab. 1. Chromosome number, idiogrammatic formula, karyotype asymmetry (A, A_1 and A_2 coefficients) and chromosome apparent length for the populations of *Lactuca* studied.

Taxon and locality	n	2n	Idiogrammatic formula	A	Coefficients A_1	Coefficients A_2	Chromosome length (µm)
Sect. *Phoenixopus* (Cass.) Bentham							
L. viminea (L.) J. and C. Presl subsp. *viminea*							
Jerte-Tornavacas	9II	18	4 m + 2 m-sm + 10 sm + 2 sm^{sat}	2B	0.39	0.38	2.04–5.90
Escaro	9II						
Cazalla		18	8 m + 2 m-sm + 4 sm + 4 sm^{sat}	2B	0.36	0.33	1.45–3.54
subsp. *chondrilliflora* (Boreau) Bonnier							
Rosas	9II	18	4 m + 10 sm + 4 sm^{sat}	2B	0.41	0.32	1.07–3.19
La Molina-Alp	9II	18					
Viella-Bossost		18					
subsp. *ramosissima* (All.) Bonnier							
Tineo-Cangas		18					
Villaluenga		18	6 m + 6 sm + 4 sm^{sat} + 2 st	2B	0.41	0.31	1.82–4.50
Puerto de la Ragua		18	8 m + 2 m-sm + 4 sm + 4 sm^{sat}	2B	0.39	0.30	1.72–4.18
Sierra de Baza	9II						
Puerto de Alájar		18					
Viniegra		18	4 m + 2 m-sm + 8 sm + 4 sm^{sat}	2B	0.43	0.32	2.79–6.22
Valdecastillo		18					
Algámitas		18	6 m + 2 m-sm + 6 sm + 4 sm^{sat}	2B	0.38	0.34	1.72–4.72
Cazalla-Constantina		18					
Sect. *Lactuca* L.							
Subsect. *Lactuca*							
L. serriola L.							
Orrius-La Roca	9II	18	8 m + 6 sm + 2 sm^{sat} + 2 st^{sat}	2A	0.39	0.22	2.32–4.37
Lanavé		18	6 m + 8 sm + 2 sm^{sat} + 2 st^{sat}	3B	0.42	0.27	1.93–4.29
Villanueva-Beas		18					
Grajal		18	4 m + 2 m-sm + 10 sm + 2 st^{sat}	3B	0.42	0.27	1.50–3.54
El Escorial		18					
Brenes	9II	18	6 m + 8 sm + 2 sm^{sat} + 2 st^{sat}	3B	0.44	0.25	2.14–4.39
Sevilla		18					
L. saligna L.							
Elciego	9II	18	6 m + 8 sm + 2 sm^{sat} + 2 st^{sat}	3A	0.38	0.24	2.04–4.07
Villanueva		18	6 m + 6 sm + 2 sm^{sat} + 2 st + 2 st^{sat}	3B	0.48	0.33	1.82–4.18
Grazalema		18	6 m + 8 sm + 2 sm^{sat} + 2 st^{sat}	3B	0.46	0.26	2.25–5.04
Otero de Sariegos		18	6 m + 8 sm + 2 sm^{sat} + 2 st^{sat}	3A	0.46	0.22	2.47–4.18
L. virosa L.							
Bienservida-Villaverde	9II						
La Espina	9II						
Puerto del Pico		18					
Orrius-La Roca		18	2 M + 8 sm + 2 sm^{sat} + 4 st + 2 t	3A	0.55	0.23	2.14–4.07
Sierra de Baza		18	2 M + 8 sm + 4 st + 2 st^{sat} + 2 t	3A	0.58	0.23	2.51–4.72
Los Marines-Aracena		9II					

Tab. 1. (continued)

Taxon and locality	n	2n	Idiogrammatic formula	A	Coefficients A_1	Coefficients A_2	Chromosome length (μm)
Fuenteheridos		18	2 M + 8 sm + 2 sm^{sat} + 4 st + 2 t	3A–3B	0.56	0.23	3.11–6.33
Jaca		18					
Puerto de Tíscar	9II						
Sierra de Cazorla		18					
Comillas		18	2 M + 8 sm + 2 sm^{sat} + 4 st + 2 t	3B	0.54	0.27	2.57–5.57
S. Nicolás del Puerto		18	2 M + 8 sm + 2 sm^{sat} + 4 st + 2 t	3A	0.58	0.23	2.89–5.68
L. livida Boiss. and Reuter							
S. Pablo de los Montes	9II	18	2 M + 8 sm + 2 sm^{sat} + 4 st + 2 t	3A	0.59	0.22	2.36–4.32
subct. *Cyaniceae* DC.							
L. perennis L.							
subsp. *perennis*							
Rosas-Cadaqués	9II	18	2 M + 8 m + 2 m-sm + 2 sm + + 2 sm^{sat} + 2 sm-st^{sat}	2A	0.34	0.17	2.89–4.93
Puerto de la Bonaigüa	9II	18	2 M + 8 m + 2 m-sm + 2 sm + + 4 sm^{sat}	2A	0.30	0.20	2.25–4.29
subsp. *granatensis* Charpin and Fdez. Casas							
Sierra de la Sagra		18	2 M + 10 m + 2 sm + 4 sm^{sat}	2A	0.34	0.17	3.00–5.04
L. tenerrima Pourret							
Villajoyosa	8II						
Zahara-Puerto Palomas		16					
Bruguera		16					
Linares de la Sierra		16					
Valle de Añísclo		16	2 M + 4 m + 2 m^{sat} + 2 m-sm + + 6 sm	2A–2B	0.33	0.21	1.18–2.57
Belerdas	8II						
Sierra de Cazorla		16	2 M + 4 m + 2 m^{sat} + 8 sm	2A	0.34	0.16	1.40–2.47
Oseja de Sajambre		16					

