

Euphorbia L. subsect. *Esula* (Boiss. in DC.) Pax in the Iberian Peninsula. Leaf surface, chromosome numbers and taxonomic treatment

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Resum

MOLERO, J. & A. M.^a ROVIRA (1992). *Euphorbia* L. subsect. *Esula* (Boiss. in DC.) Pax a la Península Ibèrica. Epidermis foliar, nombre cromosòmic i tractament taxonòmic. Collect. Bot. (Barcelona), 21:121-181.

Presentem l'estudi taxonòmic dels representants d'*Euphorbia* subsect. *Esula* a la Península Ibèrica. Prèviament, s'inclou un primer capítol dedicat a l'estudi de les epidermis foliars i un segon capítol sobre nombres cromosòmics.

El capítol dedicat a les epidermis foliars ofereix l'estudi amb el microscopi òptic i amb el MER de les fulles de 45 poblacions de tàxons ibèrics i europeus de la subsecció. Els caràcters analitzats han estat el model cel·lular, la morfologia de les cèl·lules i dels estomes (relleu primari i secundari) i les ceres epicuticulars (relleu terciari). Alguns microcaràcters epidèrmics s'han mostrat especialment útils en taxonomia. Així, el tipus bàsic d'estoma i el model de distribució d'estomes a les dues cares de la fulla, són caràcters que permeten separar tàxons tan pròxims com *E. esula* L. subsp. *esula* d'*E. esula* L. subsp. *orientalis* (Boiss. in D.C.) Molero & Rovira. El tipus morfològic de ceres epicuticulars també permet distingir *E. graminifolia* Vill. d'*E. esula* aggr.; i dins d'*E. nevadensis* Boiss. & Reuter, la subsp. *bolosii* Molero & Rovira de la resta de subespècies.

La prospecció citogenètica ha detectat la presència de tan sols el citòtip diploide ($2n=20$) per a *E. cyparissias* L. i *E. esula* L. subsp. *esula* a la Península Ibèrica. Per a *E. nevadensis* s.l. es descriu per primera vegada un complex poliploide de base $x=10$, on el nivell diploide ($2n=20$) es present a totes les subespècies; el nivell tetraploide ($2n=40$) es presenta a *E. nevadensis* subsp. *nevadensis* i el nivell hexaploide ($2n=60$) es dona a *E. nevadensis* subsp. *bolosii*. El nombre cromosòmic no és una dada que pugui ésser utilitzada taxonòmicament. La diferenciació citogenètica ha seguit en *E. nevadensis* un camí propi, aparentment no relacionat amb el procés de diferenciació morfològica.

El tractament taxonòmic final preten ésser coherent amb els resultats de l'estudi epidèrmic i amb la micromorfologia de les granes, integrant els caràcters útils. En aquest apartat, s'inclouen aspectes nomenclaturals, de tipificació, descriptius, claus, ecologia i distribució geogràfica. Es descriu un nou taxon: *E. nevadensis* Boiss. & Reuter subsp. *bolosii* Molero & Rovira; s'estableix la nova combinació *E. esula* L. *orientalis* (Boiss. in DC.) Molero & Rovira. *E. sennenii* Pau s'integra a la sinonímia d'*E. nevadensis* Boiss. & Reuter subsp. *aragonensis* (Loscós & Pardo) Bolòs & Vigo.

Mots claus: Euphorbiaceae, *Euphorbia* subsect. *Esula*, Península Ibèrica, superfície foliar, nombre cromosòmic, microevolució, Taxonomia.

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Abstract

MOLERO, J. & A. M.^a ROVIRA (1992). *Euphorbia* L. subsect. *Esula* (Boiss. in DC.) Pax in the Iberian Peninsula. Leaf surface, chromosome numbers and taxonomic treatment. Collect. Bot. (Barcelona), 21:121-181.

We present a taxonomic study of the representatives of *Euphorbia* subsect. *Esula* in the Iberian Peninsula. Prior to this, a first section is included on the study of the leaf surface and a second section on chromosome numbers.

The section on leaf surface is based on a study of the leaves of 45 populations of Iberian and European taxa of the subsections using a light microscope and SEM. The characters analyzed are cell shape, morphology of the cells and stomata (primary and secondary sculpture) and epicuticular waxes (tertiary sculpture). Some microcharacters of the leaf surface proved particularly useful for taxonomical purposes. Thus the basic type of stoma and the distribution model of the stomata on the two sides of the leaf are characters which make it possible to separate taxa as closely related as *E. esula* L. subsp. *esula* and *E. esula* L. subsp. *orientalis* (Boiss. in DC.) Molero & Rovira. The morphological type of the epicuticular waxes also enables us to differentiate between *E. graminifolia* Vill. and *E. esula* aggr. and to distinguish subsp. *bolosii* Molero & Rovira from the remaining subspecies in *E. nevadensis* Boiss. & Reuter.

Cytogenetic investigation reveals the presence of only the diploid cytotype ($2n=10$) in *E. cyparissias* L. and *E. esula* L. subsp. *esula* in the Iberian Peninsula. We describe for the first time in *E. nevadensis* s.l. a polyploid complex with a base of $x=10$ in which the diploid level ($2n=20$) is present in all subspecies; the tetraploid level ($2n=40$) is present in *E. nevadensis* subsp. *nevadensis* and the hexaploid level ($2n=60$) is found in *E. nevadensis* subsp. *bolosii*. Chromosome number is not a parameter that can be used for taxonomic purposes. In *E. nevadensis*, cytogenetic differentiation has followed its own course, with no apparent relationship to the process of morphological differentiation.

Our final taxonomic treatment aims to achieve coherence with the result of the study of the leaf surface and the micromorphology of the seeds, taking into account those characters that are of use. In this section we include aspects related to nomenclature and typification, descriptive characters, keys, ecology and geographical distribution. We describe a new taxon: *E. nevadensis* Boiss. & Reuter subsp. *bolosii* Molero & Rovira; we establish the new combination *E. esula* L. subsp. *orientalis* (Boiss. in DC.) Molero & Rovira. *E. sennenii* Pau is considered a synonym of *E. nevadensis* Boiss. & Reuter subsp. *aragonensis* (Loscós & Pardo) Bolòs & Vigo.

Keywords: Euphorbiaceae, *Euphorbia* subsect. *Esula*, Iberian Peninsula, Leaf Surface, Chromosome numbers, Microevolution, Taxonomy.

INTRODUCTION

Euphorbia subsect. *Esula* is a taxon native to Eurasia (KUZMANOV, 1964; SMITH & TUTIN, 1968) which is presently distributed for Europe and temperate regions of Asia, some species having been introduced into the United States and Canada at the beginning of the 19th century (CROMPTON, STAHEVITCH & WOJTAS, 1990; OUDEJANS, 1990).

A prime feature of this subsection is the fact that it includes a series of species which are morphologically very akin to each other and it is difficult to find stable characters to differentiate between closely related taxa. To the «cryptic» nature of its characters, a high degree of polymorphism detected in some species (eg. the «*E. esula* - *E. virgata*» complex) is added. This dilemma is reflected by the large number of taxa described, which is further increased by the current existence of numerous synonyms, and by the wealth of nomenclatural combinations. Another sign is the extreme heterogeneity of the treatment given this subsection (and, by extension, section *Esula*) in the various Floras and monographs. The most recent summary

illustrating how various authors have interpreted the chronology and taxonomy of the taxa in this subsection is to be found in the above mentioned study by Crompton & al., which emphasizes on the «*E. esula* - *E. virgata*» complex in the United States of America and Canada.

On the North American continent, two species introduced from Europe, *E. esula* («leafy spurge») and *E. cyparissias* («cypress spurge») have become weeds that invade meadows and fields, spreading with great vigour and causing damage to agriculture and animal husbandry. This situation has stimulated the interest of the authorities who have contributed to a number of interdisciplinary studies (WATSON, 1985).

In this context, the conclusions of two recent studies are of particular interest to us. In the first, STAHEVITCH, CROMPTON & WOJTAS (1988) show that there are no cytogenetic gaps, barriers to crossbreeding, irregular meiotic behaviour or heteropollinosis which could justify the large number of microspecies and hybrids claimed by some authors (see RADCLIFFE-SMITH, 1985) for the complex «*E. esula* - *E. virgata*» within the territory of the United States and Canada, and they recognize from a cytogenetic viewpoint a single, polymorphic species, *E. esula*. A later work by CROMPTON & al. (l.c.), based on the application of morphometric studies, corroborates the cytogenetic results.

Though we have no doubt that the conclusions reached by these authors are essentially valid, our reservations arise from the fact that the study was largely carried out on erratic, recently introduced populations which do not reflect a pattern of morphological-geographical correlation, and this makes it difficult to determine whether the small differences detected can be related to geographical races with any taxonomical significance.

In the Iberian Peninsula, subsection *Esula* s. str. can be stated, on the basis of a standard criterion such as that of SMITH & TUTIN (l.c.), to be represented by three species: *E. cyparissias*, *E. esula* and *E. nevadensis* (*E. terracina* L. is excluded due to its uncertain systematic position, see RADCLIFFE-SMITH, 1982). However, certain new taxa described by various specialists in Iberian Flora (LANGE in WILLKOMM & LANGE, 1880), such as *E. aragonensis* Loscos & Pardo in Willkomm, *E. sennenii* Pau, have been either forgotten or underestimated, which has led to their being incorrectly interpreted.

An instance of this is the treatment given to *E. sennenii* Pau by a number of present-day authors. SMITH & TUTIN (l.c.) assimilate it to *E. gayi* Salisb., in response, possibly, to the comments made by Pau himself, who saw a close relationship with the Sardinian-Corsican endemic taxon. This same position is maintained, though with reservations, by GREUTER, BURDET & LONG (1986) and more recently the assimilation of the two taxa has again been upheld by BOCCHIERI & MULAS (1990). This erroneous conclusion highlights the prevailing state of ignorance about the variability of the complex *E. nevadensis*, to which *E. sennenii* belongs.

A similar set of problems surrounds the «*E. esula* - *E. virgata*» complex in the Iberian Peninsula. The clarification of the correct identity and taxonomic value of the binomen *E. androsaemifolia* Willd. ex Schlecht, used by Portuguese (COUTINHIO, 1939) and Spanish authors (MERINO, 1906) is of particularly interest.

Taxonomical practice, as well as the bibliographical references contained in standard Floras and some monographs (RADCLIFFE-SMITH, 1985), show that the most useful characters for differentiating between the taxa of this subsection are provided by the leaf. This led us to consider, in addition to traditional characters (shape, indumentum, venation, etc.), the comparative study of cuticular microcharacters and we therefore include a section on the study of the leaf surface of the Iberian taxa and some neighbouring Western European taxa. In contrast, other characters related to the structure of the inflorescence, bracts, cyathium, capsules and seeds rarely have any diagnostic value and usually present considerable uniformity throughout the group.

The absence of cytogenetic data on the Iberian representatives prompted us to make an

initial exploration at a more elementary level so as to obtain their chromosome numbers. Our first goal, obviously, was to make use of these data for taxonomical purposes.

In this study we have not considered characters related to pollen, since preliminary tests had not shown them to be particularly useful in separating such closely related taxa (M. Suárez & J. Martín, pers. com.).

A third section is devoted to the classical consideration of morphological characteristics, including micromorphological characters relating to leaf surface, cyathium, capsule, and seed. This section on taxonomical treatment includes descriptive aspects and matters related to nomenclature, typification, keys, distribution, and ecology. The taxonomic scheme proposed seeks to be coherent with the results of the remaining sections.

LEAF SURFACE

BACKGROUND AND OBJECTIVE OF THIS SECTION

Previous epidermic studies have been carried out on the leaves of *Euphorbia* s.l. (VIND, 1960; KAKKAR & PALIVAL, 1974; OLIVEIRA & ALLEM, 1977; INAMDAR & GANGADHARA, 1978) though we know of no concrete references to taxa belonging to subsection *Esula* except for some generic indications by PRITCHARD (1958), and the more precise of SEGHAL & PALIWAL (1975), where data on stomatal type, frequency and stomatal index from *E. cyparissias*, *E. esula* and *E. virgata* are given. On the subject of the stomata, the ontogenetic and taxonomic studies by RAJU & RAO (1981, 1987), which highlight the systematic importance of the predominant type of stomata in distinguishing *Chamaesyce* from *Euphorbia*, are important.

On matters related to the use of the SEM, the study by EHLER (1974) on the morphology of the surface of the bracts of *Euphorbia* in Madagascar deserves mention.

This section has a twofold objective. On the one hand it is concerned with producing information about the cuticular characters of the leaves of the taxa in this subsection and their possible relationship to environmental factors and geographical distribution; on the other hand, it seeks to use variation of the cuticular microcharacters to taxonomical goals. The use of cuticular microcharacters for systematic purposes is not new (STACE, 1965; WILKINSON, 1971; BARTHOLOTT, 1981, 1983; among others), though they have always been applied to middle-level taxonomic categories (sections, genera, families). In such cases the wide range of morphological variation and geographical distribution makes it possible to obtain highly differentiated results which are of systematic use. Our intention here has been to determine to what extent cuticular microcharacters can be used when working with really closely related taxa in a limited geographical area. Subsection *Esula* seems, in principle, to be a good taxon to which to apply such research, since the inter- and infraspecific differences are mainly based on variations in leaf characters.

MATERIALS AND METHODS

Studies using light microscope (LM)

The samples in all cases come from dry herbarium materials. The vouchers specimens are listed in Table 1, which indicates the locality, sheet number, and Herbarium where each is deposited, abbreviated in accordance with HOLGREN, HOMGREN & BARNET (1990). Unnumbered sheets are identified by the date they were collected and the name of the collector. As for the materials of *E. cyparissias* and *E. esula* aggr. of non-Iberian origin included in this study, typical specimens were selected which fitted the nomenclatural type. For each popula-

tion (one specimen from a herbarium sheet), two mature leaves were selected from the zone corresponding to the top third of the main stem. The leaves were submerged in a supersaturated solution of chloral hydrate ($\text{Cl}_3\text{CCHO} \cdot \text{H}_2\text{O}$) for 48 hours until they were totally transparent. The adaxial and abaxial surfaces were separated, dyed with ruthenium red and mounted in glycerol gel. With the help of a Nikon Optifot microscope equipped with a camera lucida, drawings were obtained which correspond to five optical fields (x400) of the adaxial surface and five of the abaxial surface, selected in the middle zone of the leaves, between the midvein and the margin (STACE, l.c.).

Studies using a scanning electron microscope (SEM)

The samples were taken from fresh materials fixed in the field or individual plants raised in greenhouses. Various mature leaves from the upper middle part of the stem were fixed in glutaraldehyde at 25 % in an aqueous solution (1:9) for 3-5 hours at 4 °C. They were then dabbed with a solution of cacodylate buffer (sodium cacodylate 0.002 M, pH 7.2). The material was dehydrated by soaking it repeatedly through increasingly concentrated solutions of ethyl alcohol (50-100 %), after which the critical point was reached and the selected samples were mounted on an adhesive metal support before being metallized with a fine layer of gold of 600-800 Å. The observations were carried out using a Hitachi model S 2300 SEM microscope at the University of Barcelona's «Servei de Microscòpia Electrònica».

For the observation of the epicuticular waxes, epidermic fragments of leaves from dry herbarium material were used. After being cleaned with high pressure air, they were fixed to a support with colloidal silver and metallized directly in gold by the usual methods.

In both descriptive and terminological aspects, and in the outline presenting the results, we basically follow BARTHOLOTT's proposals (1981).

RESULTS AND DISCUSSION

Studies using light microscope

Table 1 summarizes those characters of the leaf surface of the 45 populations studied which are of most significance, both qualitatively and quantitatively. Table 2 summarizes the results for each taxon. Figures 1 and 2 illustrate some examples of leaf surfaces. In addition to Iberian populations, it was felt necessary, for comparative purposes, to study some European populations of *E. cyparissias* and the «*E. esula* - *E. virgata*» aggr. Our aim in so doing was to check whether the leaf surface corresponds to a more or less homogeneous pattern regardless of geographical distribution and ecology, or whether, on the contrary, a heterogeneous cell model appears which would make the data valid at merely local level. To this end we included in our research materials from *E. graminifolia* and *E. esula* subsp. *tommasiniana*. Though the number of populations studied is sufficiently representative, it is still low in comparison with the wide distribution of certain taxa. The results presented here, though providing indications of particular tendencies, cannot be considered definitive.

For each quantitative character we calculated the maximum, minimum, and mean values, as well as the standard deviation. In Table 1, for lack of space, we present only the mean values, followed by the deviation, in parentheses, for those parameters where fluctuation was significant. In Table 2 we also include the maximum and minimum values and omit some of the less significant characteristics.

The qualitative characters, such as the interval of variation of the undulation of the anticlinal walls (UAW), the distribution model of the stomata on the adaxial surface (SDAd),

Table 1 – Leaf surface characteristics of some European taxa of *Euphorbia* subsect. *Esula*. Populations study (for explanation of the abbreviations, see text)

Taxa	P	Localities	cells/mm ² (σ)	Ad/Ab ratio	UAW	TAW	st/mm ² (σ)	Guard cells	SD _{Ad}	% stomata ANO	stomata type ANI PAR DIA	SI (σ)	SI ratio	Leaf type (-stomatic)		
<i>E. cyparissias</i>	1	Hs: B, Montseny, Campins, BCF 36898	Ad:1892(159) Ab:2206(280)	0,85	1-2	—	49(26) 378(35)	21 × 17 20 × 17	I.1	79 73	21 24	— —	— —	2,6(1,5) 14,8(1,7)	0,2	hypoamphi-
<i>E. cyparissias</i>	2	Hs: L, Serra d'Aubens, BCF 36896	Ad:1546(96) Ab:2253(35)	0,68	1-2	—	50(0) 319(13)	26 × 25 23 × 20	I.1	100 83	— 17	— —	— —	3,3(0,2) 12,4(0,3)	0,3	hypoamphi-
<i>E. cyparissias</i>	3	Hs: Hu, Panticosa, SALA 22595	Ad:1840(121) Ab:1694(71)	1,08	1-2	—	84(21) 195(20)	25 × 21 24 × 18	R/I	87 88	13 10	— 2	— —	4,4(1,2) 10,4(1,3)	0,4	hypoamphi-
<i>E. cyparissias</i>	4	Ga: Vosges, Romont, BC 131618	Ad: 987(26) Ab:1205(87)	0,81	1-2 2-3	—	22(4) 227(17)	25 × 22 25 × 21	I.1	42 76	58 24	— —	— —	2,2(0,5) 16,0(1,9)	0,1	hypoamphi-
<i>E. cyparissias</i>	5	Cz: Sonenberg, prope Cratzen, BC 57237	Ad: 799(4) Ab: 886(48)	0,90	1-2	—	65(4) 96(17)	28 × 23 29 × 33	R	21 41	79 59	— —	— —	7,6(0,5) 9,7(1,1)	0,8	hypoamphi-
<i>E. esula</i> ssp. <i>esula</i>	6	Hs: Gr. Srra. Nevada, Pra dos de Otero, MA 250394	Ad: 863(16) Ab:1182(140)	0,73	1-2	—	50(11) 132(8)	26 × 22 27 × 20	R	88 67	6 21	6 18	— —	5,5(1,3) 10,1(0,5)	0,6	hypoamphi-
<i>E. esula</i> ssp. <i>esula</i>	7	Hs: Gr. Srra. Nevada, Trevelez, GDA 6959	Ad:1151(20) Ab: 913(178)	1,13	1-2	—	—	—	—	—	—	—	—	—	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	8	Hs: Le. Montes Aquilia nos, MA 317290	Ad:1592(124) Ab:1470(70)	1,08	2-3 2-4	—	—	—	—	—	—	—	—	—	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	9	Hs: Le Ferradillo, BCF 35258	Ad:1269(81) Ab:1259(250)	1,00	2-3 3-5	—	—	—	—	—	—	—	—	—	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	10	Hs: Hu, Sierra de Arcena, SEV 47003	Ad: 630(10) Ab: 922(128)	0,68	2-3 3-5	—	—	—	—	—	—	—	—	—	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	11	Lu: BAI, Odemira, MA 75457	Ad: 980(22) Ab: 964(146)	1,00	2-4 3-5	—	123(6) 135(7)	27 × 19 24 × 19	—	75 94	25 6	— —	— —	11,9(1,1) 12,4(1,1)	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	12	Ga: Fontainebleau, MA 76298	Ad:1011(46) Ab:1030(35)	0,98	1-2	—	—	—	—	—	—	—	—	—	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	13	Po: Cracovia, Niepolomice, MA 250395	Ad: 529(144) Ab: 557(9)	0,94	1-3 2-3	—	203(8) 114(25)	26 × 20 25 × 25	—	75 56	21 44	— —	— —	16,4(0,1) 16,9(3,3)	—	hypo-
<i>E. esula</i> ssp. <i>esula</i>	14	Ge: Sandkrug, MA 196344	Ad: 921(61) Ab:1070(109)	0,86	1-3 2-5	—	—	—	—	—	—	—	—	—	—	hypo-
<i>E. esula</i> ssp. <i>orientalis</i> (var <i>pseudotenuifolia</i>)	15	Hs: Ge, Lliers, MA 75455	Ad:1052(73) Ab:1039(13)	1,00	1-2 2-4	—	155(11) 153(7)	24 × 19 25 × 19	R	5 84	93 15	2 1	— —	12,9(0,4) 12,8(0,6)	1,0	epiamphi-
<i>E. esula</i> ssp. <i>orientalis</i> (<i>E. virgata</i>)	16	Ga: Des Ardenes, Vouziers, MA 276134	Ad:1125(150) Ab:1044(109)	1,00	1-2 1-2	—	233(30) 183(41)	23 × 19 23 × 20	R	6 29	93 70	1 1	— —	17,2(0,5) 14,4(1,4)	1,2	epiamphi-