secondary constrictions, especially in the larger pair of chromosomes, is notable in every case.

L. livida is an endemic Iberian species closely related to *L. virosa* for which there are no clear morphological boundaries (Feráková 1977, Linqvist 1960). Cytological observations have been made in material from the locality where *L. livida* was described by Boissier and Reuter: San Pablo de los Montes (see Appendix). In these plants the idiogrammatic formula was almost identical to those found in *L. virosa* (Table 1) which taxonomically reinforces the relationship of these taxa, and allows discussion on the validity of *L. livida* as species (see Discussion).

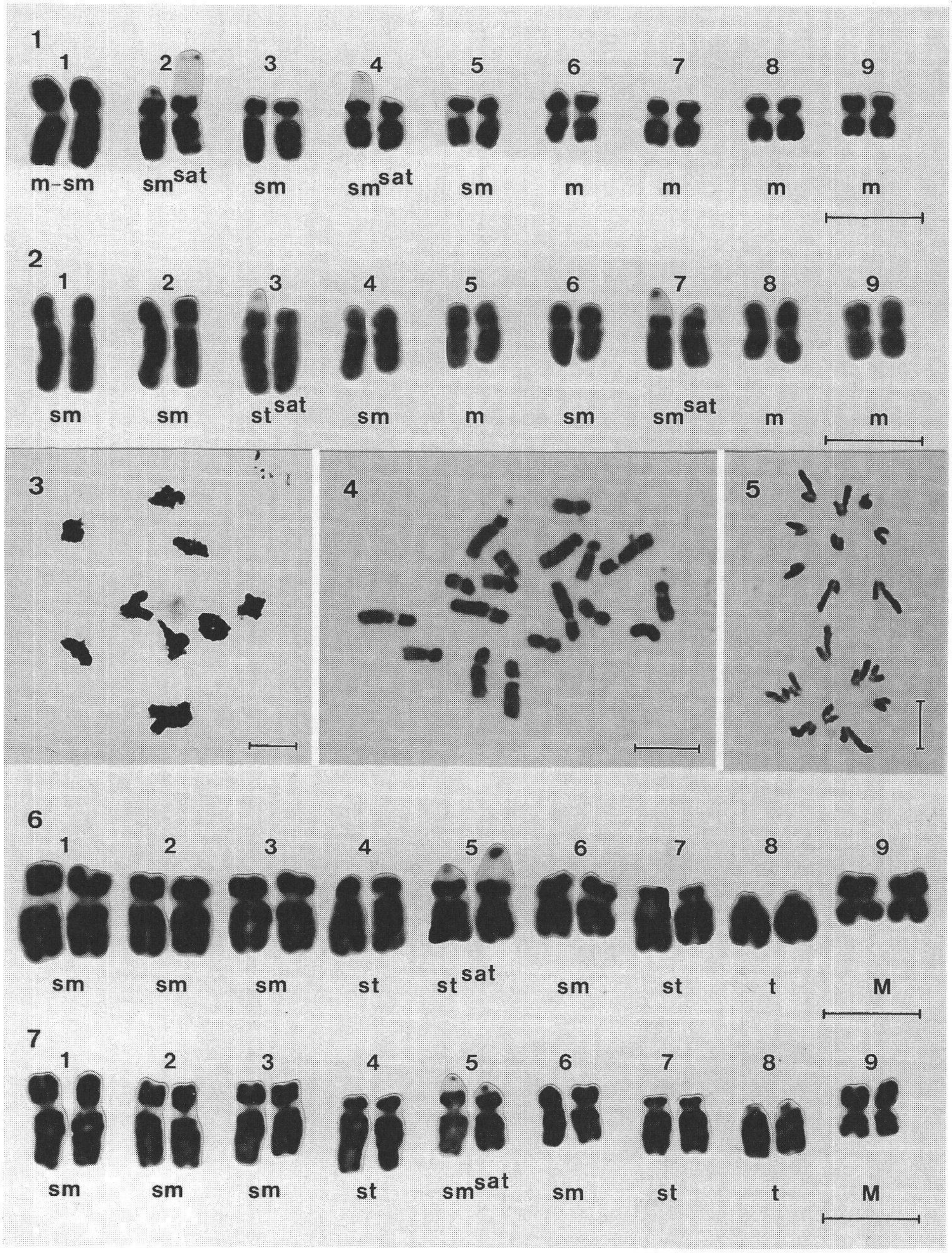

Fig. 1–7. 1. Karyogram of *L. viminea* subsp. *ramosissima* (SEV 126386), 2n = 18. 2. Karyogram of *L. saligna* (SEV 126535), 2n = 18. 3. Diakinesis of *L. viminea* subsp. *viminea* (SEV 126389), n = 9. 4. Somatic metaphase of *L. serriola* (SEV 126527), 2n = 18. 5. Anaphase II (partial) of *L. serriola* (SEV 126524), n = 9. 6. Karyogram of *L. virosa* (SEV 124656), 2n = 18. 7. Karyogram of *L. livida* (SEV 124612), 2n = 18. Scale bar = 5 μm.