Table 1 — Leaf surface characteristics of some European taxa of *Euphorbia* subsect. *Esula*. Populations study (for explanation of the abbreviations, see text)

Taxa	P	Localities	cells/mm ² (σ)	Ad/Ab ratio	UAW	TAW	st/mm ² (σ)	Guard cells	SD _{Ad}	% stomata type ANO ANI PAR DIA	SI (σ)	SI ratio	Leaf type (-stomatic)			
<i>E. nevadensis</i> ssp. <i>aragonensis</i>	32	Hs: T, Ports, Monte Caro, BC 57222	Ad: 912(169) Ab: 1019(137)	0,89	1-2	—	35(16) 138(25)	24 × 19 25 × 19	1.4	38 63	56 34	6 3	— —	3,9(2,4) 12,0(1,8)	0,3	hypoamphi-
	33	Hs: Bu, Valverde, BCF 36893	Ad: 700(16) Ab: 772(46)	0,90	1-2	—	43(4) 101(15)	28 × 22 26 × 22	R	16 18	75 82	9 —	— —	5,7(0,3) 11,4(0,9)	0,5	hypoamphi-
<i>E. nevadensis</i> ssp. <i>aragonensis</i>	34	Hs: Bu, Pancorbo, JACA 82274	Ad: 974(285) Ab: 912(253)	1,00	1-2 2-5	+	35(12) 113(23)	30 × 23 30 × 24	1.4	50 61	40 39	10 —	— —	4,2(1,6) 11,4(1,6)	0,3	hypoamphi-
	35	Hs: Vi, Lagrain, JACA 489073	Ad: 513(39) Ab: 544(8)	0,94	2-5 2-5	+	5(10) 78(8)	29 × 25 31 × 25	1.1	38 96	56 4	6 —	— —	4,9(1,9) 12,5(1,2)	0,4	hypoamphi-
<i>E. nevadensis</i> ssp. <i>aragonensis</i>	36	Hs: Lo, La Poblacion, BCF 35126	Ad: 556(35) Ab: 639(127)	0,86	1-3 2-5	— +	19(25) 78(17)	37 × 28 38 × 28	1.2	92 69	8 31	— —	— —	3,6(3,5) 10,8(1,2)	0,3	hypoamphi-
	37	Hs: Te, M. de Manzaneda, 1860, Loscos, COI-Willkomm	Ad: 416(4) Ab: 572(4)	0,72	3-5 3-5	— —	16(13) 82(12)	38 × 27 34 × 25	1.3	25 43	75 57	— —	— —	3,7(2,8) 12,5(1,6)	0,3	hypoamphi-
<i>E. nevadensis</i> ssp. <i>bolosii</i>	38	Hs: Te, Peñarroya, MA 75453	Ad: 777(46) Ab: 856(110)	0,9	2-5 2-5	— +	30(20) 91(4)	34 × 18 28 × 22	1.3	26 86	56 14	18 —	— —	3,6(2,3) 9,7(0,8)	0,3	hypoamphi-
	39	Hs: T, Cornudella, BCF 35123	Ad: 976(98) Ab: 983(90)	1,0	1-2 1-2	— —	61(37) 148(34)	26 × 25 29 × 25	1.3	24 43	74 40	2 15	2 2	5,8(3,8) 12,9(1,7)	0,5	hypoamphi-
<i>E. nevadensis</i> ssp. <i>bolosii</i>	40	Hs: T, La Pena, BCF 35131	Ad: 739(185) Ab: 761(180)	0,9	1-2 1-2	— —	31(38) 144(39)	33 × 25 32 × 25	1.3	70 48	10 42	20 9	— 1	5,2(6,3) 16,5(3,3)	0,3	hypoamphi-
	41	Hs: L, Organyà, BC 99285	Ad: 556(14) Ab: 589(54)	0,9	1-2 2-5	— +	40(17) 67(13)	36 × 27 34 × 25	1.2	49 37	49 63	2 —	— —	6,5(2,7) 10,1(1,4)	0,6	hypoamphi-
<i>E. nevadensis</i> ssp. <i>bolosii</i>	42	Hs: Hu, Oroel (wide leaf), JACA 426271	Ad: 441(26) Ab: 529(40)	0,8	1-3 1-3	— —	34(18) 65(10)	42 × 27 41 × 26	1.1	89 79	11 16	— 5	— —	6,8(3,5) 11,0(2,0)	0,6	hypoamphi-
	43	Hs: Hu, Oroel (narrow leaf), JACA 426271	Ad: 526(24) Ab: 625(43)	0,8	1-2 2-4	— —	49(7) 57(10)	39 × 28 39 × 26	R	5 9	95 84	— 7	— —	8,5(1,0) 8,3(0,7)	1,0	hypoamphi-
<i>E. nevadensis</i> ssp. <i>bolosii</i>	44	Hs: Ports d'Horta, Les Heres, BCF 71739	Ad: 682(2) Ab: 817(125)	0,8	1-2 2-3	— —	21(8) 129(21)	29 × 23 29 × 23	1.3	70 72	22 24	8 4	— —	4,0(1,6) 13,7(1,7)	0,3	hypoamphi-
	45	Hs: Na, between Aoiz and Gorritz, JACA 249671	Ad: 610(17) Ab: 712(181)	0,8	1-3 2-5	— +	41(18) 100(15)	38 × 27 36 × 25	1.2	54 70	27 27	19 3	— —	6,0(2,5) 12,4(1,9)	0,5	hypoamphi-

Table 1 – Leaf surface characteristics of some European taxa of *Euphorbia* subsect. *Esula*. Populations study (for explanation of the abbreviations, see text)

Taxa	P	Localities	cells/mm ² (σ)	Ad/Ab ratio	UAW	TAW	st/mm ² (σ)	Guard cells	SD _{Ad}	% stomata type ANO	stomata type ANI PAR DIA	SI (σ)	SI ratio	Leaf type (-stomatic)		
<i>E. esula</i> ssp. <i>orientalis</i> (var <i>angustifolia</i>)	17	Be: Flandre Orientale, Brugstraat, MA 381236	Ad: 964(31) Ab:1276(93)	0,75	1-2	—	179(8) 218(31)	25 × 19 24 × 18	R	56 74	44 24	— 2	— —	15,7(1,0) 14,5(0,9)	1,1	epiamphi-
<i>E. esula</i> ssp. <i>orientalis</i> (<i>E. tristis</i> var. <i>loreyi</i>)	18	Ga: Boneuil, BC 82848	Ad: 673(27) Ab: 766(35)	0,88	1-2	+	136(4) 117(8)	31 × 24 29 × 23	R	17 70	80 23	3 7	— —	16,8(0,5) 13,2(0,2)	1,3	epiamphi-
<i>E. esula</i> ssp. <i>orientalis</i> (<i>E. virgata</i>)	19	Po: Skalbmierz, MA 250396	Ad:2033(58) Ab:1939(115)	1,00	1-2	—	446(47) 340(20)	16 × 13 17 × 14	R	28 40	66 56	6 4	— —	17,9(1,0) 14,9(0,5)	1,2	epiamphi-
<i>E. esula</i> ssp. <i>orientalis</i> (<i>E. virgata</i>)	20	Tu: Sivas, pr. Zara, BCF 36897	Ad: 933(181) Ab: 743(37)	1,25	1-2 1-3	— +	155(9) 109(8)	27 × 21 30 × 23	R	21 46	76 52	3 —	— 2	14,7(2,7) 12,8(0,7)	1,2	epiamphi-
<i>E. esula</i> ssp. <i>orientalis</i> (<i>E. sarati</i>)	21	Ga: L'Ariane pr. Niza, VI.1864, Sarato, FI	Ad:1128(23) Ab:1260(101)	0,89	1-2	—	222(4) 218(15)	27 × 21 28 × 21	R	26 48	70 48	2 4	2 —	16,4(0,1) 14,7(0,2)	1,1	epiamphi-
<i>E. esula</i> ssp. <i>orientalis</i> (<i>E. virgata</i>)	22	Av: Manes, BC 57261	Ad:2345(181) Ab:2773(154)	0,98	1-2	—	474(15) 467(46)	16 × 12 18 × 13	R	50 51	42 45	8 4	— —	16,8(0,3) 16,4(0,7)	1,0	epiamphi-
<i>E. esula</i> ssp. <i>tommasiniana</i>	23	It: Trieste, Mte. Spaccatto, BC 57218	Ad: 630(23) Ab: 552(8)	1,14	1-2	—	93(8) 86(1)	33 × 23 33 × 24	R	25 36	66 59	9 5	— —	12,9(1,3) 13,4(0,2)	1,0	amphi-
<i>E. graminifolia</i>	24	Ga: Verquières, VI.1905, Delmas, MPU	Ad:1454(93) Ab:1349(42)	1,07	1-2	—	188(8) 148(8)	25 × 22 28 × 22	R	79 79	4 13	11 3	6 5	11,4(0,2) 9,9(0,7)	1,2	epiamphi-
<i>E. nevadensis</i> sssp. <i>nevadensis</i>	25	Hs: Gr, Srta. Nevada, Veta, 3000m, GDA 17234	Ad:1793(115) Ab:1599(104)	1,12	1-2	+	178(46) 218(31)	25 × 18 25 × 21	R	92 84	8 16	— —	— —	9,0(1,7) 11,9(1,0)	0,7	hypoamphi-
<i>E. nevadensis</i> sssp. <i>nevadensis</i>	26	Hs: Gr, Srta. Nevada, Bco. de San Juan, BCF	Ad:1229(186) Ab:1240(267)	0,99	1-2	+	110(28) 127(42)	31 × 24 33 × 24	R	86 88	13 12	1 —	— —	8,4(2,4) 9,2(1,3)	0,9	hypoamphi-
<i>E. nevadensis</i> sssp. <i>nevadensis</i>	27	Hs: Av, Hoyocasero, BCF 35128	Ad:1108(202) Ab:1021(179)	1,08	1-2	+	137(27) 102(34)	28 × 23 28 × 24	R	72 78	26 22	2 —	— —	10,9(0,9) 9,2(2,4)	1	epiamphi-
<i>E. nevadensis</i> sssp. <i>nevadensis</i>	28	Hs: Al, Srta. de Aitana, BC 99287	Ad: 871(91) Ab:1094(48)	0,79	1-3 2-5	+	50(38) 163(20)	28 × 24 33 × 23	I.1	37 25	60 75	3 —	— —	5,2(3,5) 13,0(1,2)	0,4	hypoamphi-
<i>E. nevadensis</i> sssp. <i>nevadensis</i>	29	Hs: Ab, Srta. Alcaraz, VI. 1890, Porta & Rigo 642,G	Ad: 700(54) Ab: 820(19)	0,84	1-2	—	82(12) 97(4)	34 × 27 34 × 27	R	67 64	33 36	— —	— —	10,4(0,6) 10,6(0,6)	1,0	amphi-
<i>E. nevadensis</i> sssp. <i>nevadensis</i>	30	Hs: Z, Moncayo, Peñas de Herrera, JACA 190188	Ad: 733(85) Ab: 683(142)	0,80	2-3 2-3	+	65(20) 81(12)	35 × 26 36 × 27	R/I	41 60	59 37	— 3	— —	8,2(2,7) 10,8(2,0)	0,8	hypoamphi-
<i>E. nevadensis</i> ssp. <i>aragonensis</i>	31	Hs: Te, Belmonte, 1860, Loscos, COI-Willkomm	Ad: 651(14) Ab: 745(69)	0,87	1-3 1-3	+	39(16) 79(11)	34 × 25 33 × 25	I.3	— 21	92 77	8 2	— —	5,5(2,1) 9,6(0,7)	0,6	hypoamphi-

Table 2 — Leaf surface characteristics of some European taxa of *Euphorbia* subsect. *Esula*. Synthesis by taxa.

Taxa	cells/mm ²	basic UAM	st/mm ²	Guard cells	SD Ad	basic stomatal type	SI	SI ratio	basic Leaf type
<i>E. cyparissias</i>	Ad: 794-1488 (452)-2113 Ab: 838-1699 (540)-2585	1-2 1-2	17- 57 (27)-113 78-250 (101)-419	25(2,7).21(2,5) 24(3,2).20(2,1)	I	ano	1- 4(2,0)- 8-13(2,7)-18	9 0,4(0,2)	hypoamphi-
<i>E. esula</i>	Ad: 404- 971 (276)-1540 Ab: 544-1024 (265)-1672	2-3 3-5	62-148 (48)-249	27(2,9).21(2,0)	—	—	7-13(3,5)-21	—	hypo-
<i>E. esula</i>	Ad: 739-1292 (497)-2470 Ab: 684-1259 (511)-2481	1-2 1-2	140-250 (119)-514 93-215 (120)-513	23(4,3).19(3,3) 24(4,9).19(3,5)	R	ani ani/ano	11-16(2,3)-19 12-14(1,4)-17	1,1(0,1)	epiamphi-
<i>E. esula</i>	Ad: 607- 630 (23)- 654 Ab: 544- 552 (8)- 560	1-2 1-2	85- 93 (8)-101 85- 86 (1)- 87	33(1,6).23(1,0) 33(1,6).24(1,6)	R	ani ani	12-13(1,3)-14 13-13(0,2)-13	1,1(0,1)	epiamphi-
<i>E. graminifolia</i>	Ad: 1360-1454 (93)-1548 Ab: 1307-1349 (43)-1392	1-2 1-2	178-186 (8)-194 140-148 (9)-155	25(0,1).22(1,5) 28(1,6).22(0,3)	R	ano ano	11-11(0,2)-12 9-10(0,7)-11	1,2(0,1)	epiamphi-
<i>E. nevadensis</i>	Ad: 638-1036 (328)-1875 Ab: 544-1042 (288)-1680	1-2 1-2	31- 99 (50)-225 62-124 (49)-249	30(4,7).24(3,6) 32(4,9).25(3,3)	R	ano ano	3- 8(3,0)-13 5-11(2,2)-14	0,8(0,3)	hypoamphi-
<i>E. nevadensis</i>	Ad: 474- 760 (223)-1260 Ab: 513- 793 (216)-1369	1-3 1-2/2-5	8- 31 (17)- 70 54- 99 (30)-171	30(4,8).23(3,5) 31(5,1).24(3,2)	I	ani ano	1- 4(2,0)-10 9-11(1,6)-15	0,4(0,1)	hypoamphi-
<i>E. nevadensis</i>	Ad: 404- 663 (189)-1097 Ab: 490- 735 (176)-1112	1-2 3-5	8- 33 (84)-124 46-104 (41)-217	34(6,1).25(3,9) 33(4,5).25(2,2)	I	ano/ani ano	1- 5(3,6)-13 7-12(3,1)-22	0,5(0,2)	hypoamphi-

or the basic type of stomata, have generally proved statistically more reliable than the quantitative ones. However, the quantitative variables reveal concrete tendencies which make it possible to partially distinguish between certain taxa. These can be differentiated by a set of particular trends affecting several characters rather than by the possession of a single «right» character.

Other potential characters are not shown in the table because they are constant and common to all the taxa studied. Examples are the curve of the periclinal walls, which is always convex, or the orientation of the stomata, which is aleatory.

The epidermises studied are devoid of trichomes, papillae or emergences though very occasionally some populations of *E. graminifolia* may present barely perceptible hemispherical papillae.

In terms of intrapopulation variation, the results obtained from the study of populations P 42 and P 43 of *E. nevadensis* subsp. *bolosii* are of interest. The samples were obtained from two different individuals from the same sheet bearing the name of a single locality: Oroel. We do not know whether they were gathered in the same environment or came from two microhabitats with different ecology. The individual with narrow, linear-oblong leaves corresponds to the commonest morphological type, as we were able to observe on visiting the locality, whereas the individual with wide oval-triangular leaves, similar to those of subsp. *nevadensis*, must be extremely rare, since we were unable to find a single specimen. Two of the values in Table 1 are particularly unusual with reference to these two forms. The first surprising feature is the distribution of the stomata on the adaxial surface: I.1-type in the wide-leaved specimens (in the similar subsp. *nevadensis* the distribution is usually regular) as against R-type in the narrow-leaved specimen (which in this subspecies is always irregular). The other noteworthy character is the basic type of stoma, which is shown to be anomocytic in the broad-leaved population and predominantly anisocytic in the narrow-leaved population. The coefficient of correlation between the stomatal indices is also different in the two samples. We have no convincing explanation for this anomalous intrapopulation behaviour since it would be desirable first of all to clarify the origin and microenvironment from which the two individuals in the sheet come. Even so this case calls attention to the tendency shown by *E. nevadensis* in its northeastern area towards irregular and haphazard behaviour in micromorphological characters, a phenomenon which may merely constitute proof of its genetic instability in this area, where it is subjected to a process of microspeciation.

Cuticular characters. Variation, ecological and taxonomical significance

Cell frequency (cells/mm²) and its relationship on the adaxial and abaxial surfaces respectively

Generally speaking in Table 2 it can be observed that the frequencies are somewhat higher on the abaxial surfaces of the sample studied, or, to put it another way, the cells are somewhat larger on the adaxial surfaces. A relationship can also be established (though not an absolute one) between cell frequency and altitude. Populations at higher altitudes usually present a higher cell frequency, a trend which is accentuated on the adaxial surface. This fact is illustrated in the *E. nevadensis* complex where the contrast between subsp. *nevadensis* and subsp. *bolosii* is obvious.

The variability of cell frequency does not appear to be significantly influenced by the size or width of the leaf. Thus in *E. esula* subsp. *esula* the cell frequency of populations from the Sierra de Aracena (P 10) and Odemira (P 11), made up of very robust individuals with large, very broad leaves, does not differ substantially from that of populations from Poland (P 13) comprising typical individuals with small, narrow leaves. In *E. nevadensis* subsp. *bolosii*, no ostensible differences are observed in cell size between individuals with broad and narrow leaves within the same populations (P 42, 43).

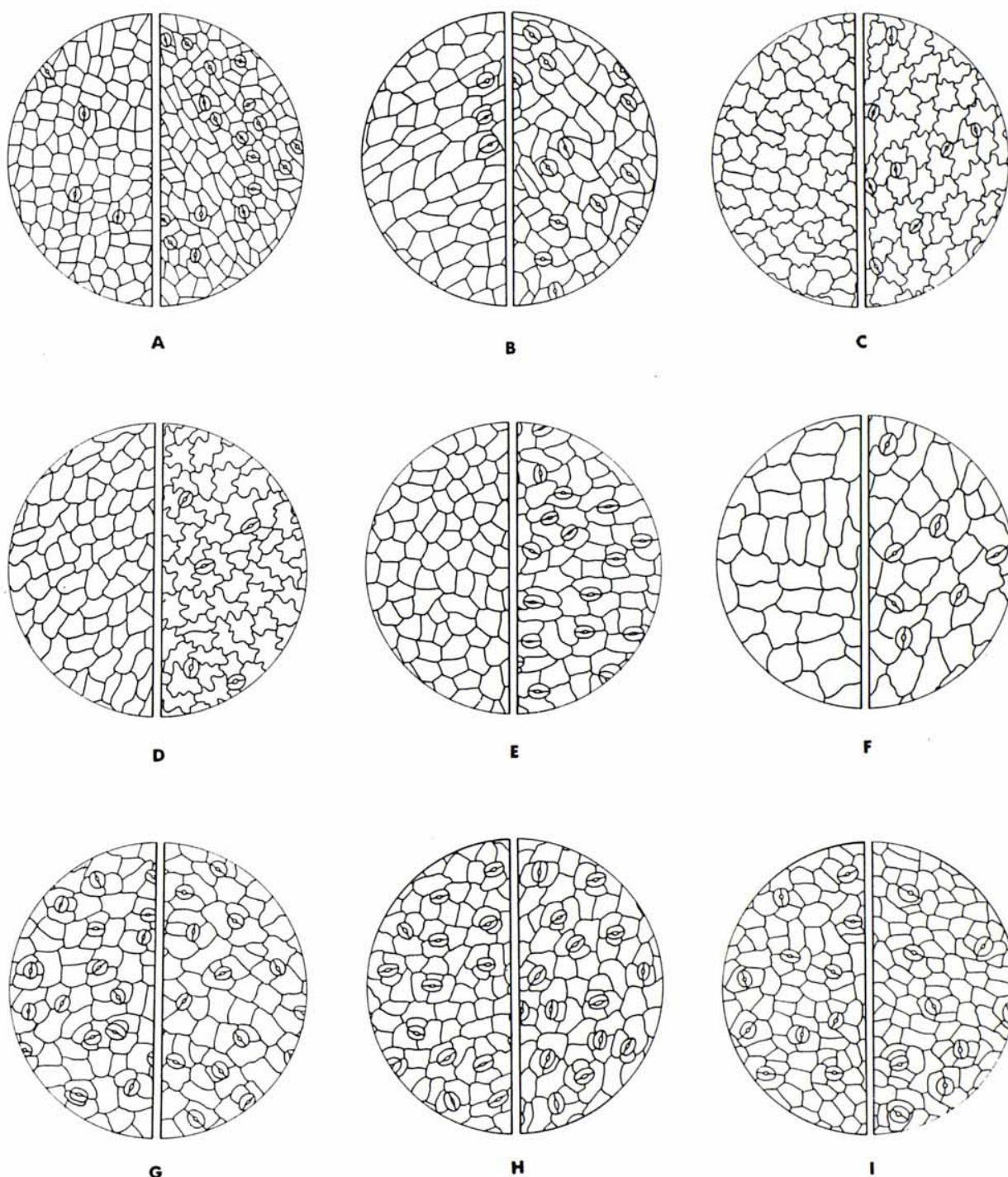


Fig. 1 – Light microscopic view of the leaf surface of European taxa of *Euphorbia* subsect. *Esula* (for each sample, represented by a circle, the left-hand semicircle corresponds to the adaxial surface and the right-hand semicircle to the abaxial surface). A-B: *E. cyparissias* L. (A: Hs, Montseny, BCF 36898; B: Ga, Romont, BC 131618); C-F: *E. esula* L. subsp. *esula* (C: Lu, Odemira, MA 75457; D: Hs, Srra Nevada, MA 250394; E: Ga, Fontainebleau, MA 76298; F: Po, Niepolomice, MA 250395); G-H: *E. esula* L. subsp. *orientalis* (Boiss. in DC.) Molero & Rovira. (G: Ga, Vouziers, MA 276134; H: Ga, Nice, VI.1864, Sarato, FI); I: *E. graminifolia* Vill. (Ga: Verquière, VI.1905, Delmas, MPU).

It is a well known fact that polyploidy affects cell size: polyploids generally present proportionally larger cells as the degree of ploidy increases. Thus, in *E. nevadensis* the tetraploid population from El Moncayo (P 30) has cells larger than the populations from the Sierra Nevada (P 25, 26), and the Central System (P 27). In *E. nevadensis* subsp. *bolosii*, the hexaploid population from Oroel (P 43) has cells somewhat larger than those of the diploid populations from Els Ports (P 44) or La Pena (P 40). In *E. cyparissias* very different values occur in Iberian populations with small cells (those studied karyologically are diploid) and European ones with cells twice as large (Table 1; Figure 1, A-B), which are probably tetraploid. The relationship between degree of ploidy and cell size in this species has already been pointed out by RADCLIFFE-SMITH (1985:22) and STAHEVITCH & al. (1987:2253) with regard to populations in Canada.

Taxonomically speaking, cell frequency shows considerable variation and cannot be used to differentiate in absolute terms between the taxa studied. However, this variable does throw light on certain trends and correlations. For instance, the highest values occur in *E. cyparissias*. In *E. esula* the mean frequency is higher in subsp. *orientalis* than in subsp. *esula*. In the *E. nevadensis* complex, subsp. *nevadensis* stands apart from other subspecies, especially subsp. *bolosii*, on account of its higher frequencies.

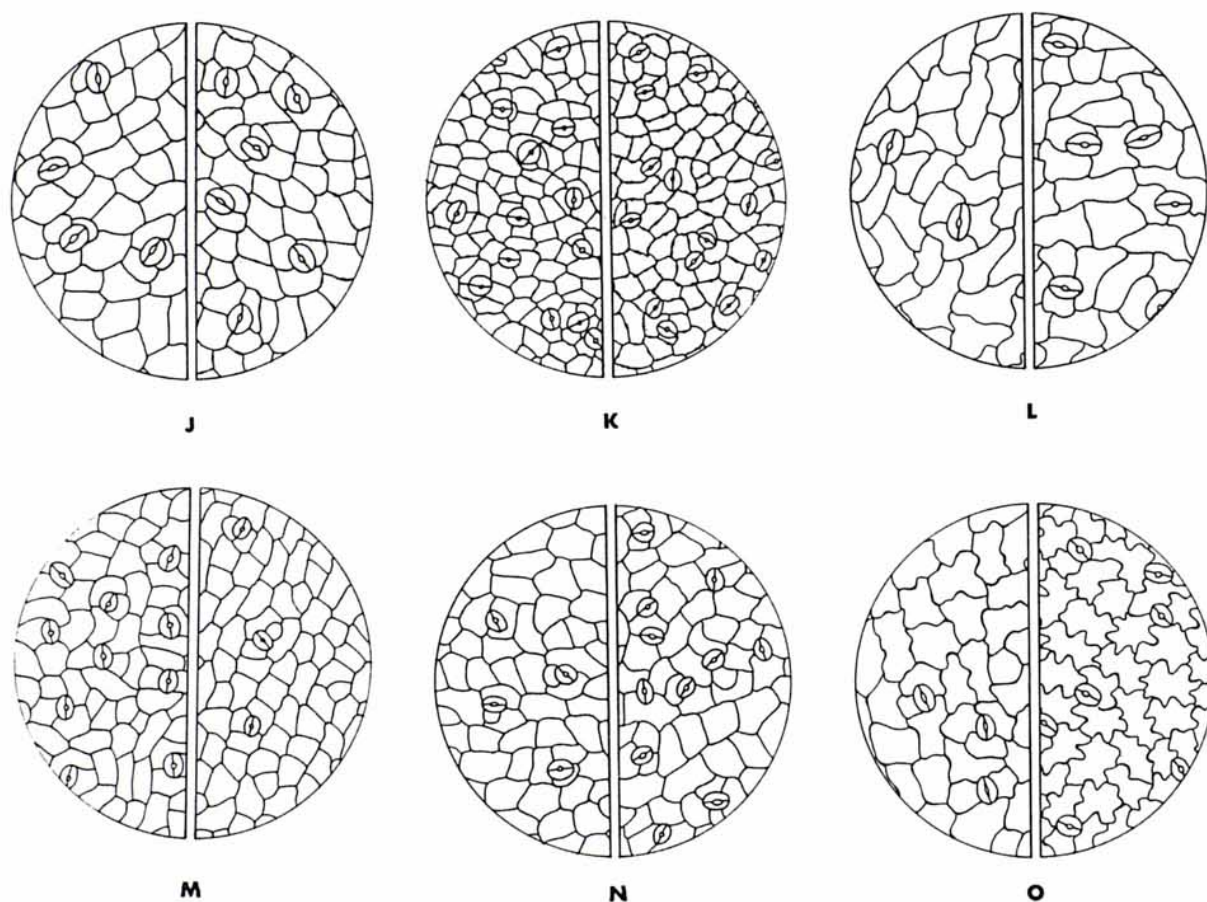


Fig. 2 — Light microscopic view of the leaf surface of European taxa of *Euphorbia* subsect. *Esula* (continuation). I-K: *E. nevadensis* Boiss. & Reuter subsp. *nevadensis* (J: Hs, Srra. Alcaraz, Porta & Rigo 642, G; K: Hs, Srra. Nevada, GDA 17234); L-M: *E. nevadensis* Boiss. & Reuter subsp. *bolosii* Molero & Rovira (L: Hs, Oroel, JACA 426271; M: Hs, Cornudella, BCF 35123); N-O: *E. nevadensis* Boiss. & Reuter subsp. *aragonensis* (Loscos & Pardo) Bolòs & Vigo (N: Hs, Tossa de Caro, BC 57256; O: Hs, Lagrain, JACA 469073).

Undulation of the anticlinal walls (UAW)

This variable is expressed in terms of the interval of variation in the scale established by STACE (enm. WILKINSON, l.c.:153).

The anticlinal walls on the abaxial surface are usually more undulating than on the adaxial surfaces. Study of the Tables shows that this variable is almost always significant in *E. esula* subsp. *esula*, which usually has clearly undulating walls (interval 3-5 in the Stace scale) on the abaxial surface, while those on the adaxial surface (Figure 1: C-D) are slightly less undulating (interval 2-3 in the same scale). These values are in contrast with those obtained for subsp. *orientalis* and the related taxa subsp. *tommasiniana* and *E. graminifolia* which present straight or only slightly undulating walls (interval 1-2 in the Stace scale). It should be pointed out, however, that the Iberian population from Llers (P 15) is deviant, in that the walls of the abaxial surface are markedly undulating.

Within the *E. nevadensis* complex, there is a tendency for populations to present gradually more undulating anticlinal walls (particularly on the abaxial surface) the further they are located along a line oriented from south to northeast. This trend increases in the mountains around the eastern end of the Ebro basin. Thus in subsp. *nevadensis*, the anticlinal walls are straight or only slightly undulating, except in certain more northerly transitional populations (P 28, 30). In subsp. *aragonensis* this trend is more pronounced and in subsp. *bolosii* the abaxial surfaces with undulating walls are clearly predominant. In this complex, the degree of undulation of the anticlinal walls does not appear to be directly related to the more or less nemoral or xeric environment of the habitats. For instance, populations in Els Ports (P 32) and Valverde (P 33) which colonize the edges of woods and clearings with relatively moist and shady environments have straight or only slightly undulating walls while other populations growing at low altitude, such as those from Peñarroya (P 38) and Organyà (P 41), which colonize hotter, drier environments, have undulating walls.

Thickenings in the anticlinal walls (TAW)

We use this term in the the meaning given by VINDT (1960:282). Only presence (+) or absence (-) is indicated.

Incrassations are absent from the epidermis of *E. cyparissias* but can occur sporadically in the abaxial epidermis of *E. esula* s.l. and in the adaxial and abaxial surface (or more rarely the adaxial surface alone) of *E. nevadensis* s.l. This character appears at random and is difficult to use for taxonomic purposes. However, its greater frequency and more heterogeneous distribution in the *E. nevadensis* complex, especially in subsp. *nevadensis*, deserve mention.

Stomatal frequency (st/mm²)

The behaviour of this variable is conditioned by the distribution pattern of the stomata on the two leaf surfaces. In the group of taxa with epiamphistomatic leaves and regular distribution of the stomata on the adaxial surface («*E. virgata*» complex), *E. tommasiniana* stands alone on account of its low stomatal frequency. *E. esula* subsp. *esula*, which has hypostomatic leaves, presents a cell frequency on the abaxial surface which is noticeably lower than that of subsp. *orientalis* («*virgata*»), though close to *E. graminifolia*.

In the group of taxa with hypophamphistomatic leaves (*E. cyparissias*, *E. nevadensis*), *E. nevadensis* subsp. *nevadensis* stands apart from the remaining subspecies on account of the distribution of the stomata, which is regular on the adaxial surface, and its stomatal frequency, which is noticeably higher.

Size of the guard cells

Generally speaking, the relationship between higher frequencies and smaller stomata is maintained. Length varies to a markedly greater extent than width and consequently has greater value as an distinguishing trait.

In terms of mean values, the smallest stomata are found in *E. esula* subsp. *orientalis* and in *E. cyparissias*. Though *E. esula* subsp. *esula* has slightly larger stomata than the two aforementioned taxa, the overlap in measurements is obvious. The largest stomata are to be found in *E. nevadensis*, with maximum sizes in subsp. *bolosii*.

It should be pointed out that among populations of *E. nevadensis* subsp. *nevadensis*, the largest stomata correspond to the tetraploid population from El Moncayo (P 30) while in subsp. *bolosii*, the largest stomata belong to the hexaploid population from Oroel (P 42). These cases confirm the link between a higher level of ploidy and larger stomata, a phenomenon that had already been detected for other variables such as cell frequency. These relationships have already been discussed in various scientific studies (WILKINSON, l.c.).

Stomata size, like other variables already mentioned, does not provide the means for separating recognized taxa, though it does reveal very pronounced trends which make it possible to differentiate partially between certain controversial taxa: between subsp. *esula* and subsp. *orientalis* in *E. esula*; between *E. esula* subsp. *orientalis* and subsp. *tommasiniana*; and between subsp. *nevadensis* and subsp. *bolosii* in *E. nevadensis*.

Stomatal distribution pattern on the adaxial surface (SDAd)

In the species under study, the distribution of the stomata on the abaxial surface is always regular. On the adaxial surface, the stomata can be distributed regularly (R) or irregularly (I). Irregular distribution means that the stomata are distributed in strips, of variable width, on either side of the midvein of the leaf. The outer edge of this strip may present various undulations, giving rise to the four patterns of irregular distribution recognized in the present study, which are described in the outline accompanying Figure 3.

Though not an entirely constant character, the obvious predominance of a particular pattern in some taxa may be of partial use for diagnostic purposes. *E. cyparissias* normally presents an irregular pattern (I.1), though on rare occasions the stomatal strip widens to occupy the whole lamina. In *E. esula* subsp. *orientalis*, only a regular pattern (R) is found. *E. nevadensis* proves to be an extremely variable taxon. Subsp. *nevadensis* has an essentially regular pattern (R), except in some more norther transitional populations (P 28, 30) where model I.1 with a wide strip occurs. Subsp. *aragonensis* displays extraordinary variability, differing from all the patterns described except I.3. This pattern is also predominant in subsp. *bolosii*, though others may also appear.

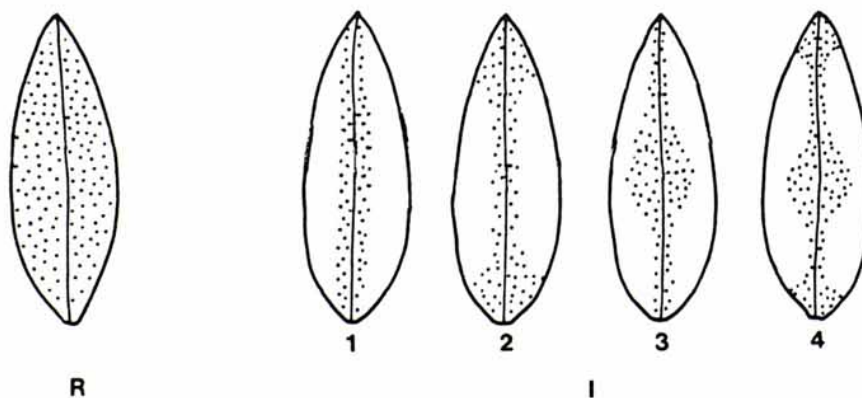


Fig. 3 — Patterns of stomatal distribution on the adaxial surface. R: regular; I: irregular (I.1: irregular with parallel margins; I.2: irregular with convex margins; I.3: irregular with concave margins; I.4: irregular with sinusoidal margins).

Stomatal type (%)

In this research we have taken into account only the morphological type of stomata in mature leaves, but not ontogenic development. In accordance with WILKINSON (l.c.), four major morphological types have been recognized: anomocytic (ANO) and anisocytic (ANI), which are predominant, and paracytic (PARA) and diacytic (DIA), which are subsidiary.

E. cyparissias and *E. esula* subsp. *esula* present a basically anomocytic type of stomata, while *E. esula* subsp. *orientalis* corresponds to the anisocytic type, as does subsp. *tommasiniana*. The same is not true of *E. graminifolia*, which has anomocytic stomata on both surfaces. In the *E. nevadensis* complex, percentages are distributed in a more random fashion. Southern populations of subsp. *nevadensis* correspond exclusively to the basic anomocytic type, but the more norther populations, like those of the remaining subspecies distributed over the mountains around the Ebro basin, display highly unstable behaviour. That of *E. nevadensis* subsp. *bolosii* (Table 1; P 42 and P 43) provides an illustration: the wide-leaved sample corresponds to the anomocytic type, while the narrow-leaved one corresponds to the anisocytic type.

Our results are in agreement with those of SEGHAL & PALIWAL (l.c.) in respect to *E. cyparissias* whereas they are not in respect to *E. esula* (to which paracytic stomatal type is attributed by these authors) or *E. virgata* (to which anomocytic stomatal type is attributed).

RAJU & RAO (l.c.), on the basis of their own studies and the bibliography they compiled, established that in *Euphorbia* the basic types of stomata are paracytic and anomocytic, the latter being more widespread in European species. These types predominate over the anisocytic type which characterizes the genus *Chamaesyce*. Nonetheless VINDT (1960) and SEGHAL & PALIWAL (l.c.) already recognized that in some *Euphorbia*, the anisocytic type can be basic. In our case, the anisocytic type characterizes *E. esula* subsps. *orientalis* and *tommasiniana* in contrast with subsp. *esula*. We also note that it appears more frequently on adaxial surfaces.

The stomatal Index (SI) and its coefficient of correlation between the adaxial and abaxial surfaces (SI ratio)

WILKINSON (l.c.) indicates that the stomatal index can be of use when applied to taxa in which it oscillates little, as was shown by Rowson for some species of *Cassia*, but it can prove inoperable in some species where it is highly variable, as was observed by Staveen & Baas in some Icacinaceae genera.

Table 2 shows that the comparable data are exclusively those of the abaxial surfaces, which always display regularity in terms of stomatal distribution. Mean values range from 9 to 13 (9 to 16 in Table 1), partially or totally overlapping so that they cannot be used to make taxonomical distinctions. It should be pointed out however that *E. nevadensis* tends to present somewhat lower indices. On the adaxial surfaces where stomata are regularly distributed, the margins of variation are wider. At taxon level, *E. esula* subsp. *orientalis* shows the highest indices (SI 16), and *E. nevadensis* subsp. *nevadensis* presents the lowest (SI 8).

On adaxial surfaces where stomata are irregularly distributed, the indices are considerably lower (*E. cyparissias*, *E. nevadensis* subsps. pls.), despite the fact that stomatal frequency was measured exclusively on the strip of the lamina which contains stomata.

The coefficients of correlation can yield better results when the aim is to separate closely related taxa. *E. esula* subsp. *orientalis* and *E. graminifolia* can be distinguished from subsp. *esula* by their SI ratio > 1. In *E. nevadensis*, subsp. *nevadensis* is distinguished from the rest of subspecies because its index is significantly higher, though in this case separation is not total.

Basic leaf type

This simple character, directly related to stomatal frequency on the two leaf surfaces, has proved very useful in separating some controversial taxa. We follow the terminology of WILKINSON (l.c.: 99-100).

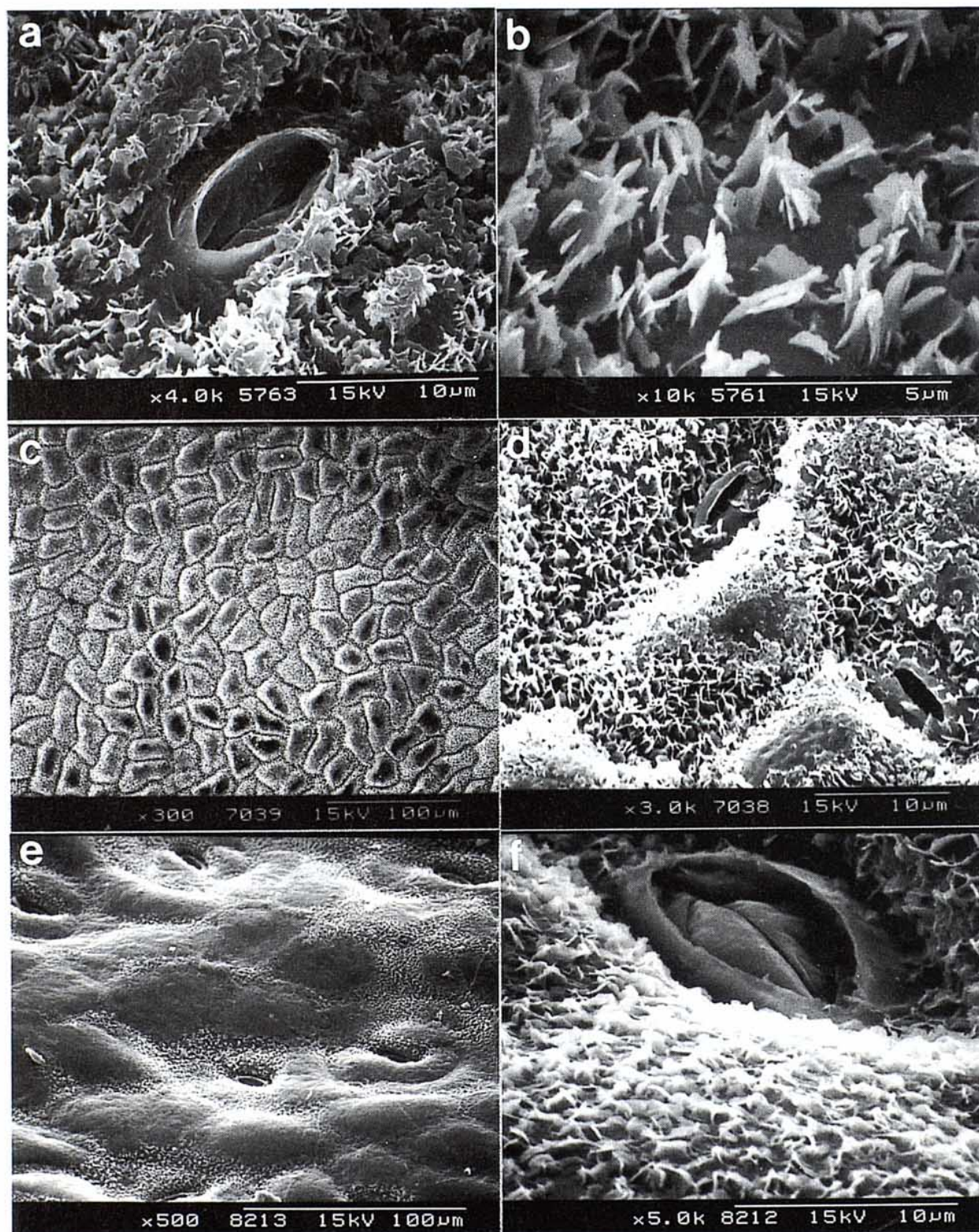


Fig. 4 – SEM micrographs of the cuticular surface of European taxa of *Euphorbia* subsect. *Esula*. *E. cyparissias* L. (Hs, Panticosa, SALA 22595): a) adaxial surface, x 400; b) abaxial surface, detail of wax type, x 10.000. *E. esula* L. subsp. *esula* (Hs, Ferradillo, LEB 33074): c) adaxial surface, x 3000; d) abaxial surface, stomata and detail of wax type, x 2000. *E. esula* L. subsp. *tommasiniana* (Bertol) Kuzmanov (It, Mt. Spaccatto, BC 57218): e) adaxial surface, x 500; f) abaxial surface, x 5000.