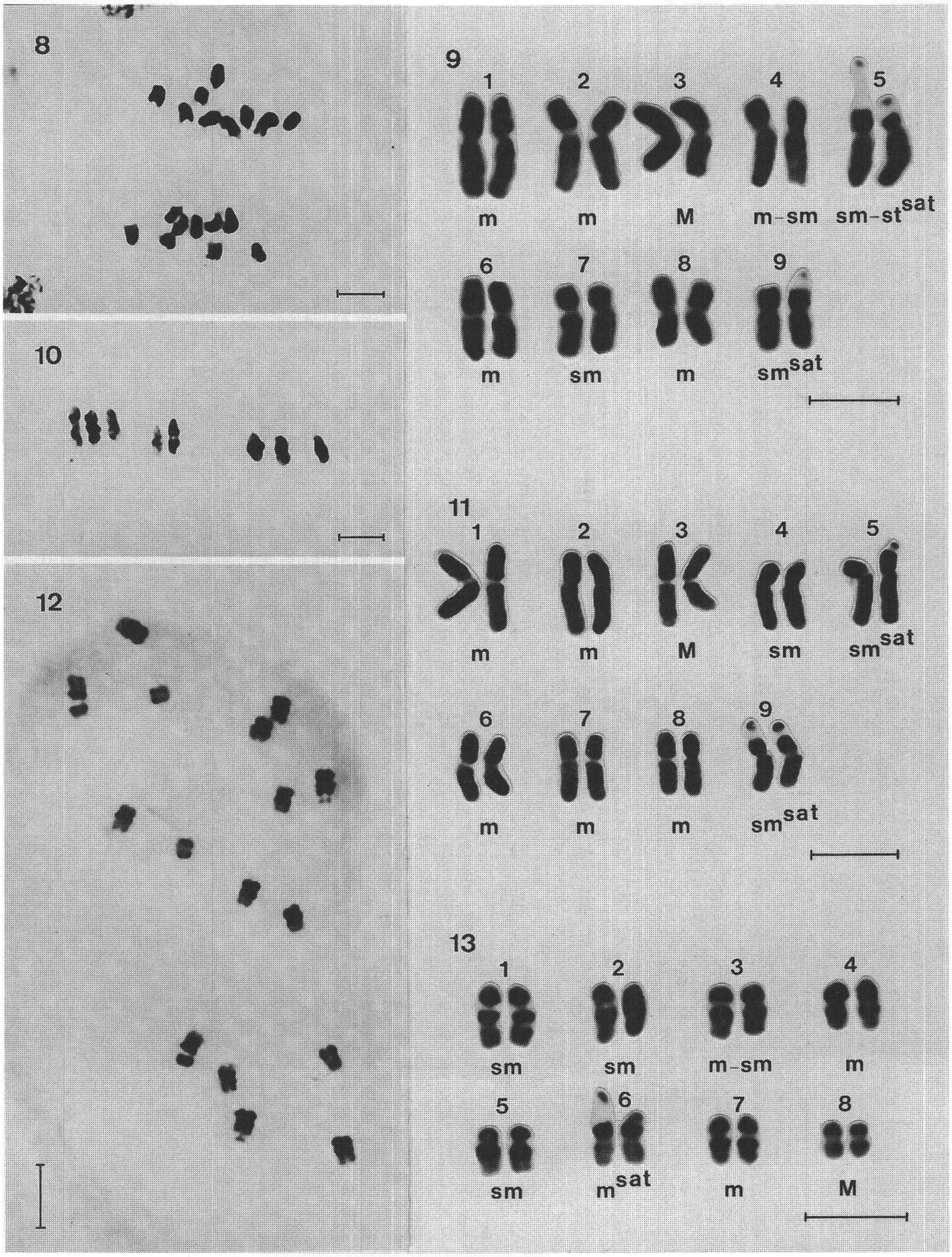

Fig. 8–13. 8. Anaphase I of *L. perennis* subsp. *perennis* (SEV 126546), n = 9, 9. Karyogram of *L. perennis* subsp. *perennis* (SEV 126546), 2n = 18. 10. Metaphase I of *L. tenerrima* (SEV 124653), n = 8. 11. Karyogram of *L. perennis* subsp. *granatensis* (SEV 126591), 2n = 18. 12. Somatic metaphase of *L. tenerrima* (SEV 124646), 2n = 16. 13. Karyogram of *L. tenerrima* (SEV 126571), 2n = 16. Scale bar = 5 µm.

Tab. 2. Previous chromosome counts for the Iberian taxa of *Lactuca*

Taxa	n	2n	Origin of material	Authors
L. viminea (L.) J. and C. Persl subsp. *viminea*		18	Slovenia	Feráková, 1970a: 14
		18	Portugal	Fernandes and Queirós, 1971: 83
		18	Portugal	Queirós, 1973: 311
		18	Bulgaria	Kuzmanov and Georgieva, 1980: 715
subsp. *chondrilliflora* (Boreau) Bonnier	9II		France	Whitaker and Jagger, 1939: 299
	9II		France	Thompson et al., 1941: 93
		18	Italy	Brullo and Pavone, 1978: 260
L. serriola L.	9II		Japan	Ishikawa, 1921: 156
	7II + 1IV		U.S.A.?	Cooper and Mahony, 1935: 846
	9II		U.S.A, U.S.S.R., Sweden	Whitaker and Jagger, 1939: 299
		18	U.S.A.	Heiser and Whitaker, 1948: 185
		18	Canada	Mulligan, 1957: 781 sub *L. scariola* L.
		18	cultivated	Chatterjee and Sharma, 1969: 580
		18	Afghanistan	Podlech and Dieterle, 1969: 230
		18	Slovenia	Feráková, 1970a: 13
		18	Portugal	Fernandes and Queirós, 1971: 84
		18	India	Koul and Gohil, 1973: 61
		18	Portugal	Queirós, 1973: 311
		18	Britain	Edmonds et al., 1974: 160
		18	Bulgaria	Feráková and Murin, 1976: 491
	9II		U.S.A.	Tomb et al., 1978: 719
		18	Italy	Brullo et al., 1979: 146
		18	Greece	Strid and Franzén, 1981: 842
		18	Britain	Haque and Godward, 1985a: 730
	9II		Britain	Haque and Godward, 1985b: 841
	9II		India	Mehra et al., 1965: 44
L. saligna L.	9II		U.S.A.	Thompson et al., 1941: 93