E. esula subsp. *esula* has showed itself to be constantly hypostomatic, with the exception of one hypoamphistomatic population in the Sierra Nevada (P 6) growing at an altitude of 3000 m in territory close to that of *E. nevadensis* subsp. *nevadensis*. This might be accounted for by a hybridogenous-type introgression of *E. nevadensis* into *E. esula*.

The European populations which can be attributed to subsp. *orientalis*, including the closely related taxa subsp. *tommasiniana* and *E. graminifolia*, present a common epiamphistomatic mode. This uniformity of behaviour affecting populations over such an extensive area confirms the relevancy of this character. However, further research is required before any definitive statement can be made.

Studies using the SEM

About 200 microphotographs were studied, a selection of which are presented in Figures 4, 5 and 6.

The *cell shape* is uniform for all the taxa studied and does not differ substantially from that presented by the leaves of most dicotyledons.

Primary sculpture. Irregular polygonal cells with 3-6 (7) sides, isodiametric or elongated. Cell boundary slightly excavated into a channel. Convex periclinal walls (Figure 4,c; Figure 5,g).

Stomata epidermic (superficial or slightly sunken) in *E. cyparissias*, *E. esula* s.l. (Figure 4,d), and *E. nevadensis* subsp. *aragonensis*. Stomata subepidermic (buried under the cuticle) in *E. graminifolia* (Figure 5: g,h), *E. nevadensis* subsp. *nevadensis* and *E. nevadensis* subsp. *bolosii* (Figure 6,q). Shape of the external stomatal apparatus, between elliptical and elliptical-oblong or subcircular. Outer stomatal rim raised. Stomatal poles generally subobtuse (Figure 4: a,f) or rounded (Figure 6,q). Pores elongated.

Secondary sculpture. Cell walls smooth, without cuticular folding. Absence of papillae and trichomes.

Tertiary sculpture. All taxa studied present epicuticular waxes. From the study of the samples, four models can be deduced. Discontinuous deposits made up of: 1) crystalloids of wax in the shape of irregular vertical platelets radially joined together in the form of a pyramidal star. This model of crystalloid is widespread in *Euphorbia* and *Chamaesyce* and can appear in other families (BARTHOLOTT, 1981: 350 illustrates this model in *Cercis siliquastrum*, *Leguminosae*). 2) small irregular horizontal platelets (Figure 4,b; Figure 6,n) which alternate with the crystalloids. 3) large horizontal platelets, larger and thicker than in model 2, which normally appear superimposed on the crystalloids (Figure 5,k). Continuous deposits, which correspond to a single model. 4) continuous layers of wax, uniformly distributed, with a smooth surface (Figure 6,r), finely micropapillate (Figure 5,h) or finely granular (Figure 6,q) which can appear indistinctly in the same taxon.

E. cyparissias and *E. esula* s.l. correspond to models 1 and 2: the crystalloids are more densely grouped together on the upper surface; the platelets are more frequent alongside the stomata. *E. graminifolia* belongs to type 4, with a smooth or micropapillate surface. *E. esula* subsp. *tommasiniana* (Figure 4:e,f) corresponds on both surfaces to a mixed model in which the large platelets occupy the greatest area. *E. nevadensis* subsp. *nevadensis* corresponds to model 3. *E. nevadensis* subsp. *aragonensis* (Figure 5,l) often presents models 1 or 2 but populations growing at high altitudes bear resemblances to model 3. *E. nevadensis* subsp. *bolosii* (Figure 6:q,r) corresponds to model 4.

There is a clear link between the type of wax deposit and certain characters such as the colour and shine of the leaf, as detected by the naked eye. Surfaces comprising only crystalloids and small platelets look dull, greyish green, subglaucous (*E. cyparissias*, *E. esula* s.l.). As the size and thickness of the smooth horizontal platelets increase, predominating over

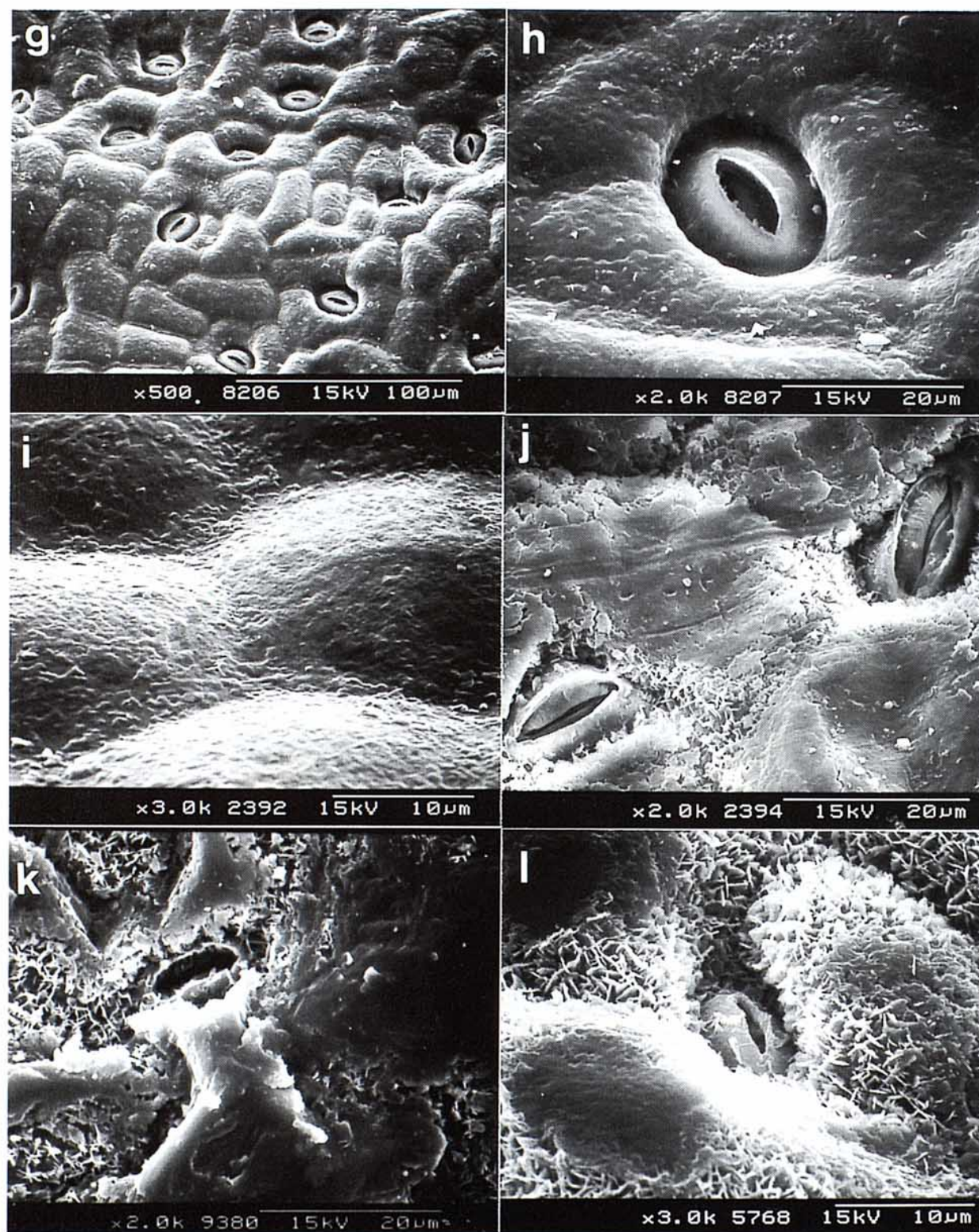


Fig. 5 — SEM micrographs of the cuticular surface of European taxa of *Euphorbia* subsect. *Esula* (continuation). *E. graminifolia* Vill. (Ga, Verquière, VI.1905, Delmas, MPU): g) adaxial surface, x 500; h) abaxial surface with a subepidermic stoma, x 2000. *E. lucida* Walds. & Kit. (Au, March, BC 649308): i) adaxial surface, x 3000; j) abaxial surface, x 2000. *E. nevadensis* Boiss. & Reuter subsp. *nevadensis* (Hs, Grado del Pico, SALA 34031): k) adaxial surface, x 2000; l) abaxial surface, x 3000).

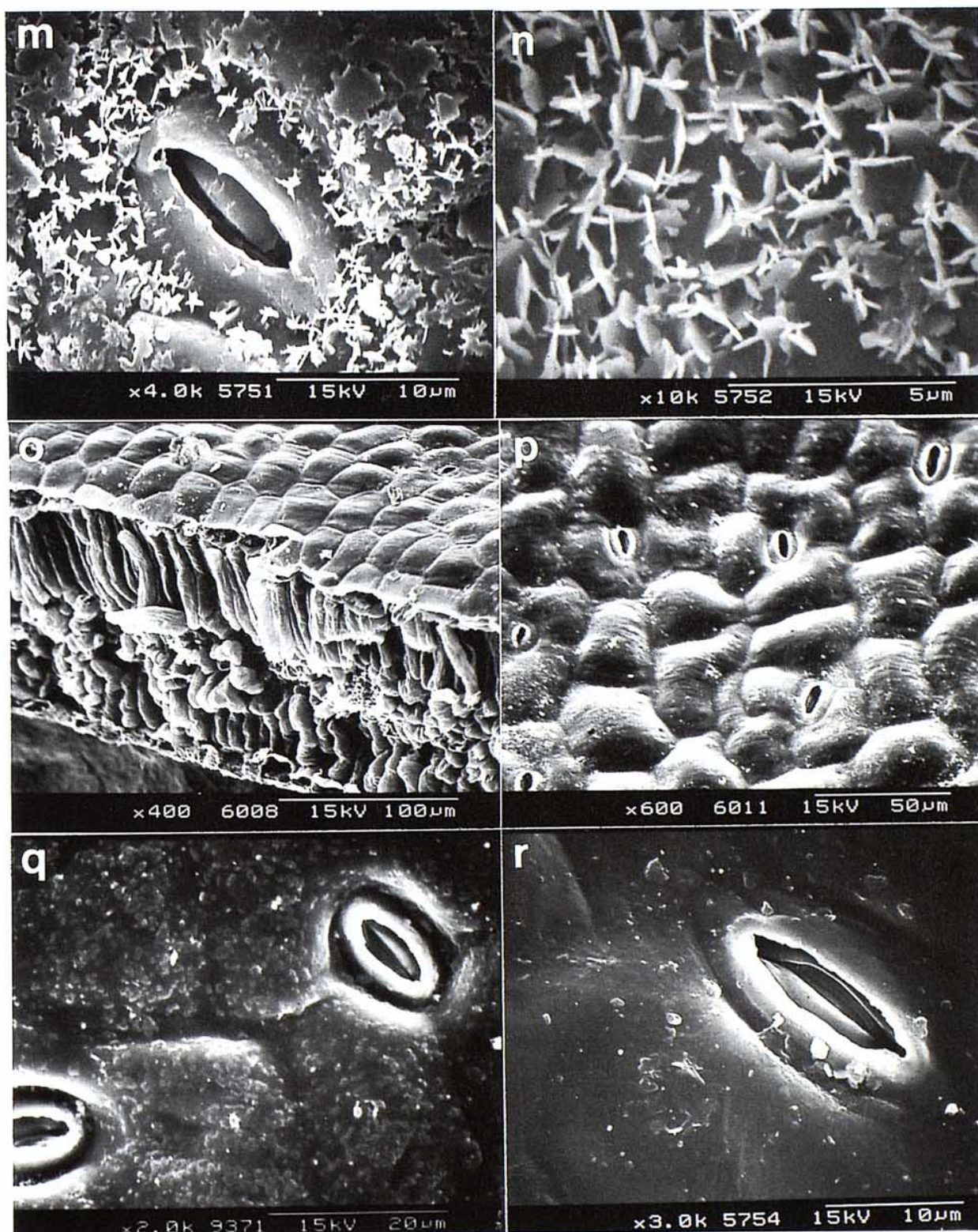


Fig. 6 – SEM micrographs of the cuticular surface of European taxa of *Euphorbia* subsect. *Esula* (continuation). *E. nevadensis* Boiss. & Reuter subsp. *aragonensis* (Loscos & Pardo) Bolòs & Vigo (Hs, Valverde, BCF 36893): m) adaxial surface, x 4000; n) abaxial surface, detail of wax type, x 10.000. *E. nevadensis* Boiss. & Reuter subsp. *bolosii* Molero & Rovira (Hs, Cornudella, BCF 111491): o) section of the leaf, x 400; p) adaxial surface, x 600; q) adaxial surface, x 2000; r) adaxial surface, x 3000 (Hs, Llaveria, BC 631227).

the crystalloids (model 3 and transition to model 4), the surface takes on a greyish green, more or less satiny look, corresponding to a glaucous appearance (*E. nevadensis* subsp. *nevadensis*). Surfaces with continuous deposits look satin-like or shiny, according to the thickness of the layer of wax (*E. lucida*, which has a thick layer, is clearly shiny, Figure 5:i,j) and their colour, which varies from yellowish green to dark green, is brighter, the range of greys disappearing (*E. graminifolia*, *E. esula* subsp. *tommasiniana*, *E. nevadensis* subsp. *bolosii*).

Many present-day authors (BARTHOLOTT, 1981; CURLER & BRANDHAM, 1977) accept the notion that the morphology of the waxes is under genetic control. Nevertheless, in many species the configuration, size and distribution of crystalline waxes can be significantly altered by environmental conditions (HALLAM, 1970; BAKER, 1974).

THOMAS & BARBER (1974) suggest that glaucous surfaces increase light reflection and thus constitute a selective advantage for plants in alpine climates. For our part, we have observed that glaucous appearance is common to populations of *E. nevadensis* subsp. *nevadensis* growing at high altitudes but that it does not occur in populations of *E. esula* subsp. *esula* growing in the alpine belt of the Sierra Nevada.

Continuous wax deposits appear in taxa belonging to the group which are distributed over low mountains, are adapted to the Mediterranean climate, and live in open formations, exposed to direct solar radiation and warm temperatures (*E. nevadensis* subsp. *bolosii* and *E. graminifolia*). In such cases the structure of these deposits could be interpreted as a plastic response to the stimulation of certain environmental factors, such as long exposure to direct solar radiation and heat (BAKER, l.c.). However, observation that continuous, finer deposits are also present in some specimens which grow in the shade leads us to assume that this character is under genetic control. Moreover, it is constant in other species of the group, such as *E. lucida*, which normally lives in nemoral and not Mediterranean environments. In this species, the shiny adaxial surface (indicative of continuous wax deposits) is a character used diagnostically to distinguish it from other closely related species.

There is widespread controversy at present over the use of waxes for taxonomical purposes. We agree with BARTHOLOTT (l.c.) that it is a character which can be used when its constancy has been demonstrated and that it can be useful, not only when applied to the taxonomy of large genera like *Eucalyptus* (HALLAN & CHAMBERS, l.c.), but also at lower taxonomical levels such as that with which we are concerned.

In accordance with these observations, the continuous wax deposits present in *E. graminifolia* constitute one of the characters which prevents us from assimilating this taxon to *E. esula* subsp. *orientalis*. In the *E. nevadensis* complex, this character can be used diagnostically to separate subsp. *bolosii* from the remaining subspecies.

CONCLUSIONS

The variation of cuticular microcharacters is to a large extent the reflection of the stability or instability of macrocharacters transferred to another level of observation. They do however open the way to the discovery of new distinctive traits for separating closely related taxa in cases where traditional characters do not prove particularly useful. Ascertaining to what extent they are genetically determined or correspond to phenotypic variations related to environmental factors or geographical distribution is quite another matter. It seems clear that in many cases the variation of some of these microcharacters reflects stable adaptations to particular conditions in the habitat of the taxon in question (especially microclimatic conditions or those related to geographical distribution). In our opinion, these morphological differences must be assessed taxonomically at the level which corresponds to them, normally the infraspecific level.

Cuticular characters can be used to distinguish between the taxa recognized in this study. However they are especially useful for providing arguments for differentiating between very closely related taxa. The clearest example is the recognition of two entities within *E. esula*. Subsp. *orientalis* can be separated from subsp. *esula* by its epiamphistomatic leaves, its SI ratio of 1, its smaller anisocytic stomata, its higher cell and stomatal frequency and the presence of straight or only slightly undulating anticlinal walls. Caution is required in drawing conclusions about the relationship between subsp. *orientalis*, subsp. *tommasiniana* and *E. graminifolia*, since only a small sample of the latter was used, though it is also true that its geographical distribution area is very restricted. Generally speaking, these two taxa are very akin to subsp. *orientalis*, but they differ from the latter and between themselves with respect to certain characters. *E. graminifolia* has anomocytic stomata and a low stomatal index, while *E. esula* subsp. *tommasiniana* has a low cell and stomatal frequency and the stomata are larger. Wax deposit types are another distinguishing trait between the three taxa, though in this respect *E. esula* subsp. *tommasiniana* has greater affinities with *E. graminifolia*.

Within the *E. nevadensis* complex, the sharpest contrast is between subsp. *nevadensis* and subsp. *bolosii*. The former is more stable, presents regularly distributed stomata on the adaxial surface, a higher SI ratio, larger cell and stomatal frequencies, non-undulating anticlinal walls and non-continuous wax deposits. The latter is more unstable, has irregularly distributed stomata on the adaxial surface, low cell and stomatal frequencies, larger stomata, usually undulating anticlinal walls, and continuous wax deposits. Subsp. *aragonensis* reveals intermediate characters but is closer to subsp. *bolosii*.

It seems clear that the instability of the characters shown by these two latter taxa is due to the process of microevolution which the stirps has undergone in its northermost area owing to a process of adaptative radiation accentuated by changes in the substratum (limestone versus granite) and the gradual increase in microclimate variation towards the northwest.

CHROMOSOME NUMBERS

MATERIALS AND METHODS

The materials used were root meristems obtained from plants transplanted into the greenhouse from wild populations, and flower buds fixed directly in the field. We excluded the study of root meristems from seed, owing to the very low rate of germination presented by all the taxa studied.

The roots obtained from live plants were first treated with a solution of 0.002 M/l of 8-hydroxyquinoline (TJIO & LEVAN 1950) for 6 hours at 3-6 °C. Then, they were fixed in Farmer's reagent (absolute ethyl alcohol and glacial acetic acid, 3:1) for 24 hours. Mitotic plaques were obtained by crushing. The flower buds were fixed in situ using Farmer's reagent for a minimum of two hours; they were dyed with 2% acetic carmine 24 hours, and subsequently crushed and mounted. The vouchers, duly numbered, are conserved in the BCF herbarium.

RESULTS

The result of the chromosome counts are given in Table 3. The photographs and drawings of the mitotic plaques are presented in Figure 7.

The chromosomes of the taxa studied in mitosis are small, between 1-3 (6) µm. The centromeric position can rarely be clearly observed, especially in the ovaric metaphases. For

Table 3. — Chromosome number of the studied taxa of *Euphorfia* subsect. *Esula*.
Mat.: material origin; fb: flowering buds; rm: root meristems.

Taxa	Vouchers	Mat.	2n	Figure
<i>E. cyparissias</i> L.	<i>Barcelona</i> : Montseny, Campins, 31TDG51, schist, 460 m, 12.IV.1991, J. Vicens, BCF 36898.	fb	20	4,11
	<i>Girona</i> : Alta Garrotxa, pr. Sta. Pau, 31TDG66, granitic areas, 450 m, 21.IV.1991, J. Simón, BCF 36899.	fb	20	4,10
<i>E. esula</i> L.	<i>Huesca</i> : Sierra de Aracena, among Aracena and Castelazar, 29SQB09, schist, 430 m, 19.V.1990, Blanché & Vicens, BCF 36701.	rm	20	4,1
	<i>Leon</i> : Ferradillo, 29TPH90, 1250 m, 11.VII.1989, Andres & Llamas, BCF 36982.	fb	20	—
	<i>Granada</i> : Sierra Nevada, Prados de Otero, 30SVG60, schists, 2400 m, 16.VI.1990, Molero Mesa, BCF 36891.	fb	20	4,5
<i>E. nevadensis</i> Boiss & Reuter subsp. <i>nevadensis</i>	<i>Avila</i> : Hoyocasero, pr. Navalvillar, Cueva del Maragato 30TVQ27, granitic sands, 450 m, 20.VI.89, Molero & Rovira, BCF 35128.	fb	20	4,9
	<i>Granada</i> : Sierra Nevada, near of Refugio Universitario, 30SVG60, schists, 2650 m, 11.VI.1991, J. Molero, BCF.	fb	20	4,8
	<i>Zaragoza</i> : Moncayo, Peñas de Herrera, 30TXM02, calcareous scree, 1450 m, 28.V.1990, Molero & Rovira, BCF 35125.	rm	40	4,7
subsp. <i>aragonensis</i> (Loscos & Pardo) Bolòs & Vigo.	<i>Burgos</i> : Miranda de Ebro, montes de Valverde, 30TWN02, on limestone, 600 m, 27.V.1990, Molero, Rovira & Vallés, BCF 36893.	fb	20	4,4
subsp. <i>bolosii</i> Molero & Rovira	<i>Tarragona</i> : Montsant, Albarca, 31TCF27, marly soil, 740 m, 20.IV.1991, J. Molero, BCF 36894.	fb	20	4,2
	<i>Tarragona</i> : Ports d'Horta, Les Heres, 31TBF73, limestones, 700 m, 12.VI.1990, Molero & Rovira, BCF 71739.	fb	20	4,6
	<i>Huesca</i> : Jaca, Pto. Oroel, 31TYN01, stony marls, 1200 m, 15.IV.1991, J. Molero & al., BCF 35127.	rm	60	4,3

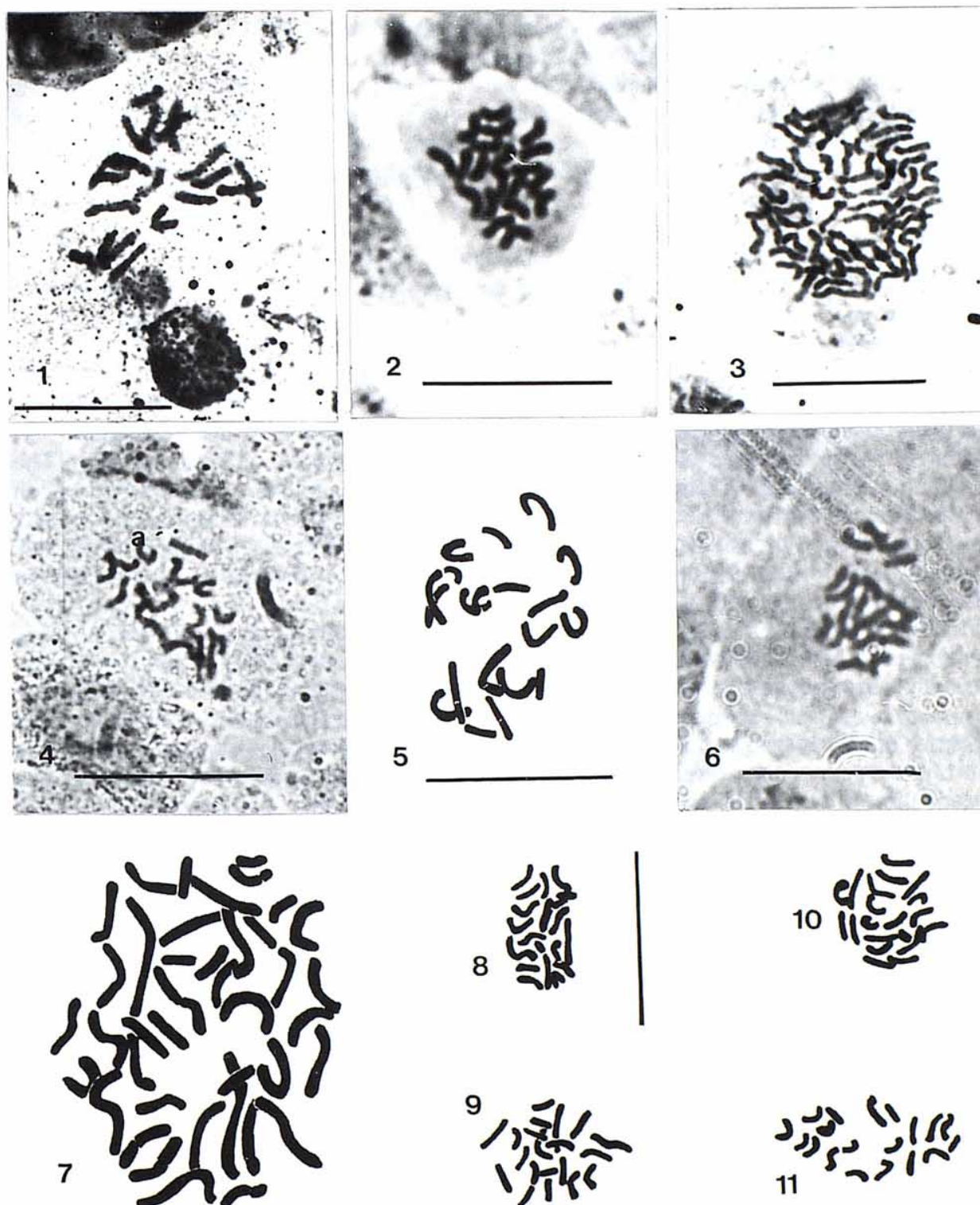


Fig. 7 — Somatic metaphases of Iberian taxa of *Euphorbia* subsect. *Esula*. 1) *E. esula* subsp. *esula*, $2n=20$ (Hu: Srta. de Aracena, BCF 36701). 2) *E. nevadensis* subsp. *bolosii*, $2n=20$ (T: Albarca, BCF 36894). 3) Id., $2n=60$ (Hu: Oroel, BCF 351271). 4) *E. nevadensis* subsp. *aragonensis*, $2n=20$ (Bu: Valverde, BCF 36893). 5) *E. esula* subsp. *esula*, $2n=20$ (Gr: Srta. Nevada, BCF 36891). 6) *E. nevadensis* subsp. *bolosii*, $2n=20$ (T: Ports d'Horta, BCF 71739). 7) *E. nevadensis* subsp. *nevadensis*, $2n=40$ (Z: Peñas de Herrera, BCF 35125). 8) Id., $2n=20$ (Gr.: Srta. Nevada, BCF 35197). 9) Id., $2n=20$ (Av: Hoyocasero, BCF 35128). 10) *E. cyparissias*, $2n=20$ (Ge: Sta. Pau, BCF 36899). 11) Id., $2n=20$ (B: Campins, BCF 36898).

reasons we are unable to explain, the chromosomes are seen to be relatively larger in metaphases from root meristems than in metaphases from ovaric walls. Sometimes these differences are very visible, as in tetraploid populations of *E. nevadensis* subsp. *nevadensis* from El Moncayo, where the relative size of the chromosomes is greater than in the remaining diploid populations. Similar evidence has come to light in the study of other groups of *Euphorbia* in the western Mediterranean, such as the complexes «*E. verrucosa*» (J. Simón, pers. comm.) and «*E. squamigera*» (J. Vicens, pers. comm.).

DISCUSSION

E. cyparissias L.

In the two Iberian populations studied, only the diploid level was detected, $2n=20$. In Europe both the diploid cytotype (RUTLAND, 1941; PERRY, 1943; PRITCHARD, 1958; SHIMOYAMA, 1959; GADELLA & KLIPHUIS, 1966; KLIPHUIS & WIEFFERING, 1972; LÖVE & LÖVE, 1974) and the tetraploid cytotype (PRITCHARD, 1958; STRID & ANDERSON, 1985) are present. The number $2n=36$ quoted by ZHUZOVA, 1967, for plants in Siberia must be viewed with caution since it has never since been reported by any other author. In the United States and Canada, the tetraploid cytotype seems clearly predominant (MOORE & RANKTON, 1969; MOORE & LINDSAY, 1953; MOORE, 1958; STAHEVITCH & al., l.c.) over the much rarer diploid cytotype (MOORE & LINDSAY, l.c.; STAHEVITCH & al., l.c.).

STAHEVITCH & al., l.c., indicate that in Canada the diploid race is sterile on account of the irregular genesis of its pollen and despite the fact that meiosis takes place without anomalies. Normally vegetative propagation by stolons functions well in this diploid race, and for this reason it is used for ornamental purposes in cemeteries. They also point out that the two chromosomic races tend to be distinct in terms of micromorphology, geography and altitude. The diploid cytotype has small leaf cells, lives at low altitudes close to the sea, and its reproduction is basically vegetative, whereas the tetraploid cytotype has larger cells, tends to be found at higher altitudes and more northern latitudes, and presents a reproductive strategy with effective pollinization and viable crossing.

In our case, the two populations studied grow at low altitudes and relatively close to the sea. Nonetheless, the correlation between cell size and degree of ploidy seems to be maintained. It should be remembered that the three Iberian populations studied have small cells in comparison with the two European populations (Table 1) whose cells are double the size. It would have been interesting to carry out karyological research on these European populations, which are probably tetraploid. From the small amount of data available, we can only indicate that the diploid race is present in the Iberian Peninsula. If the correlation between cell size and ploidy is confirmed, we can also state that the diploid race is very widespread.

E. esula L.

The Iberian populations examined in this study correspond exclusively to the diploid cytotype, $2n=20$. Various chromosome numbers have been indicated for the polymorphic *E. esula*. The commonest, $2n=60$, which corresponds to a hexaploid with a base of $x=10$, has been reported both from Europe (GADELLA & KLIPHUIS, 1966, 1968; PRITCHARD, 1959; STAHEVITCH & al., l.c.) and from the northern regions of the United States and Canada (MOORE, l.c.; MULLIGAN, 1961; STAHEVITCH et al., l.c.). Other basic numbers - $x=8,9$ - have been reported for Europe. LONG & DE JONG (1978) found $2n=16$ in plants from France but CROMPTON & al. (l.c.: 1983) analyzed the herbarium evidence of this count and according to them the material belongs to *E. segetalis*, which presents this same somatic number.

The somatic number $2n=64$ has been reported in connection with European materials by REESE 1952 in HANS 1973, SHIMOYAMA, 1958, and GADELLA & KIPHUIS, 1968; HURUSAWA & SHIMOYAMA, 1976 report $2n=56$ in the *E. esula* s.l. complex for individuals with narrow leaves and $2n=64$ for individuals with wide leaves; CROMPTON & al. (l.c.) stated that they were unable to gain access to any of the herbarium evidence of the latter authors with a view to corroborating their findings. It is important to ascertain once and for all whether this number can be attributed to *E. esula*, especially after the study of the abundant material belonging to this species carried out by STAHEVITCH & al. (l.c.) in the United States and Canada, which yielded only the gametic number $n=30$.

BAKSAY (1958) found $2n=20$ in Hungarian populations attributed to *E. esula* subsp. *tommasiniana*. KRAHULCOVA (1991) reported $2n=20$ for materials from Moravia indentified as *Tithymalus virgultosus* (Klokov) Holub (= *E. esula* subsp. *orientalis*). The same study reproduces various other counts, such as that done by Majovsky, Murin & al. who found $2n=20$ for materials from Slovakia and another by Goldblatt (1985) which gives $2n=20$ for plants from Byelorussia.

The finding of only the diploid cytotype in the Iberian Peninsula raises questions which call for comment. It seems obvious that in *E. esula* a polyploid series with a base of $x=10$ has been differentiated whereas up to now the diploid and hexaploid levels had been detected. Cytogenetic research into this species in its western area (Central and Western Europe and North America) is sufficiently representative, but the same is not true of the area considered the speciation centre of the subsection: the countries of Eastern Europe and Central West Asia. Further search in these areas may well yield surprising results in the localization of new diploid or tetraploid cytotypes. In the light of the present results, it seems difficult to maintain the hypothesis of the halopolyploid origin of this species (STAHEVITCH & al., l.c., on the basis of the pollinic polymorphism detected in the American populations). Though Iberian populations subjected to palinological study (J. Martín, pers. comm.) reveal a wide degree of intrapopulation variation in their measurements, they do not differ substantially from one another. A more logical explanation would seem to be an autopolyploid process which has given rise to a cytotype with an invading capacity in the area with the most favourable climate. Indeed, it is in the territory where these populations are considered to have been introduced (northwestern Europe and North America) that conditions of mesophism and hygrophism are encountered which permit better propagation of the hexaploid cytotype in meadows and damp pastures, thus causing harm to cattle and agriculture.

On the other hand, the populations in the Iberian Peninsula are few in number, stable, and enclosed in fresh, moist enclaves of Eurosiberian vegetation surrounded by the mediterranean region. Here the subsection owes its survival to its adaptation to specialized environments which have enabled it to survive but not to evolve.

The primary speciation centre of subsection *Esula* must be situated, in principle, in the area where it displays greatest diversity: west-central Asia (KUZMANOV, 1964: l.c.). The ancestors of its present western Mediterranean representatives must have reached the Iberian Peninsula at the end of the Pliocene, when a general cooling of the climate occurred (THUNELL, 1979), or else during periods of the Pleistocene which were dominated by glaciations. It is more difficult to attempt to attribute it to a more ancient colonization taking place during the Miocene, since at the time North Africa was joined to the Iberian Peninsula (GALLAND, 1988) and in the middle Atlas there were conditions highly favourable to the penetration and establishment of this species, which in the Iberian Peninsula has spread to positions as far south as the Sierra Nevada and Sierra de Aracena.

E. nevadensis Boiss. & Reuter.

There are no previous karyological data on this Iberian endemic species. In it a polyploid

complex with a base of $x=10$ has been detected for the first time in which the diploid cytotype $2n=20$ is much more frequent than the tetraploid $2n=40$ or the hexaploid $2n=60$.

In this complex, cytogenetic differentiation has followed its own course, independent of the morphological differentiation which gave rise to the present subspecies.

On account of its morphological stability, ecology and distribution, subspecies *nevadensis* constitutes the genuine primitive stirps. The populations in the Sierra Nevada and Central System, which are silicolous and high montane, have proved diploid. The calcicolous population from El Moncayo, on the other hand, is tetraploid and has not given rise to significant morphological differences, even at the level of pollen size.

The only population of subsp. *aragonensis* studied, from the Montes de Valverde (Burgos), is calcicolous and has been found to be diploid.

Subsp. *bolosii* has given rise to a differentiated diploid cytotype in the calcicolous low-mountain populations from the pre-coastal Catalan ranges of Montsant and Els Ports. The pre-Pyrenean population of Oroel has been found to be hexaploid. This polyploidy presents certain differential traits at micromorphological level: larger epidermic cells and stomata, slightly larger pollen, and generally somewhat larger capsules and seeds, though the differences remain within the margins of variability of the species. In this study we have not sought to attribute any taxonomic rank to this variation, since in our opinion it is not of sufficient significance.

The complex *E. nevadensis* can be considered neopolyploid (sensu FAVERGER, 1961) and probably originated from recent autopolyploidy. It is a morphologically and cytogenetically stable stirps in the southern part of its distribution area (Betic ranges and Central System). It has been affected by a process of microevolution in its northern area, in the mountains that border on the Ebro basin, where the phenomena of polyploidy and morphological differentiation converge, though without apparent signs of correlation. Microspeciation in this case is oriented in a S - NE direction and has coincided with more recent colonization of limestone substrata at lower altitudes.

CONCLUSIONS

The chromosome numbers of the taxa belonging to subsection *Esula* represented in the Iberian Peninsula are of no taxonomical use in separating the various species and subspecies. The cytogenetic evolution of these stirps is not directly correlated to morphological diversity. The cytogenetic data contributed in this study, together with others that are already known, make it possible to put forward certain evolutionary and biohistorical hypotheses.

TAXONOMIC TREATMENT

MATERIALS AND METHODS

For the taxonomical study we consulted materials deposited in the following herbaria, whose names are abbreviated in accordance with the acronyms specified by HOLMGREN, HOLMGREN & BARNETT (l.c.): AV, BC, BCC, BCF, BM, COI, FI, G, GDA, GR, JACA, JAEN, LEB, LISE, LISU, LOU, MA, MAF, MGC, MPU, MUB, SALA, SALAF. These observations were complemented by the study of certain characters of live plants from the wild, transplanted to the experimental garden of the Faculty of Pharmacy in Barcelona.

In the descriptive section, we list for each taxon: the correct name, synonyms (exclusively homonyms and synonyms used by authors who have studied Iberian materials; the extensive

study by OUDEJANS, l.c., will enable any reader who so wishes to complete the synonymy at a more general level), typification, description, overall distribution, distribution in the Iberian Peninsula (the provincial administrative units of Spain and Portugal are abbreviated according to CASTROVIEJO & al., 1986) and ecology.

For morphological terminology we basically follow the criteria established by STEARN (1983) and FONT QUER (1953). The cataloguing of flat forms is adjusted to the outline proposed by the Systematics Association Committee for Descriptive Biological Terminology 1962 (abbreviated in this study to SA). The colour of certain organs (leaves and seeds) is sometimes specified according to the chromatic code defined by KORNERUP & WANSCHER, 1978.

Observation of the cyathia and capsules under the SEM required treatment of the samples as specified under the heading «materials and methods» in the section on Leaf Surface. The seeds were metallized directly with gold, without any prior treatment. The terminology used in this section is that of EHLE (1975) and BARTHOLOTT (1981).

TAXONOMIC CHARACTERS USED AND THEIR VARIABILITY

Indumentum

Except for the cyathium, none of the taxa included in this study have any indumentum.

Rhizome

This is a character which is difficult to define since it is usually lacking in the herbarium sheets. All the taxa with which this study is concerned present a highly developed horizontal or oblique rhizome, which is easily propagated by stolons (RAJU, 1985). The thinner and more ramified rhizomes are characteristic of *E. nevadensis*, and become more accentuated in subsp. *bolosii*. This character is used by KHAN (1964) to differentiate *E. virgata*, to which he attributes a vertical rhizome, from *E. esula*, with a horizontal rhizome. According to our observations, materials belonging to *E. virgata* from the eastern area (eastern Europe, Russia, Turkey) usually present a vertical rhizome, in contrast to materials belonging to *E. esula* from central and western Europe, which present a horizontal rhizome. However, materials of *E. virgata* from central and western Europe may present a horizontal, oblique or vertical rhizome indistinctly. This character is not constant throughout the distribution area of *E. virgata*.

Habit and ramification

The commonest forms of habit and branching found in Iberian taxa, along with their variability, are expressed graphically in Figure 8. The most complex forms occur in the northwestern populations of *E. esula* (Figure 8:f) while the simplest forms correspond to populations of *E. nevadensis* subsp. *nevadensis* growing at high altitudes (Figure 8:j,k) and to those of subsp. *bolosii* (Figure 8:s). This character proves so flexible under the effect of environmental factors and the age of the plant (RAJU, l.c.) that it rarely has taxonomical significance. However, it does define some trends that are of descriptive use. Thus the basal ramification is very pronounced (up to 15 stems) in *E. cyparissias* whereas the greatest simplicity (1 to 3 stems) is found in *E. nevadensis* subsp. *bolosii*. The number of sterile branches is usually high in *E. cyparissias* (Figure 8:e), while they are missing in *E. nevadensis* subsp. *bolosii*.

Cataphylles

Scariose, linear-triangular (*E. cyparissias*), triangular (*E. esula*) or ovate-triangular (*E. nevadensis*), light to dark brown in colour. There is a logical correlation between the shape of



Fig. 8 — Habit and ramification of Iberian taxa of *Euphorbia* subsect. *Esula*. a-d: *E. cyparissias*; a) B: St. Hipòlit, BC 57233; b) L: Flamisell, BC 99407; c) B: Moncada, BC 57253; d) L: Tossal de servi, BC 126688). e-h: *E. esula* subsp. *esula*; e) Le: Ferradillo, LEB 33074; f) Se: Cazalla de la Sierra, SEV 107099; g) Le: Redillueva, LEB 16547; h) Le: Riaño, SEV 14428). i: *E. esula* subsp. *orientalis* (Ge: Llers, BCF 75455). j-o: *E. nevadensis* subsp. *nevadensis*; j) Gr: Trevelez, GDA 6959; k) Gr: Mulhacén, MGC 21743; l) Av: Hoyocasero, MAF 121622; m) Av: Pto. Villatoro, GDA 9088; n) Av: Canencia, MAF 75430; o) Gr: Sra. de Baza, MAF 98280). p-s: *E. nevadensis* subsp. *bolosii*; p) T: Montanica, BC 11149; q) T: Montanica, BC 11149; r) T: Montanica, BC 11149; s) B: Manresa, BC 57227.

the cataphylles and the shape of the nearby cauline leaves: the longer and narrower the cataphylles, the longer and narrower the leaves.

Leaves

Devoid of stipules, alternate, pinnately veined, heteromorphic. In this study the following characters are analyzed: size, length-width ratio, shape, base, margin, apex, consistency, colour and shine. We also include some of the most significant micromorphological characters such as leaf type with reference to the distribution and type of stomata and type of wax deposit. Variations in leaf morphology are particularly significant in this subsection, in contrast to the uniformity of the reproductive organs: hence their usefulness in diagnostically differentiating between the various taxa. Other authors who have dealt with the taxonomy of this group were aware of this fact, among them RADCLIFFE-SMITH, 1985 and CROMPTON & al., l.c.

Figure 9 shows the variation in the leaves and bracts of the Iberian taxa on a rising scale. Concrete examples are given of the most widespread types.

The sterile branches usually present significantly narrower leaves than those of the main stem. In *E. cyparissias* this is a differential character of prime importance.

Some authors (CROMPTON & al., l.c.) have studied the width of the leaf scar on the stem. After a trial assessment, this supposed character was rejected on account of its low discriminating value.