		18	U.S.A.	Heiser and Whitaker, 1948: 185
		18	Portugal	Fernandes and Queirós, 1971: 84
L. virosa L.	9II		Netherlands	Thompson et al., 1941: 93
		18	Portugal	Fernandes and Queirós, 1971: 84
		18	France	Kliphuis and Wieffering, 1972: 600
		18	Portugal	Queirós, 1973: 311
		18	Italy	Brullo et al., 1979: 146
	9II		Spain	Gallego, 1983: 132
		18	Spain	Blanca and Cueto, 1984: 185
		18	Spain	Fernández et al., 1985: 301
		18	Madeira	Dalgaard, 1986: 231
L. livida Boiss. and Reuter		18	Spain	Blanca and Cueto, 1984: 185

Tab. 2. (continued)

Taxa	n	2n	Origin of material	Authors
L. perennis L. subsp. *perennis*	9II		England	Whitaker and Jagger, 1939: 299
	9II		cultivated	Thompson et al., 1941: 93
		18	Hungary	Pölya, 1949: 134
		18	Austria	Leute, 1974: 812
		18	Italy	Löve and Löve, 1982b: 584
subsp. *granatensis* Charpin and Fernández Casas		18	Spain	Charpin and Fernandez Casas, 1981: 237
L. tenerrima Pourret		16	Spain	Ubera and Ruiz de Clavijo, 1984: 296
		16+ 1B, 2B	Spain	Cueto and Blanca, 1987: 405

Size of the chromosomes

The apparent chromosome length of the Iberian representatives of *Lactuca* varies from about 1.07–6.33 µm in the present study. Therefore, they are small, medium small and medium large; the class medium small being the most-represented. *L. tenerrima* shows the karyotypes with the smallest chromosomes, since in no case were they found to be longer than 2.57 µm. In the remaining taxa only 1 or 2 pairs, if any, are small, the rest are basically medium small, and, in some cases, 1 or 2 medium large pairs are present. Considerable levels of variability were found within taxa, which in some cases can be attributed to different degrees of condensation, although special care was taken to homogenize the period of antimitoic treatment.