Bracts

We use the term pleiochasial bracts to designate those arranged in a whorl at the base of the pleiochasium in the same number as the radii. Different authors have given them different names (e.g.: they were called umbellate leaves by VINDT, l.c.; involucral leaves by KHAN, 1964; ray leaves by SMITH & TUTIN, l.c.; bracts by VALDES, 1987; and so on). They normally differ only slightly from the nearby cauline leaves, though they are generally shorter and wider.

The dichasial bracts (called floral leaves by VINDT, l.c.; involucellar leaves by KHAN, l.c.; raylet leaves by SMITH & TUTIN, l.c.; bracteoles by VALDES, l.c., etc.), which are opposed and free, palmate, and are arranged on the nodes along the dichasial ramification.

Figure 9 illustrates the variability of the bracts in the different Iberian taxa. The most significant characters are: shape, length/width, base, margin and apex. There is also usually a direct relationship between the shape of the leaves and the bracts. In taxa with narrow or very narrow leaves, the length of the bracts is usually equal to or greater than their width: in taxa with wide leaves, the width of the bracts is usually equal to or greater than their length. The bracts however are of little taxonomical value.

Synflorescence

According to WEBERLING (1989), the synflorescence is the fertile part of the plant which comprises the fertile lateral radii, the pleiochasium and the dichasial or dichotomous cymes (which are occasionally monochasial as a result of abortion). The shape of the synflorescence (Figure 8) varies between widely oblong (sometimes with a circular or semicircular cross section) as in *E. cyparissias* and *E. esula* subsp. *esula*, and narrowly oblong as in *E. esula* subsp. *orientalis*, s.l. *E. graminifolia* and *E. nevadensis*. Despite the stability of this character for each taxon, it can vary according to the age of the plant and the environmental conditions, so that its taxonomic value is low.

The term pleiochasium was proposed by Croizat and maintained by FONT QUER (l.c.); it designates the pseudoumbella formed by the radii which originate in the axils of the pleiochasial bracts. The variation in the number of pleiochasial radii is a character habitually used in Floras and monographs, which is of use here in distinguishing between certain taxa. Thus in *E.*

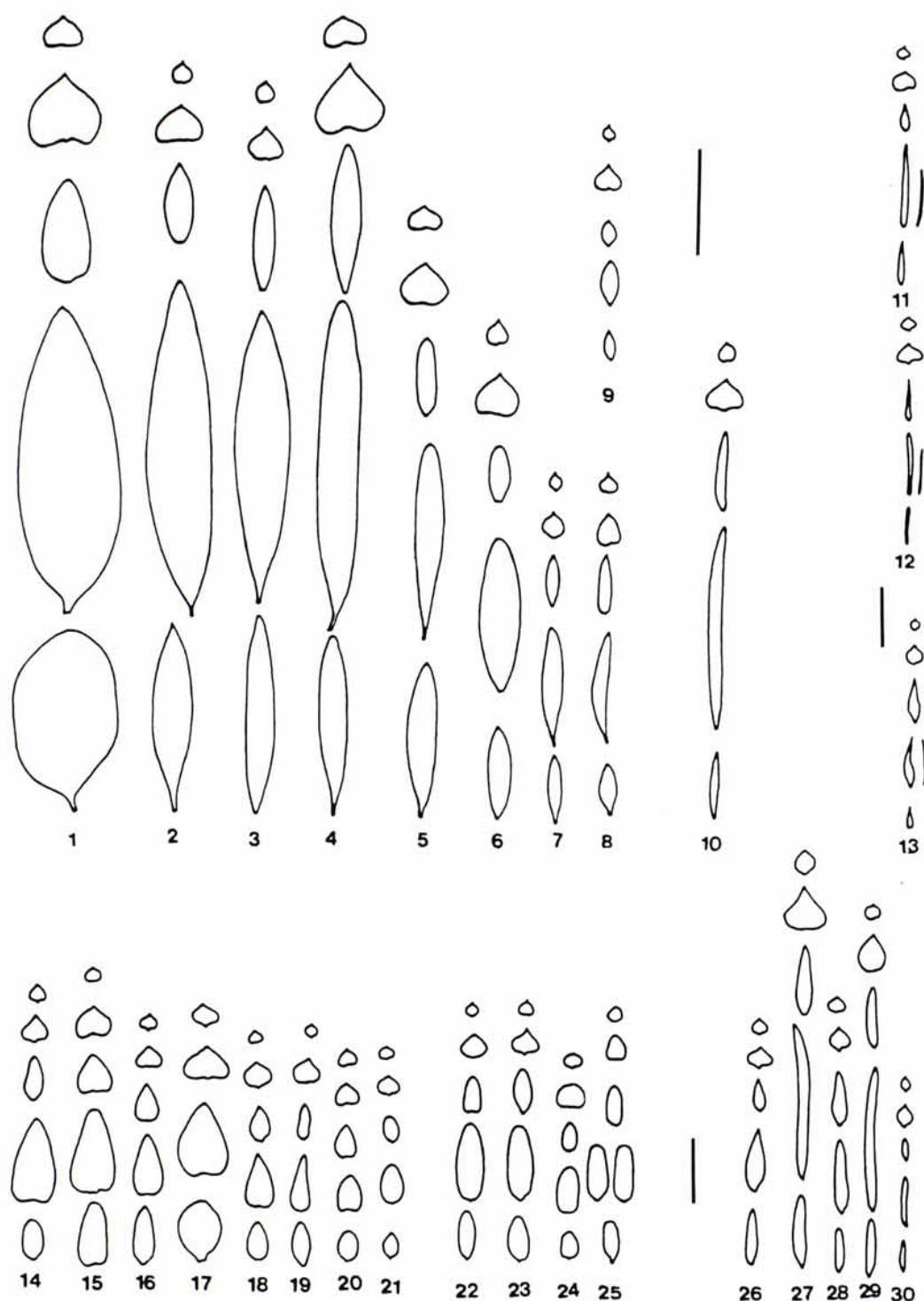


Fig. 9 — Morphological variations of the ascending leaf gradient (basal leaf, leaf from the top of the stem, pleiochasial bract, first dichasial bract, last dichasial bract) from Iberian taxa of *Euphorbia* subsect. *Esula*. 1-9: *E. esula* subsp. *esula* (1: Hu, Castelazar, BC 36701; 2: Hu, Srra. de Aracena, SEV 47002; 3: Lu, Odemira, MA 75457; 4: Gr, Monachil, SEV 55651; 5: Za, Moral de Sayago, SALA 32642; 6: Le, Ferradillo, LEB 33074; 7: Le, Mtes. Aquilianos, MA 317290; 8: Gr, Srra. Nevada, MA 250394; 9: Le, Redillueva, LEB 16547. 10: *E. esula* subsp. *orientalis* (Ge, Llers, MA 75455). 11-13: *E. cyparissias* (11: B, St. Martí de Provençals, BC 101956; 12: B, Maçanes, MA 344267; 13: Hu, Panticosa, JACA 201480). 14-21: *E. nevadensis* subsp. *nevadensis* (14: Gr, Dornajo, MAF 88869; 15: A, Aitana, BC 99287; 16: Av, Hoyocasero, MAF 121622; 17: Av, Pto. de Villatoro, MA 213640; 18: Z, Peñas de Herrera, BCF 35125; 19: Av, El Hornillo, MAF 121623; 20: Gr, Mulhacen, MGC 21743; 21: Gr, Trevelez, GDA 6959). 22-25: *E. nevadensis* subsp. *aragonensis* (22: Vi, Lagran, JACA 469073; 23: Na, La Población, JACA 484373; 24: Bu, Valverde, MA 75053; 25: T, Mte. Caro, MA 75452). 26-30: *E. nevadensis* subsp. *bolosii* (26: Hu, Oroel, JACA 426271; 27: Hu, Guara, JACA 3916; 28: Te, Toza de Peñarroya, MA 75453; 29: T, Montsant, BC 103280; 30: T, Cornudella, BCF 111491). Scale bar: 10 mm.

cyparissias the radii are usually numerous (15-20) while in *E. nevadensis* they are few in number (up to 9) and in *E. graminifolia* there is a maximum of 6.

Cyathium

The cyathium is of decisive importance in *Euphorbia* in that it supplies basic characters for delimiting taxa at various levels. However, except for the lunate glands, which sometimes provide grounds for differentiation at specific level, the use of the cyathial characters is more appropriate at supraspecific level (sections or subsections). Within this subsection, the variability of the cyathium is rarely fixed at specific level, though some characters show concrete tendencies which can be used in taxonomy.

The exocyathium. This term refers to the outer receptacle of the inflorescence, formed by the lateral union of the five bracts of the male cincinni, which is raised on a short peduncle measuring 0.3-2 mm. On the upper margin of this cup-shaped involucre, the lobes alternate with 4 or 5 nectariferous lunate glands (Figure 11,a). Neither shape, size nor colour (green, yellowish-reddish, according to the degree of maturity) have discriminating value.

With respect to the indumentum, some specimens of *E. esula* subsp. *esula* from the Sierra de Aracena and Portugal have unicellular hairs of c. 0.4 mm scattered over the outer surface of the exocyathium and extending as far as the peduncle. However, this is not a constant character and may be either present or absent in different populations in the same locality. The margin is always ciliate and an indumentum made up of unicellular hyaline hairs covers the inner margin and descends along the sutures on the inner surface below the lunate glands as far as the base. The density of this indumentum varies: for instance, it can be densely pubescent or sericeous in some western populations of *E. esula* subsp. *esula* (Sierra de Aracena, Odemira, etc.) or glabrescent in some eastern populations of *E. nevadensis* subsp. *bolosii* (precoastal Catalan ranges).

The glands or nectaries, which number 4, or occasionally 5, are yellowish-green, yellowish or reddish when mature. Their shape can vary within the same taxon, as happens in *E. esula* and *E. nevadensis*, this variation not being correlated to other morphological characters. Their shape is semicircular, truncate or emarginate, with small horns bearing a sharp point or, less frequently, broadened and lobulate. More rarely they can be subtruncate, oblate, or pectinate. The leaf surface displays a characteristic secondary sculpture, which is rugose and labyrinth-shaped, and narrow secretory pores, typical of *Euphorbia* subgen. *Esula* (Figure 11:b,c).

The exocyathial margin has 5 (4) lobules which alternate with the glands and are up to twice as long as wide, widely obtuse, truncate or emarginate, and ciliate-lash-like. Their variability, which is often more marked between populations belonging to the same taxon than between separate taxa, prevents their taxonomical use.

Male flowers. Grouped together in 4-5 cincinnoid inflorescences. The number of flowers (stamens) ranges from 3 to 8 per inflorescence and is higher in *E. esula* and *E. cyparissias*. In the mature flower, the staminal peduncle stretches slightly beyond the exocyathial margin; the staminal pedicel usually reaches half way along the peduncle; the anthers are ovoid and dorsifixed.

Intracyathial septa. Inside the cyathium, the groups of male flowers are separated by 5 intracyathial septa arranged radially, next to the bottom of the staminal peduncles. Very close to the base, these septa are divided into lacinate, ciliate or pubescent scales; these lacinations must not be confused with the true bracts of the male flowers, such as those which appear in the genus *Chamaesyce* (see BENEDI & ORELL in this volume). The size of the scales and the extent of their division, as well as the density and location of the indumentum, constitute relatively stable characters which are of taxonomic use. Figure 10 illustrates the variability of the intracyathial scales in the taxa studied. *E. esula* subsp. *esula* (Figure 10:10-26) can be distinguished from subsp. *orientalis* (Figure 10:27-36) by the greater density and coverage of the indumentum of the septal scales. Within *E. nevadensis* too, subsp. *bolosii* (Figure

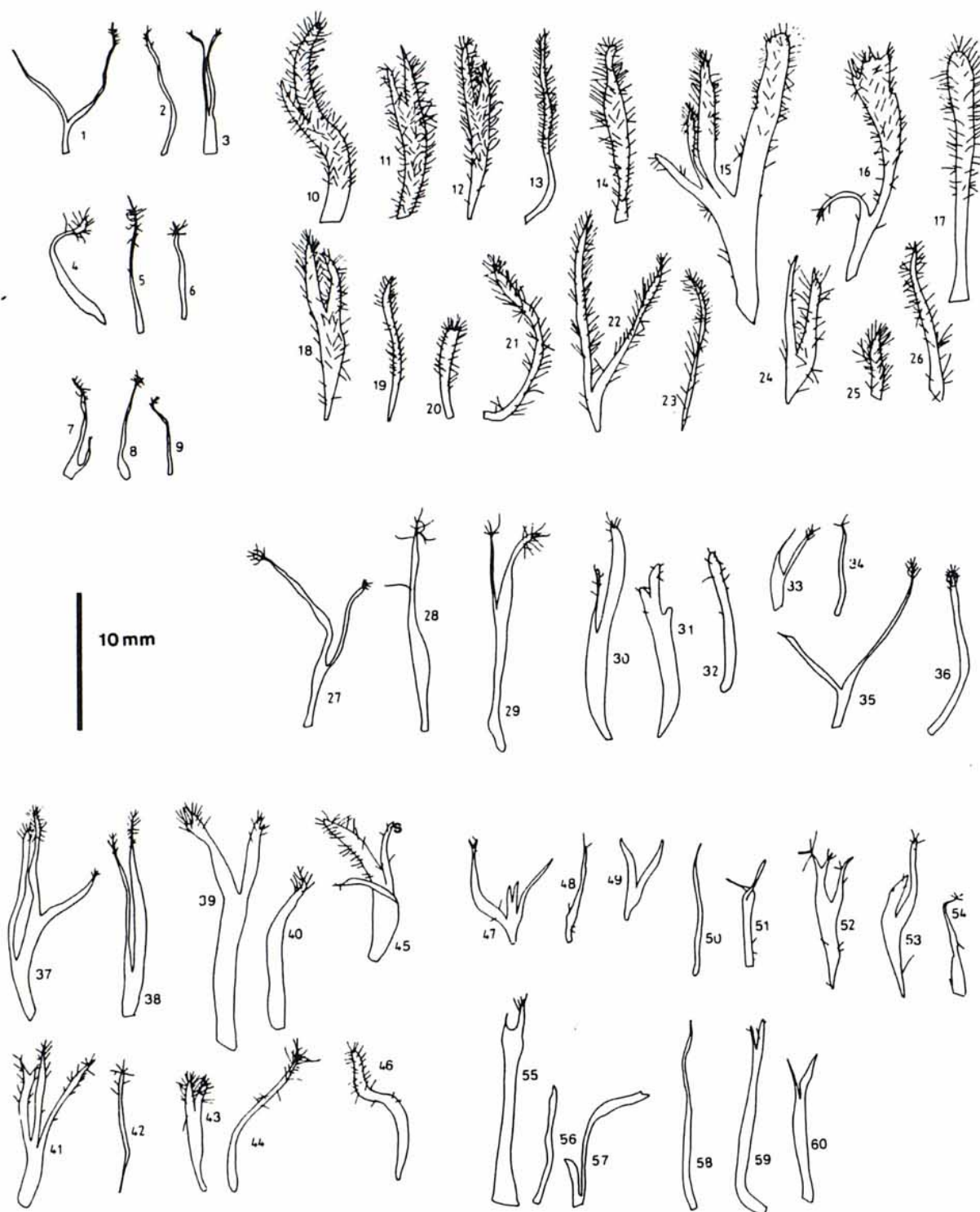


Fig. 10 — Intracyathial septal scales from taxa of *Euphorbia* subsect. *Esula*. 1-9: *E. cyparissias* (1-3: Hs, L, Srra. d'Aubens, BCF; 4-6: Au, Stain, BC 57239; 7-9: Hs, Hu, Panticosa, JACA 362667). 10-26: *E. esula* subsp. *esula* (10-11: Hs, Se, Cazalla de la Sierra, SEV 107099; 12-14: Hs, Le, Ferradillo, LEB 33074; 15-17: Hs, Gr, Sierra Nevada, SALAF 1124; 18-20: Lu, Odemira, MA 75457; 21-23: Hs, Gr, Sierra Nevada, río Monachil, SEV 55651; 24-26: Hs, Or, Ponferrada, MA 317290). 27-36: *E. esula* subsp. *orientalis* (27-29: Hs, Ge, Llers, MA 75455; 30-32: Be, Brugstraat, MA 381236; 33-34: Po, Niepolonice, MA 250395; 35-36: Ga, Vouziers, MA 276134). 37-46: *E. nevadensis* subsp. *nevadensis* (37-38: Hs, Gr, Srra. Nevada, Barranco de S. Juan, BCF; 39-40: Hs, Av, Hoyocasero, BCF 35128; 41-42: Hs, A, Serra d'Aitana, BC 99287; 43-44: Hs, Z, Moncayo, JACA 190188; 45-46: Hs, Bu, Valverde, BCF 36893). 47-60: *E. nevadensis* subsp. *bolosii* (47-49: Hs, T, Montsant, BC 103280; 50-51: Hs, Te, Peñarroya, MA 75453; 52-54: Hs, L, Organya, BC 99285; 55-57: Hs, Hu, Oroel, JACA 42627; 58-60: Hs, Na, Aoiz, JACA 249671).

10:55-60) can be distinguished from the remaining subspecies (Figure 10:37-54) by its simpler scales which have no, or only a few, cilia on the apex.

Pistillate flowers. In this subsection these do not provide characters of taxonomic value. The variability of the styles and stigmas must be studied in the mature capsule.

Capsules

The capsules are situated on peduncles which can attain 5 mm when mature. The shape of the longitudinal section varies from widely oval (SA 41) to widely oblong (SA 18,19), the latter being the most common type in *E. nevadensis*. On the back of the mericarps are hemispherical or subcylindrical emergences, often with stomata (Figure 11:d,e), which take on a granulated appearance at low levels of magnification. They are arranged in a strip occupying 1/4 to 1/2 the dorsal surface of the mericarp. Occasionally they can cover the entire surface (*E. cyparissias*), or be confined to a narrow strip usually taking up less than 1/4 of the surface of the mericarp (*E. nevadensis* subsp. *bolosii*). Generally speaking capsules with more rounded mericarps and more closed grooves are found in *E. cyparissias* and *E. esula*, whereas in *E. nevadensis*, the pericarps are narrower and the grooves more open.

The styles, which are 1-2.5 mm long and patent or erect patent, can be either free from the base or joined up to half their length, and are bifurcate at the apex forming two stigmatic lobules of variable length. In *E. cyparissias* the length of the styles is approximately 1 mm. In other taxa variations are observed both in the length of the styles and the extent to which they are united.

The size of the style is fairly uniform in all the taxa studied but with noteworthy variations between populations. It should be pointed out, however, that the smallest capsules occur in some populations of *E. esula* from northwestern Spain while the largest ones belong to some hexaploid populations of *E. nevadensis* subsp. *bolosii* (Peña Oroel). Often the capsule develops only one or two mericarps, as a result of the abortion of the rest.

The capsules do not provide good distinguishing characters for use in separating the taxa recognized in this study.

Seeds

Very similar in size and shape. Their morphological characters correspond to a common basic model: shape of longitudinal section (in ventral view: Figure 11,f; Figure 12:h,j,l) from broad and elliptical (SA 5,6) to broad and oblong (SA 18,19); chalaza usually not very pronounced, subcircular; raphe thin; hilum zone sloping 45-60°; surface smooth, finely punctulate; colour, metallic grey, dark greyish brown or reddish brown; caruncle variably conical in ventral view, navicular-truncate in lateral view, sometimes subreniform in *E. cyparissias*, short and stipitate or subsessile, ventrally emarginate, and occupying an apical-lateral position with respect to the seed.

Characteristics of the seed surface under the SEM. Epidermic cells pentagonal, hexagonal or subcircular (Figure 11,g; Figure 12:i,k,m); anticlinal walls straight, not very prominent; intercellular spaces subtriangular, appearing in the zone near the hilum; periclinal walls flat or slightly concave or convex. Secondary sculpture from rugulate (Figure 11,g) to ruminate (Figure 12,i). The number of cells per surface unit (100 x 100 µm square, according to EHLER 1975, modified by BAIGES 1989), which we refer to by the abbreviation SCI (seed cellular index), ranges in absolute terms between 18 and 46. This seems to be one of the few characters which partially differentiates between the species though there is some overlap. In view of the small number of samples from each taxon examined (2-3), the results can only be considered indicative. In *E. cyparissias*, SCI: 30-36; in *E. esula* subsp. *esula*, SCI: 33-46; in *E. nevadensis*, SCI: (20) 22-32. The largest cells occur in the hexaploid population of *E. nevadensis* subsp. *bolosii* from Oroel, with values ranging from 20 to 24.

The uniformity of shape and partial overlapping of the measurements make seed characters of limited taxonomical value.

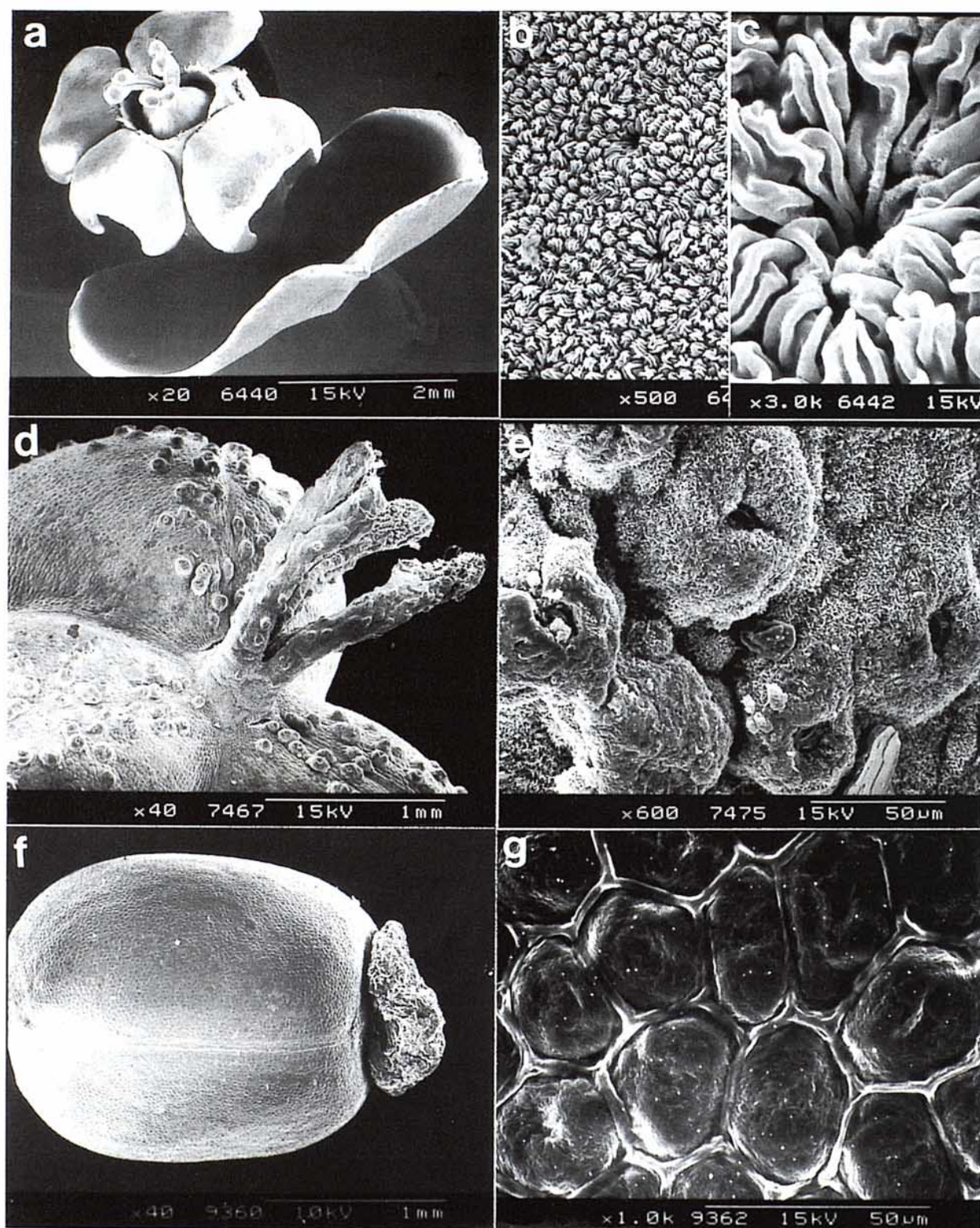


Fig. 11 — Cyathium and capsule in *Euphorbia* subsect. *Esula*. *E. nevadensis* subsp. *bolosii* (Hs: T, La Pena, BCF 36707): a) cyathium and bract (x 20); b-c) surface of the nectary gland x 500, and detail of secretory pores (x 3000). *E. nevadensis* subsp. *nevadensis* (Hs: Gr, Srna. Nevada, BCF 35179): d) apical zone of the capsule (x40); e) detail of emergences on the back of the mericarps with sunken stomata (x 600). *E. cyparissias* (Hs: Hu, Panticosa, BCF); f) ventral view of the seed (x 40); g) detail surface of the episperm (x 1500).

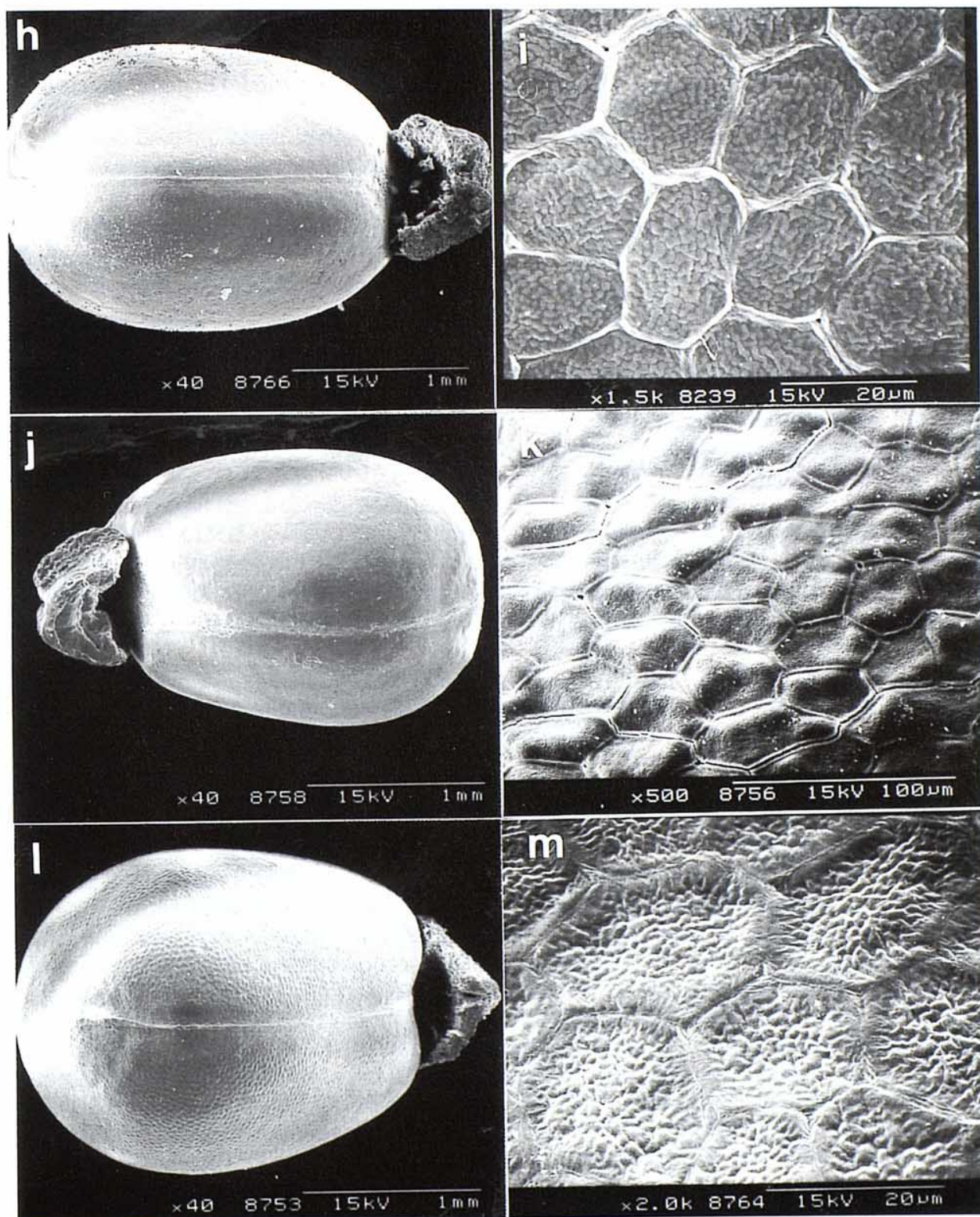


Fig. 12 — *E. esula* subsp. *esula* (Hs: Le, Ferradillo, LEB 33074); h) ventral view of the seed (x 40); i) detail surface of the epidermis (x 1000). *E. nevadensis* subsp. *nevadensis* (Hs: Gr, Sierra Nevada, BCF 35179); j) ventral view of the seed (x 40); k) detail surface of the epidermis (x 500). *E. nevadensis* subsp. *bolosii* (Hs: T, La Pena, BCF 36707); l) ventral view of the seed (x 40); m) detail surface of the epidermis (x 2000).

Euphorbia subsect. **Esula** (Boiss. in DC.) Pax in Engler & Prantl, *Natürliche Pflanzenfamilien* 3(5):110 (1981).

TYPE: *E. esula* L.

Perennials. Sterile branches generally present. Leaves pinnately nerved. Dichasial bracts free. Capsules generally granulate on the keels. Seeds smooth. $x=9,10$.

Key of Iberian species

1. Sterile branches with leaves 0.5-1 mm wide, densely and imbricately arranged in the apical zone; cauline leaves 1-2(3) mm wide *E. cyparissias*
 — Sterile branches with leaves over 2 mm wide, not imbricately arranged in the apical zone, or sterile branches absent; cauline leaves 2-30 mm wide 2
2. Leaves with subcordate base, truncate or rounded, sessile *E. nevadensis*
 — Leaves with cuneate or attenuate base, subsessile to petiolate 3
3. Shiny leaves, dark green; spaced out along the stem; sterile branches absent *E. nevadensis*
 — Leaves not shiny, greyish-green; closely-set along the stem; sterile branches usually present *E. esula*

1. *Euphorbia cyparissias* L., Sp. pl.: 461 (1753).

TYPE: «Habitat in Misnia, Bohemia, Helvetia, G. Narbonensi». LECTOTYPE: LINN 630.67 (Hb. LINN), «49 cyparissias», selected here. RADCLIFFE-SMITH (1982: 623) does not choose between the material of the Herb. LIN and that of the Herb. Cliff. which he mentions.

≡ *Tithymalus cyparissias* (L.) Hill, Hort. Kew. (ed. 1): 172 (1768) ≡ *Esula cyparissias* (L.) Haworth, Syn. pl. succ.: 155 (1812) ≡ *Karaselma cyparissias* (L.) Rafin., Fl. tellur. 4:116 (1838) ≡ *Galarrhoeus cyparissias* (L.) Small in Rydberg, Fl. Prairies N. Amer.: 520 (1932).

Rhizome horizontal, rarely oblique, up to 6 mm in ϕ . Stems erect, up to 60 cm, slightly or highly branched at the base. Sterile branches (0)3-9(15), sometimes highly developed, longer than the synflorescence. Lateral radii 0-12(18), 1-2 times dichotomous. Pleiochasial radii (6)11-18(21), 1-2 times dichotomous, with contracted dichasial radii. Leaves (5)10-26(37) x (0.4)1-2.6(3) mm, linear, linear-spatulate or linear-ovate, with cuneate or attenuate base and acute or obtuse apex; those of the sterile branches 0.4-0.8(1) mm, densely and imbricately arranged in the apical zone, filiform or linear; herbaceous consistency, fleshy, yellowish green (29 C8, 30 C8), dark green through drying; hypostomatic, with anomocytic-type stomata, irregularly arranged on the adaxial surface; crystalloid-type waxes. Pleiochasial bracts similar to the leaves of the nearest stem. Dichasial bracts 3-10 x 4-0 mm, between wide and ovate or ovate-rhombic to subcircular or reniform, with truncate base, rounded or cuneate and obtuse apex, either apiculate or not. Cyathium 1.5-2.2 (3) x 1.5-2.5 mm; glands 1.2-1.8 x 0.4-0.7 mm, emarginate, with two short, sharp horns; intracyathial scales 0.6-1.7 x 0.05-0.2 mm, entire, only slightly divided, barely ciliolate on the apex. Capsule 3-4 x 3-4 mm, deeply sulcate; granulate mericarps (1/3-1/2) on the back, often covering the whole surface; styles 1-1.2 mm, trifurcate at 1/3-1/2 of the base; stigmas with lobes of up to 0.3 mm. Seeds 1.8-2.5 x 1.4-1.7 mm, oblong or elliptical-oblong, smooth, dark brown (6 E6), greyish-white when immature; caruncle 0.2-0.5 x 0.8-1.1 mm, subreniform, sessile, ventrally emarginate; SCI: 30-36. $2n=20,40$.

Overall distribution

Species characteristic of the Eurosiberian Element. W, S & C Europa, C & S Russia; introduced into U.S.A. and Canada (OUDEJANS, l.c.:123).

Distribution in the Iberian Peninsula

Northeastern Spain (Figure 13): B, Cs, Ge, Hu, L, [Na]. The indications, of bibliographical origin, for S and T, are to be rejected.

Ecology

In open fields: pasture land (*Festuco-Brometea*), meadows (*Xerobromion*, *Mesobromion*, *Ononidetalia striatae*), scrubland (*Aphyllantion*), open woods, waysides and forest tracks, moll grassland (*Molinio-Holoschoenion*, *Brachypodium phoenicoidis*). From the submontane to the alpine zone, (200)500-2600 m, on all types of substrata. On the shores of the Mediterranean it can descend as far as the coastline where favourable conditions exist.

Localities studied

Spain

BARCELONA: Arenys de Montcada, 31TDF39, 25.IX.1946, A. & O. de Bolòs (BC 116994); Barcelona, plaine du Besòs, 31TDF38, 9.IV.1916, Sennen (BC 57252); Barcelona, Rec Comtal, prop del Besòs, 31TDF38, IV.1939, A. & O. de Bolòs (BC 100718); Tiana, 31TDF39, 1.X.1945, P. Montserrat (BC 616262); Montgat, 31TDF49, 24.II.1946, P. Montserrat (BC 616263); Vallgorguina, 31TDG51, 20.IV.1946, P. Montserrat (BC 616264); Massanes, 70 m, 31TCG97, 3.IV.1949, Font Quer (BC, BCC, BCF, MA 344267); Montcada, 31TDF39, IV.1909, Llenas (BC 57253); Montnegre, de Sant Celoni a Can Riera, 31TDG51, 22.IV.1946, P. Montserrat (BC 616265); Montseny, Seva, 31TDG43, 21.V.1915, Font-Quer (BC 57325); Montseny, Campins, 31TDG51, 25.III.1948, O. de Bolòs (BC 108828); Montseny, Campins, 31TDG51, 12.IV.91, J. Vicens (BC36898); San Celoni, 31TDG51, VI.1963, Losa Quintana (SALA 1238); San Hipòlit, orillas del Ter, 31TDG35, 3.VI.1868, Puigarrí (BC 57233); San Martí de Provençals, 31TDF38, III.1947, A. & O. de Bolòs (BC 101956); San Quirze de Besora, sobre la Font del Bufí, 31TDG36, 18.IV.1960, C. Besora (BC 144730); Cercanías de Torelló, 31TDG35, 29.VII.1868, M. Campos (BC 57242). CASTELLON: Benicarló, base del Puig, bajo el poblado ibérico, 31TBE88, 70 m, 1.VI.1991, J. Araú (BCF 36702). GIRONA: Alp, 1200 m, 31TDG18, 18.VI.1931, A. Ferrer (BC 99405); Batet, 31TDG38, V.?, Vayreda (BC 688976); Bescanó, 31TDG74, 24.V.1917, Font Quer (BC 57240); Alt Empordà, Llers, 31TDG98, 9.IV.1907, Sennen (BC Sennen); Alt Empordà, Vilarnadal, 31TDG98, 14.IX.1904, Sennen, BC-Sennen (MA 75442); Gerona, Empalme, 31TDG84, V.1953, Gabarda (MA 276153, MA 128359); Martorell de la Selva, 31TDG72, 5.V.1943, A. & O. de Bolòs (BC 123976); Martorell de la Selva, 31TDG72, 31.V.1945, Font-Quer (BC 105447); La Molina, w.d., 31TDG18, A. de Bolòs (BC 145720); Núria, 31TDG39, 30.VI.1922, Sra. Gallardo (BC 125045); Núria, roc de la Male, 12.IX.1944, P. Montserrat (BC 616266); Rosas, 31TEG17, 27.VII.1903, Rodríguez López Neyva (MA 341121); Tordera, 31TDG71, 26.IV.1988, Morales 268RM & J. Alvarez (MA 448331); El Torn, al Molí d'En Camps, 31TDG76, 29.VII.1945, P. Montserrat (BC 616268); Puerto de Tossas, 1800 m, 31DG18, 10.VII.1988, Morales 342RM, Paiva, Izuzquá (MA 458876, MA 458874); Vall d'Eina, 31TDG29, VII.1893, Trèmols (BC 649338); Vall de Ribes, Rialb, 1075 m, 31TDG38, 4.IX.1957, J. Vigo (BC 146225). HUESCA: Port de Benasque, 31TCH03, 5.VIII.1973, Trèmols (BC 649288); Benasque, 1130 m, 31TBH92, 22.V.1982, J.M.^a Palacín (JACA 350084); Benasque, la Renclusa, 31TCH02, 15.VII.1986, Giráldez (SALA 43864); Hospicio de Benasque, 31TCH02, 16.VII.1903, C. Pau (MA 407982); Hospital de Benasque, 31TCH02, VIII.1918, C. Bolívar (MA 754441); Hospital de Benasque, 1700-1750 m, 31TCH02, 31.VII.1974, L. Villar (JACA 498574); Hospital de Benasque, ladera este, 1000 m, 31TCH02, 22.IV.1982, J.M.^a Palacín (JACA); Valle de Benasque, la Renclusa, 31TCH02, 180 m, 12.VII.1988, Morales 447Rm, Paiva & Izuzquita (MA 458837); Bielsa, Circo de La Larri, 1350 m, 31TBH63, 1.VII.1973, P. Montserrat & L. Villar (JACA 112880); Hostal de

Salinas de Sin. Bielsa, 780 m, 31TBH77, 30.V.1980, P. Montserrat & L. Villar (JACA 112880); Bujaruelo, 31TYN33, 27.VII.1984, Burgaz (MA 313246, SALA 34269); La Fortunada, río La Garona, 1250 m, 31TBH70, 30.V.1980, P. Montserrat & L. Villar (JACA 101180); Ordesa, Circo de Soaso, 1750 m, 31TYN42, 25.VII.1970, L. Villar (JACA 407070); Ordesa, Calollarro, 1500-1850 m, 30TYN42, 23.VIII.1971, L. Villar (JACA 671171); Llano de Ordesa, 1300 m, 31TYN42, 16.VII.1929, Cuatrecasas (BC 57250); Valle de Ordesa, Estrecho de Arasas, 31TYN42, 13.VIII.1935, Ceballos (MA 75440); Valle de Ordesa, 31TYN42, 29.VI.1953, Malato Beliz 1052 (MA 276152); Panticosa, 1700-1800 m, 31TYN23, 21.V.1967, P. Montserrat (JACA 362667); Panticosa, 31TYN23, 4.VIII.1979, Amich, Rico & Sánchez (BCF, MAF 250301, SALA 22595); Panticosa, La Ripera, 1150-1580 m, 30TYN23, 3.VII.1980, P. Montserrat & L. Villar (JACA 201480); Panticosa, Balneario, 1600 m, 30TYN23, 11.VII.1982, J.M.^a Palacín (JACA 342484); Plan, de San Mamés a La Sentina y Las Coronas, 1350 m, 31TBH70, 22.VI.1981, P. Montserrat & L. Villar (JACA 94281); Peña de Laspún, 1100 m, 31TBG89, 27.IV.1979, D. Gómez (JACA); Foradada del Toscar, 1450 m, 31TBH70, 27.IV.1979, D. Gómez (JACA); Foradada del Toscar, 1450 m, 31TBH70, 27.IV.1979, D. Gómez (JACA); Valle La Garona, 1250 m, 31TBH70, 10.IV.1980, D. Gómez 101180 (JACA); Umbría de la Estiva, 1450 m, 31TBH70, 27.VII.1985, D. Gómez 48685 (JACA); El Pueyo, 700 m, 31TBH60, 10.IV.1982, D. Gómez 3582 (JACA); Laspuña, Peña Montañesa, 1400 m, 31TBH70, 25.VII.1985, D. Gómez 54185 (JACA); Ainsa, río Cinca, 570 m, 31TBG69, 22.IV.1981, D. Gómez 6281 (JACA); Cotiella NW, 2280 m, 31TBH81, 22.VIII.1979, G. Montserrat 119479 (JACA); Cotiella SW, 2220 m, 31TBH70, 25.VII.1979, G. Montserrat 38879 (JACA); Laspuña, 1300 m, 31TBH70, 10.IV.1980, G. Montserrat 19480 (JACA); Seira, 1180-1250 m, 31TBH80, 24.IV.1980, G. Montserrat 28980, 30380 (JACA); Seira, 960 m, 31TBH80, 27.IV.80, G. Montserrat 44880, 42480 (JACA). LERIDA: Alt Urgell, Serra d'Aubens, 1340 m, 31TCG56, 12.VI.1976, Molero & Silvestre (BCF); Caldes de Bohí, 31TCH21, VIII.1944, J. Borja (MA 192570); Coll de Nargó, hacia Aubens, 31TCG67, 12.VI.1976, Molero & Silvestre (MA 311994); Conca del Ter, pr. la Sellera, torrent de Rauricós, 22.IV.1920, w. col. (BC 17238); San Maurici-E, Espot, 2125 m, 31TCH31, 25.VIII.1964, J. Puigdefabregas (JACA); Vall d'Espot, pista de Lladres, 200 m, 31TCH41, 2.VIII.1976, J.M.^a Montserrat (BCC); Espot, 1360 m, 31TCH41, 11.IX.1981, Carrillo & Ninot (BCC); Espot, Lago de San Mauricio, 1185 m, 31TCH31, 11.VII.1988, Morales 359RM, Paiva & Izuzquia (MA 456451); Orillas del Flamisell, 31TCG39, IV.1918, Gallardo (BC 99407); La Bonaigüa, 31TCH32, 23.VII.1980, Casaseca, Fdez. Díez, Amich, Rico y Sánchez (SALA 47828); Subida al Pto. de la Bonaigua, 1600 m, 31TCH32, 22.VII.1975, G. López, G. Moreno & E. Valdés (MA 200937); Montsec, Rubies, 31TCG25, 25.VI.1925, Riofrío (BCC); Sant Joan de l'Erm, coll sobre El Ras, 1962 m, 31TCH60, 3.IV.190, J. Carreras (BCC); Pallars Sobirà, Vallferrera, pujant cap a Virós, 1250 m, 31TCH51, 22.IV.1973, E. Farreny (BC 620010); Camí de Sant Quim, Vall Fosca, 1600 m, 31TCH30, 14-VIII-1984, Pineda (BCC); Serra Pedregosa, Gósol, 2.VIII.1926, Cuatrecasas (BC 57248); Tosal de Servi, Manyanet, 2300 m, 10.VIII.1954, F. Masclans (BC 126688); Congosto de Terradets, Tremp, 350-400 m, 31TCG25, 6-VII-1986, P. Montserrat & G. Montserrat (JACA); Vall d'Aran, Port d'Uvets, 2300 m, 31TCH22, M. Llenas (BC 57254); Valle de Aran, 2100 m, 31TCH20, Gz. Albo (MA 75439).