The A_2 index of interchromosomic variability ranges from 0.16 to 0.38. The most symmetrical species in this respect are *L. tenerrima* and *L. perennis*, representatives of the subsect. *Cyaniceae* of the sect. *Lactuca*. Higher indices were found in the representatives of the subsect. *Lactuca* from the same section: *L. serriola*, *L. saligna*, *L. virosa* and *L. livida*. All the subspecies of *L. viminea* (sect. *Phoenixopus*) show higher interchromosomic asymmetry levels, always exceeding 0.30. In this latter case, the constant presence of a pair of chromosomes longer than the others, and easily recognizable, was observed.

Discussion

The chromosome numbers presented here for the genus *Lactuca* agree with previous counts made by various authors in all the taxa (Table 2) except *L. viminea* subsp. *ramosissima*, the chromosome number of which is reported for the first time (Table 3). Nevertheless, some specific points can to be made: the formation of 9 bivalents has been observed in the meiotic studies of *L. serriola*, in disagreement with Cooper and Mahony (1935: 846) who indicated the formation of 7 bivalents and 1 tetravalent during meiosis

Tab. 3. Chromosome numbers and geographical distribution of *Lactuca* taxa. Distribution areas have been taken from "Index Kewensis" (Hooker and Jackson, 1946 and following) and modified according to Britton and Brown (1970), Feráková (1976; 1977) and Vuilleumier (1973). Authors: (1) Babcock et al., 1937 sec. Feráková, 1977: 85. (2) Blanca and Cueto, 1984; 185. (3) Charpin and Fernández Casas, 1981: 237. (4) Chatterjee and Sharma, 1969: 580. (5) Ching-I-Peng and Chien-Chang Hsu, 1977: 564. (6) Dvorák et al., 1981: 844. (7) Feráková, 1970a: 13–14. (8) Feráková, 1970b: 413. (9) Ghaffari, 1986: 901. (10) Gupta and Gill, 1980: 352. (11) Hanelt, 1973: 649. (12) Ishikawa, 1911 sec. Ishikawa, 1916: 438. (13) Ishikawa, 1916: 438. (14) Ishikawa, 1921: 156–157. (15) Keil and Pinkava, 1981: 705. (16) Kuzmanov et al., 1981: 702. (17) Laurenko et al., 1988: 606. (18) Laurenko et al., 1990: 1623. (19) Löve and Löve, 1975b: 674. (20) Löve and Löve, 1982a: 359–360. (21) Lungeanu, 1972: 682. (22) Malla et al., 1977: 446. (23) Martinoli, 1954: 79. (24) Mehra et al., 1965: 44. (25) Montmollin, 1986: 437. (26) Mulligan, 1957: 781. (27) Murín, 1971: 353. (28) Nazarova in Feráková. 1977: 85. (29) Nazarova, 1984: 972. (30) Ono, 1955: 270. (31) Ortega and Navarro, 1977: 76. (32) Packer, 1964: 483. (33) Parfitt, 1981: 516. (34) Provatova and Sokolovskaya, 1990: 1620. (35) Shetty, 1967: 570. (36) Sokoloskaya and Probatova, 1986: 1423. (37) Sokolovskaya et al., 1985: 126. (38) Stebbins et al., 1953: 427. (39) Strid and Franzén, 1981: 842. (40) Thompson et al., 1941: 93. (41) Tomb et al., 1978: 719. (42) Ubera and Ruiz de Clavijo, 1984: 296. (43) Whitaker and Jagger, 1939: 299. (44) Zakharyeva, 1985: 1699

Taxa	Geographical distribution	n	2n	Authors
L. acanthifolia (Willd.) Boiss.	Aegean Region		18	(25)
L. altaica Fisch. and Mey.	Altai Region	9		(40)
L. aurea (Schultz Bip. ex Panc.) Stebbins	Balkan Peninsula		16	(1)
L. bourgeaui (Boiss.) Irish and Taylor	Asia Minor	8		(40, 43)
L. brunoniana (Wall.) Clarke = *Prenanthes brunoniana* Wall.	Himalayan Region, Malaysia	8		(24, 35)
			16	(24, 38)
L. canadensis L.	Boreal America		34	(20, 40, 43)
L. cretica Desf.	Asia Minor	8		(40, 43)
L. chelidonifolia Makino	Japan	5		(14)
L. chinensis Makino	Japan	16		(14)
L. debilis Benth. and Hook. f.	Japan	24		(13, 14)
L. dentata Robinson				
var. thumbergii	Japan	12		(14)
var. albiflora	Japan	12		(14)
var. alpicola	Japan	7		(14)
L. denticulata Maxim.	Japan	5		(13, 14)
L. dissecta D. Don	Himalayan Region	8		(24, 35)
L. floridana (L.) Gaertn. = *L. biennis* (Moench) Fern.	Boreal America	17		(33, 40)
			34	(20, 26, 32)
L. formosana Maxim.	China, Formosa		18	(5)
L. georgica Grossh.	Transcaucasian Region		18	(29)
L. gracilliflora DC.	Himalayan Region, Malaysia	9		(4, 24)
			18	(4)
L. graeca Boiss.	Greece		18	(39)
L. graminifolia Michx.	Boreal America	17		(15, 40, 41, 43)
L. hastata DC.	Eastern India	8		(24, 35, 43)
			16	(38)
L. indica L.	Malaysia	9		(40)

Tab. 3. (continued)

Taxa	Geographical distribution	n	2n	Authors
L. indica L.	Malaysia		18	(5)
L. keiskeana Makino	Japan	5		(14)
L. lanceolata Makino	Japan	5		(13, 14)
L. lessertiana Clarke	Himalayan Region		16	(38)
L. livida Boiss, and Reuter	Iberian Peninsula	9	18	(2)
L. longidentata Moris	Sardinia	8	16	(23)
L. longifolia DC.	Himalayan Region	8		(24, 35)
			16	(24, 38)
L. ludoviciana (Nutt.) Ridell.	Western Boreal America		34	(20)
L. macrantha Clarke	Himalayan Region		16	(38)
L. macrorhiza (Royle) Hook. f.	Himalayan Region	8		(24, 35)
		9		(24)
L. matsumarae Makino	Japan	8		(14)
L. orientalis Boiss. = *Scariola orientalis* (Boiss.) Soják	Himalayan Region, Asia Minor		18	(9, 27, 29)
L. palmensis Bolle	Canary Isles	8		(31)
L. perennis L.				
subsp. *perennis*	Southern Europe	9	18	(43, see Table 2)
subsp. *grantensis* Charpin and Fernández Casas	Iberian Peninsula		18	(3)
L. polycephala Benth.	Eastern India, Burma	8		(10)
L. pulchella (Pursh) DC. = *L. tatarica* subsp. *pulchella* (Prush) Stebbins	Western Boreal America		34	(20, 38)
L. quercina L.				
subsp. *quercina*	Caucasus	9	18	(7, 8)
subsp. *wilhelmsiana* (Fisch. and Mey., ex DC.) Feráková)	Caucasus		18	(28)
L. raddeana Maxim.	Japan	9		(14, 40)
L. rapunculoides Clarke	Himalayan Region		16	(38)
L. repens Benth. and Hook. f.	?	8		(14)
L. saligna L.	Northern Hemisphere	9	18	(40, see Table 2)
L. sagittarioides Clarke	Himalayan Region	5		(22)
L. sativa L.	cultivated	9		(40, 43)
			18	(43)
L. serriola L.	Northern Hemisphere	9	18	(43, see Table 2)
L. sibirica (L.) Benth.	Sibiria		18	(19)
			27	(17, 18, 36)
L. sororia Miq.	Japan, China		18	(5)
L. spicata (Lam.) Hitchc.	Northern America	17		(40)
L. squarrosa Miq.	Eastern Asia	9		(30)
			18	(30, 34)
L. stolonifera Benth, and Hook. f.	Japan	8		(14)
L. tamagavensis	?	8, 7		(14)
L. tatarica (L.) Mey. = *L. tatarica* (Mey.) Nijar	Western Asia, Eastern India	9		(40)
			18	(6, 11, 16, 21, 43)
L. takhtadzhianii Sosn.	?		18	(44)
L. tenerrima Pourret	Southern Europe, Morocco	8	16	(42, see Table 2)

Tab. 3. (continued)

Taxa	Geographical distribution	n	2n	Authors
L. thumbergii Maxim.	Japan	12, 11		(12)
L. triangulata Maxim.	Eastern Siberia	9		(14)
			18	(37)
L. undulata Ledeb.	Eastern an Boreal Asia	9		(9)
L. villosa	?	9		(13, 14)
L. viminea (L.) J. and C. Presl				
subsp. *viminea*	Northern Hemisphere	9	18	(7, see Table 2)
subsp. *alpestris* (Gand.) Feráková	Crete		18	(25)
subsp. *chondrilliflora* (Boreau) Bonnier	Mediterranean Region	9	18	(43, see Table 2)
subsp. *ramosissima* (All.) Bonnier	Mediterranean Region	9	18	(hic)
L. virosa L.	Northern Hemisphere	9	18	(40)

for this species. Also, no B chromosomes were detected in the populations of *L. tenerirma* studied, while Cueto and Blanca (1987: 405) indicated the presence of B chromosomes in plants of this species from Sierra de Baza (Granada, Spain). Table 4 gives the chromosome numbers of the Iberian taxa of *Lactuca* and many other representatives of the genus from around the world, including their geographic distribution. A high diversity can be seen in numbers including 2n = 10, 14, 16, 18, 22, 24, 32, and 34, which display an interesting geographic pattern. The representatives from the Mediterranean Region, that ecompasses the highest number of representatives of Europe and North Africa, have mainly the number 2n = 18, but two taxa, *L. aurea* and *L. tenerrima*, have 2n = 16. No incidence of polyploidy has been found in this area. The number 2n = 16 is the most common number found among the representatives from the Himalaya, India and Malaysia. In North America, a group of species occurs sharing the number 2n = 34. It has been proposed to be composed of amphiploids originating from species with 2n = 18, and 2n = 16 (Whitaker and Thompson 1941) from Eurasia that colonized North America via the Bering Strait (Whitaker 1944, Vuilleumier 1973). It seems that all of them have a common origin since a high interfertility level was found (Thompson et al. 1941, Whitaker and Jagger 1939, Whitaker and Thompson 1941). Some additional taxa showing the number 2n = 18 are also distributed in this region, but they are presumed to have been introduced from the Old World (Vuilleumier 1973). The representatives from Japan form the most diverse group from the karyological point of view since all the numbers are represented. Some of these correspond to endemic taxa studied by Ishikawa (1916, 1921) but not later complet confirmation of his observations has been reported. According to Tomb (1977) these results are questionable.

Each of these regions is related to different centres of speciation of the genus. The number n = 9, considered the basic one of the tribe (Stebbins et al. 1953, Tomb et al. 1978), although Turner et al. (1961) postulated x = 4 or x = 5 as the ancestral basic number in the Lactuceae, prevails only in the Mediterranean Region, that has been considered as centre of origin of *Lactuca* by Feráková (1977). In this area 4 sections of the genus *Lactuca* can be found: *Mulgedium* (Cass.) Clarke, *Lactucopsis* (Schultz-Bip ex Vis. et Panc.) Rouy, *Phoenixopus* (Cass.) Benth. and *Lactuca* L.; all four are represented in the Eastern part of the area, while in the West only the last two sections can be found.

The Eastern Mediterranean Region is probably a centre of origin of the genus. Babcock et al. (1937 sec. Stebbins et al. 1953) considered both $x=8$, and $x = 9$, as basic chromosome numbers in *Lactuca* and proposed a polyphyletic origin for the genus, but Stebbins et al. (1953) considered $x = 9$ as the only primitive one, arguing that the number $n=8$ had not been found in *Cicerbita*. In fact, although some species of *Cicerbita* showing $n=8$ have been reported (e.g. Bolkhoskikh et al. 1969), they could hardly be considered as ancestors of *Lactuca*. In the area of the Himalayas, India and Malaysia, where a high incidence of the number $n = 8$ has been found, the reduction of the chromosome number should take place during an early evoutionary stage. Nevertheless, the high diversity of the genus and the geographical pattern of distribution allows a polyphyletic origin to think about, that is illustrated by the taxonomic study of a small group of scandent species of *Lactuca* from Africa, not related to any other taxa of the genus, which probably originated in this area from an isolated section of *Prenanthes* (Stebbins 1937). Unfortunately no karyological studies are on record.

As indicated before (see Introduction) chromosomes of *Lactuca* are quite appropriate for studies of chromosome morphology but few references can be found on this subject, except on *L. serriola*, the chromosome set of which had been studied before by Haque and Godward (1985a). These authors proposed the idiogrammatic formula $8\ m + 2\ m - sm + 6\ sm^{sat} + 2\ st^{sat}$ for British plants, a formula very similar to our results. The asymmetry type found by these authors was 3A, and the asymmetry coefficients calculated in the work presented here from the arm length ratios are $A_1 = 0.44$ and $A_2 = 0.21$. They also indicated that *L. serriola* and *L. sativa* were karyologically very similar. Certain other authors (Chatterjee and Sharma 1989, Whitaker and Jagger 1939) had made observations on the chromosome morphology of these taxa but nomenclature differences preclude a comparison. In addition, it has been possible to study the idiogrammatic formula of *L. virosa* and *L. livida* from the detailed photographs published by Blanca and Cueto (1984). In both cases the formula deduced is $2\ M + 8\ sm + 2\ sm^{sat} + 4\ st + 2\ t$ (Table 1), which coincides with our observations.

It is interesting that the study of the karyotypes in the Iberian representatives reflects their taxonomic relationships (Table 1) and could also be an useful tool in certain taxonomic considerations. Three groups can be separated: 1) *L. viminea*, represented by three subspecies with very similar idiogrammatic formula and karyotype asymmetry; 2) *L. serriola*, *L. saligna*, *L. virosa*, and *L. livida* which are widespread weed representatives of the sect. *Lactuca* subsect. *Lactuca*, an evolved group in the genus. They present the most asymmetrical karyotypes of the Iberian taxa as could be expected to occur in colonizer weeds (Stebbins 1971: 90); 3) *L. perennis* and *L. tenerrima*, included in the subsect. *Cyanicae* sect. *Lactuca*, are very closely related morphologically. Superficially, their chromosomes seem quite different because of their lengths and some secondary constrictions found in *L. tenerrima* (Fig. 12 and 13), but in both cases, the karyotype asymmetry is 2A, and A_1 and A_2 coefficients are very similar (Table 1).

L. viminea presents pronounced morphological diversity comprising four subspecies treated as species by many authors (e.g., Willkomm 1861, Coste 1903) and considered well-marked subspecies by Feráková (1977). Three of them are represented in the Iberian Peninsula, but not clear morphological and taxonomic delimitations have been found in the material studied. Some characters currently used may be fixed, e.g. the length of the beak in the cypsela but some others, such as the mode of ramification, may depend on climatic features and sun exposure. Based on the karyological data no differentiation is possible since the diversity found is as similar between subspecies as it is within subspecies (Table 1).

Various authors have dealt with the taxonomic status of *L. livida* Boissier and Reuter. Blanca and Cueto (1984) indicated that *L. livida* is a species clearly differentiated from *L. virosa*. In contrast, Linqvist (1960) and Feráková (1977) considered them as closely related species without clear differential characters, and Velasco (1981) proposed the new combination *L. virosa* subsp. *livida* (Boissier and Reuter) Ladero and Velasco. In fact, the number of florets per flower head, the shape of the leaves, and the anthocyanin purple colouring, considered as the most important differential characters in the taxonomic diagnosis, have been found to show a continuous variation in the area, and sometimes to be different in wild populations, and in the material from these populations growing in the experimental fields. Also, no important karyological differences have been found among the material studied as can be seen in Table 1. It is reasonable to assume that a thorough taxonomic revision is necessary for clarifying definitively the taxonomic boundaries and status of these taxa. Plants with some typical characters of *L. livida* can be found in several separate localities of the Iberian Peninsula, which indicates that their distribution area is wider than usually presumed (Feráková 1976: 330, 1977: 75). In fact, although Feráková indicated that the distribution of *L. livida* is restricted to a small area in the centre of Spain, Velasco (1981) estimated that it has a wider distribution.

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Appendix. – Origin of the material studied (and voucher specimens)

Lactuca viminea subsp. *viminea:* CACERES: Entre Jerte y Tornavacas; 15. IX. 1985; García y Mejías (SEV 126388). LEON: Escaro; 22. IX. 1985; García y Mejías (SEV 126389). SEVILLA: Cazalla de la Sierra; 10. VIII. 1986; Herrera, Mejías y Moreno (SEV 126384).

Lactuca viminea subsp. *chondrilliflora:* GERONA: Rosas, Playa de La Pelosa; 7. VIII. 1985; Mejías, Polo y Romero (SEV 126381). GERONA: Entre La Molina y Alp; 10. VIII. 1985; Mejías, Polo y Romero (SEV 126380). Entre Viella y Bossost; 11. VIII. 1985; Mejías, Polo y Romero (SEV 126382).

Lactuca viminea subsp. *ramosissima:* ASTURIAS: Entre Tineo y Cangas de Narcea; 14. VIII. 1987; Barrera y Mejías (SEV 126385). CADIZ: Villaluenga del Rosario; 7. IX. 1985; Herrera, Mejías y Muñoz (SEV 126383). GRANADA: Puerto de la Ragua; VIII. 1985; Muñoz (SEV 126386). Sierra de Baza, Calar de Rapa; 29. VII. 1987; Mejías y Talavera (SEV 126579). HUELVA: Puerto de Alájar; 1. IX. 1985; Mejías (SEV 126379). LOGROÑO: Entre Viniegra de Arriba y Viniegra de Abajo; 18. IX. 1985; García y Mejías (SEV 126378). LEON: Valdecastillo; 22. IX. 1985; Gracía y Mejías (SEV 126387). SEVILLA: Peñón de Algámitas; 25. VIII. 1986; Mejías y Muñoz (SEV 126377). Entre Cazalla de la Sierra y Constantina; 10. VIII. 1986; Herrera y Mejías (SEV 126384).

Lactuca serriola: BARCELONA: Entre Orrius y La Roca; 6. VIII. 1985; Mejías, Polo y Romero (SEV 126524). HUESCA: Lanavé; 13. VIII. 1985; Mejías, Polo y Romero (SEV 126527). JAEN: Entre Villanueva del Arzobispo y Beas de Segura; 2. VIII. 1985; Mejías, Polo y Romero (SEV 126528). LEON: Grajal; 23. IX. 1985; García y Mejías (SEV 126529). SEVILLA: Brenes; 12. VIII. 1989; Mejías (SEV 126584). Sevilla; 12. VIII. 1989; Mejías (SEV 126585).

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