2. *Euphorbia esula* L., Sp. pl.: 461 (1753).

TYPE: «*Habitat in Germania, Belgio, Gallia*». LECTOTYPE: LINN 630.62 (Hb. LINN), chosen by RADCLIFFE-SMITH according to CROMPTON, STAHEVITCH & WOJTAS (l.c.:1985)¹

1. The specimen chosen by Radcliffe-Smith as the nomenclatural type of *E. esula* corresponds to the traditional idea of the taxon, having obovate leaves with an undulating margin, wider in the apical third of the lamina and a largely attenuate base. Thus it coincides with the iconography of the works referred to by Linnaeus in the protologue «*esula minor*» Delechamps, hist. 1653 (vidit!) and Dodoens 374 (vidit!), which also has leaves that are wider in the upper third and long and attenuate at the base.

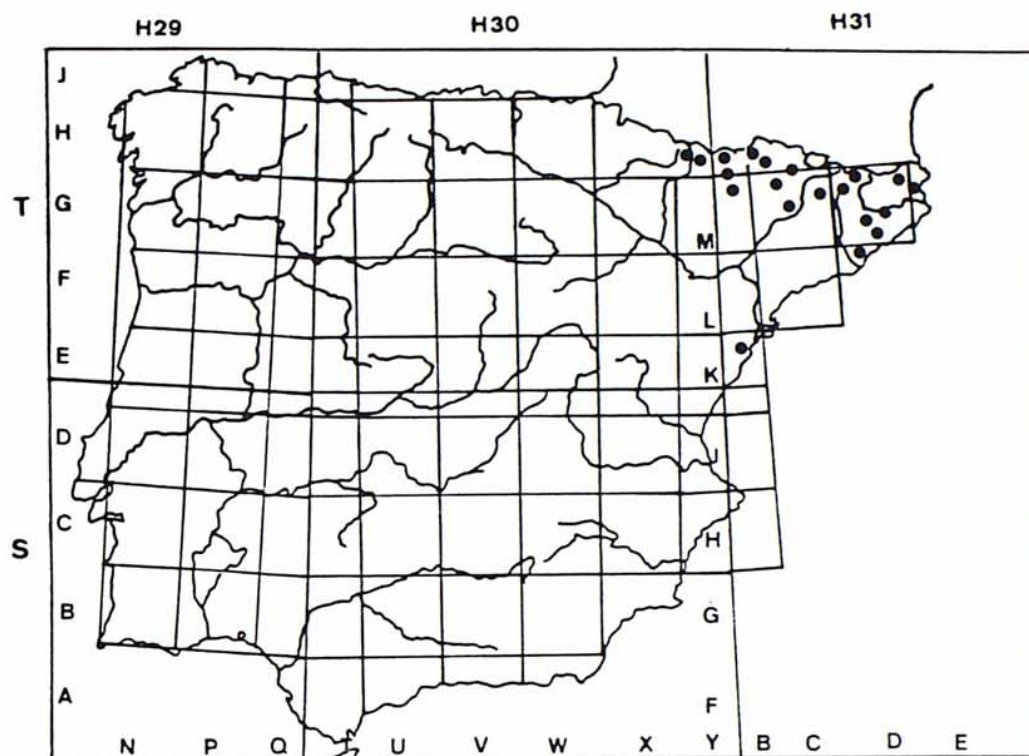


Fig. 13 – Distribution map of *E. cyparissias* L. in the Iberian Peninsula (U.T.M. 10x10 Km grid square).

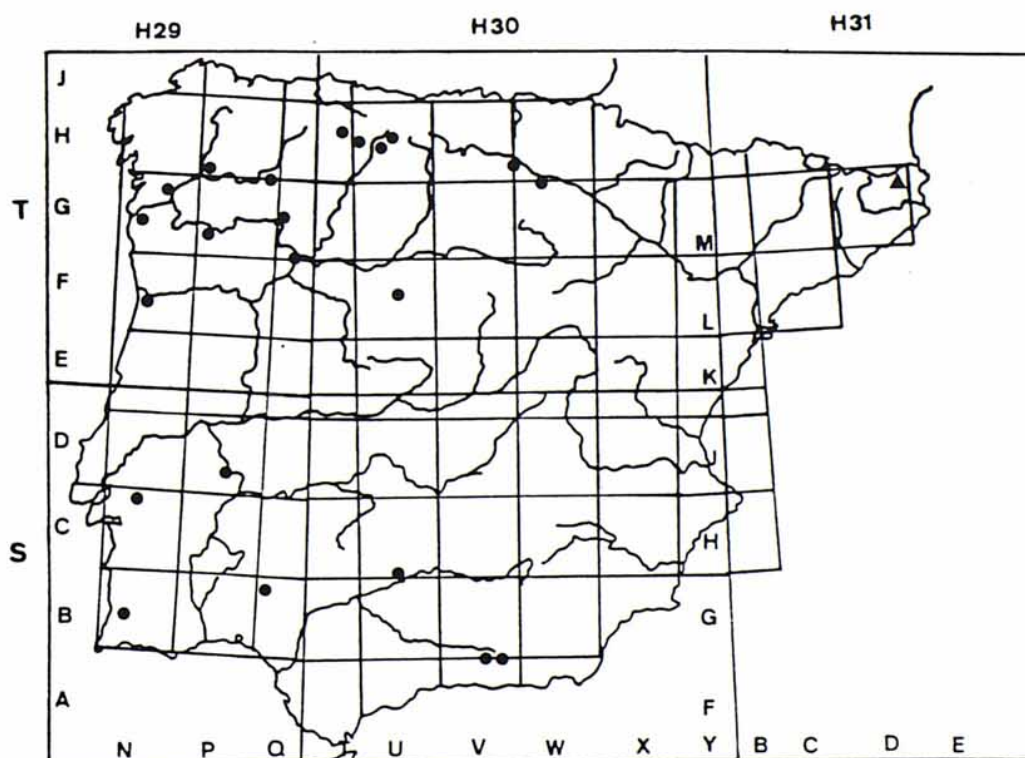


Fig. 14 – Distribution map of *E. esula* L. subsp. *esula* (•), and subsp. *virgata* (Walds. & Kit.) Molero & Rovira (▲), in the Iberian Peninsula.

= *Tithymalus esula* (L.) Hill, Hort. Kew. (ed. 1): 172.4 (1768) = *Karaselma esula* (L.) Rafin., Fl. tellur. 4:116 (1838) = *Euphorbion esula* (L.) Saint-Lager, Ann. Soc. Bot. Lyon 7:126 (1880) = *Galarrhoeus esula* (L.) Rydberg, Brittonia 1:93 (1931) = *Esula esula* (L.) Rafin. ex Merrill, Index rafin.: 153 (1949).

Rhizome horizontal or oblique, rarely vertical, up to 8 mm in ϕ . Stems up to 120 cm, from solitary to numerous. Branches sterile (0)3-14. Lateral radii, 0-20, 1-2 times dichotomous. Pleiochasial radii 4-20, 1-3(4) times dichotomous. Leaves subsessile or shortly petiolate (1-5 mm), 10-90 x 3-27 mm, of variable size and shape, with attenuate or cuneate base, margin entire, denticulate in the apical third, apex sharp, obtuse or rounded; herbaceous consistency; colour greyish green (29 C8 when fresh changing to 29 D7,8 or 29 E7,8 after drying); leaves of sterile branches narrower, densely but not imbricately arranged in the apical zone. Pleiochasial bracts like the nearby cauline leaves, usually shorter and wider. Dichasial bracts 3-15 x 4-18 mm, from ovate or ovate-rhombic to narrow and ovate or reniform, with cordate, truncate, rounded or cuneate base and obtuse or rounded (rarely pointed), apex, apiculate or not, mucronulate or not. Cyathium 1.5-3 x 1.5-2.8 mm, yellowish when mature; glands 1-2 x 0.6-1.1 mm, of variable shape, emarginate with short horns (pointed or broadened), rarely subtruncate, oblate or pectinate. Capsule 2.5-3.2 x 3-4 mm, deeply sulcate; mericarps granulated on the back; style 1-2(2.6) mm, trifurcate close to the base; stigmas with lobes up to 0.4 mm. Seeds 2-2.5 x 1.4-1.7 mm, between ovate-elliptical and oblong, greyish-white, reddish brown in maturity; caruncle 0.3-0.6 x 0.7-1 mm, subconical, navicular-truncate in lateral view, slightly stipitate, ventrally emarginate.

Overall distribution

Species of the Eurosiberian Element. Europa, N, C and SW Asia, China, Korea, Japan; introduced into Canada, U.S.A. and N Mexico (OUDEJANS, l.c.:150).

Key of subspecies²

Leaves 10-90 x (3) 4-27 mm, length 1.5 - 9 times greater than width, lanceolate, spatulate, narrow and ovate or obovate. Hypostomatic, with anomocytic-type stomata. Pleiochasial radii (5) 7-16 subsp. *esula*

Leaves 25-70 x 2-4(5) mm, length 14 to 20 times greater than width, linear (rarely linear-lanceolate). Epianphistomatic, with anisocytic-type stomata. Pleiochasial radii (5) 7-9 subsp. *orientalis*

subsp. *esula*

= *E. androsaemifolia* Willd. ex Schlecht., Enum. pl. hort. berol., Suppl.: 27 (1814). TYPE: No reference to locality in the protologue. LECTOTYPE: Willdenow 9373, sheet 1 (B-Hb. Willde-

2. In the taxonomical treatment described below, particular attention is paid to the results of the micromorphological study of the leaf surface. There appears to be a correlation between the shape of the leaf and the cuticular characteristics which forces us to recognize within *E. esula* the existence of two entities (subsp. *esula* and subsp. *orientalis*) which are certainly variable at subspecific level even if one takes into account the existence of some transitional forms.

now, Figure 18). The sheet contains a single specimen from which the lower half of the stem is missing; below it is a small label with the words: «Euphorb. / androsaemifol. / (W).» in Willdenow's writing.³

= *E. pinifolia* Lam., Encycl. 2:437-438 (1788). TYPE: «on trouve cet Euphorbe dans les provinces méridionales de la France». LECTOTYPE: in P, Hb. Lamark (Figure 17). The right half of the sheet contains a specimen which is clearly annual and corresponds to *E. segetalis* L. while the left half is occupied by three vegetative fragments (stems with leaves). We choose as the lectotype the fragment of the specimen from the lower left-hand corner, alongside a handwritten label in Lamarck's writing which reads: «*euphorbia pinifolia* / lam. dict. / au *euphorbia esula* Lin / *tithymalus foliis pini, forte dioscoridi phytiusa* / bauh. p. 292».

= *E. esula* L. subsp. *pinifolia* (Lam.) Fournier, Quatre Fl. France: 274 (1936).

— *E. bupleurifolia* Pau ex Losa España in Anales Jard. Bot. Madrid 7:422-423 (1946), *nom. illeg.*; *non* Jacquin 1797.

— *E. iberica* Sennen & Elias, *nom. in sched.* (MA 74704).

— *E. lucida* auct. *iber.*, *non* Waldest. & Kit.

Stems up to 120 cm. Leaves (10)25-70(90) x (3)5-22(27) mm, length up to 9 times greater than width, with maximum width in the middle or upper part, narrowly or widely lanceolate, subspatulate, oblong-lanceolate, oblong-linear, elliptical, ovate-lanceolate or obovate-lanceolate; base attenuate or cuneate, margin sometimes undulating; apex obtuse or subobtuse, rarely rounded or pointed; hypostomatic, with anomocytic-type stomata. Lateral radii (0)4-20. Pleiochasial radii (84)7-18(20). Cyathium sometimes pubescent on the outside.

Notes

E. androsaemifolia Willd. ex Schlecht. and *E. pinifolia* Lam. constitute, in our view, two extreme forms of variation of *E. esula* subsp. *esula*. Western Iberian authors have habitually identified the robust and highly ramified forms (Figure 8,f) with narrow lanceolate leaves (Figure 9:1,2) from Portugal and northwestern Spain with *E. androsaemifolia* (COUTINHO, 1939:465; MERINO, 1906:537). However, in the same and nearby localities there occur other less robust and ramified forms with narrow leaves which recall the typical forms as they occur in the majority of localities in the hinterland of the peninsula or the Sierra Nevada. Figure 9(1-8) illustrates the extreme limits of the variation of the leaf morphology, which does not present any clear morphological-geographical correlation. Hence in this study we consider *E. androsaemifolia* as a synonym of *E. esula* subsp. *esula*.

3. The sheet also contains a label in the handwriting of Boissier reading: «*E. lucida* W. & K. / Boiss.», which raises doubts as to the correct identity of the specimen it contains. The photograph of the type (we were unable to gain access to the original material) does not make it possible to ascertain whether the specimen in question is or is not *E. lucida*. Thanks to the kindness of Dr. Hiepko, the curator of the Botanical Museum of Berlin, we were able to study the characters of the epidermis of a leaf fragment from Willenow's type. The results are conclusive: hypostomatic leaves, with anomocytic stomata, cells with fine, undulating anticlinal walls, and wax deposits in the form of crystalloids. These characteristics are typical of *E. esula* and in contrast with those presented by *E. lucida*: hypoamphistomatic leaves, with anomocytic-type stomata, distributed in a very narrow continuous strip on the adaxial surface close to the midvein, cells with straight anticlinal walls, irregular thickenings on the abaxial surface and continuous wax deposits without crystalloids (Fig. 5:i,j). The leaf micromorphology of the original material of *E. androsaemifolia* shows close analogies with western Iberian populations of *E. esula*, especially those in Portugal, and it may thus be suggested that this material, with no locality indicated in the protologue, comes from Portugal. OUDEJANS (l.c.:51), who recognized this taxon at specific level, attributes to it an Iberian origin, probably on the basis of bibliographical references by Portuguese and Spanish authors.

E. pinifolia Lam., which has narrow linear-spatulate or narrow and obovate-lanceolate leaves (3-6 mm), with an apex between rounded and subobtusate and a long, attenuate base, is located at the opposite extreme of the variation of subsp. *esula*. Its morphological proximity to subsp. *orientalis* is well known and it is consequently difficult to distinguish it from *E. esula* var. *pseudotenuifolia* Sennen. The lack of data about its cuticular characters prevents us from taking a more definitive stand.

Distribution in the Iberian Peninsula

S, W & N Spain; N & E Portugal (Figure 14). **Portugal:** BA, DL, R and TM. **Spain:** Ba, Bu, Gr, Le, Lo, Lu, O, Or, P, Po, [S], Se, Za. Literature reports from the provinces of: Al(?), B, Ca, Ge, Hu, Te and V should be rejected.

Ecology

Grassland and damp meadows by watercourses, mesoxerophilous stony grazing land, high mountain megamorphic communities, rock crevices. From the colline to the alpine zone, 200-3000 m; mainly on granite and schist soils; also on calcareous, slightly decarbonated soils.

Localities studied

Portugal

BAIXO ALENTEJO: «Ademira», 29SNB35, VII.1893, Sampaio (COI); Odemira, 29SNB35, V.1905, G. Sampaio (MA 75457). DOURO LITORAL: Via Nova de Gaia, Quebrantoés, 29TNF35, VI.1899, Sampaio (COI). RIBATEJO: Rives du Sorraia, pr. Coruche, 29SNC49, -IX.1888, Daveau (COI). TRAS OS MONTES ALTO DOURO: Regua, pr. Bragantes, 29TQG04, 3.VI.1939, Rothmaler & Silva (LISE 6144); Izeda, Vale do Sabox, 29TQG30, 19.VI.1932, Carrisso & Mendouça (COI); Salvador, pr. Narvão, 29TPG13, 24.VI.1958, Fernandes, Matos & Sarmiento (COI).

Spain

BADAJOS: Carrión, 29SPD63, 15.VI.1983, P. Gómez (MA 453377). BURGOS: Castilla, Miranda, 30TWN02, 24.V.1909, Hno. Elías (BC 74704, MA 74704); Miranda de Ebro, 460 m, 30TWN02, 5.VII.1920, Hno. Elías (MA 75466, 7465); Miranda de Ebro, orillas del río Ebro, 460 m, 30TWN02, V.1934, Losa (MA 470663); Miranda de Ebro, 30TWN02, V.1935, M. Losa (MAF 23569). GRANADA: Capileira, Trancada de Aguas Verdes, 30SVG60, 2950 m, 17.IX.1978, J. Molero Mesa (GDA 6970); Sierra Nevada, 30SVG60, VII.1844, Willkomm (BM); Sierra Nevada, barranco de Val de Capillos, 30SVG60, 23.VIII.1844, Willkomm (COI-Willkomm); Sierra Nevada, 2800 m, 30SVG60, VII.1890, Porta & Rigo 584 (BM); Sierra Nevada, barranco de S. Juan, 30SVG60, VIII.1913, C. Vicioso (MA 75451); Sierra Nevada, La Alcazaba, 2700 m, 30SVG70, 30.VII.1923, Gros & Font Quer (BC 99286); Sierra Nevada, río Monachil, 2100 m, 30SVG60, 12.VII.1978, M. Roivainen (SEV 55651); Sierra Nevada, Prados de Otero, 2500 m, 30SVG60, 9.VII.1980, Ladero & López-Guadalupe & Molero Mesa (SALAF 1124); Sierra Nevada, Guejar, bajo Vacares, 2100 m, 30SVG70, 20.VII.1985, Sánchez & Alejandro (MA 337868); Granada, 2500 m, 30SVG60, 18.VII.1985, G. Montserrat & J.M. Montserrat (JACA 630); Trevelez, Lagunillos del Góteron, barranco del Infierno, 2700 m, 30SVG70, w.d., J. Molero Mesa (GDA 6951). HUELVA: Sierra de Aracena, Santa Olalla, 29SQB09, 12.VI.1967, Galiano & Gilbert (SEV 47004); Sierra de Aracena, Castaño del Robledo, Pico Castaño, 960 m, 29SQB09, 25.V.1979, Rivera & Cabezudo (SEV 47002); Sierra

de Aracena, entre Valdeazufre y Aracena, 29SQB19, 21.VII.1979, Rivera & Cabezudo (MGC 9747); Sierra de Aracena, entre Los Marines y Fuenteheridos, 29SQB09, 7.VIII.1979, J. Rivera (SEV 47003); Sierra de Aracena, entre Aracena y Castellar, 29SQB09, 19.V.1990, Blanché & Vicens (BCF 36701). LEON: Caldas de Necedo, 30TUN05, 17.VII.1979, López Pacheco (LEB 17399); Ferradillo, 29TPH90, 7.VII.1984, J. Andrés (LEB 33074); Necedo, río Curueño, 30TUN05, 18.VII.1931, Borja (MAF 23568); Ponferrada, Mtes. Aquilianos, vertiente N. de La Guiana, «Los Apóstoles», 1600 m, 29TPH90, 18.VII.1982, Nieto Fellner (MA 317290); Redillueva, 30TTN96, 17.VII.1979, López Pacheco (LEB 16547); Contra Riaño, 1050 m, 30TUN35, 13.VII.1971, Laínz (MA 395699, SEV 144228); Riaño, pr. Anciles, 1050 m, 30TUN35, 18.VII.1987, Laínz (MA 353916, SALA 43209). LOGROÑO: Ribera, Molino del Prior, 26.IV.?, Zubía (MA 75454); Camino Viejo de Varea, orillas del Ebro, 30TWN40, 20.V.?, Zubía (MA 75464). ORENSE: Castrelo de Miño, 29TNG78, 18.VII.1935, A. Rodríguez (MA 7545). PALENCIA: Espigüete, 30TUN55, 24.VII.1982, T.E. Díaz & al. (LEB 14004). PONTEVEDRA: Caldas de Tuy, Caldelas, 29TNG25, w.d., P. Merino (LOU 01439); Peares, 29TPH00, w.d., Merino (LOU 01439). SEVILLA: Cazalla de la Sierra, 30STH50, 22.VI.1976, F. Galiano & al. (SEV 90410); Cazalla de la Sierra, «El Duende», 30STH50, 22.VIII.1979, S. Silvestre (SEV 107099). ZAMORA: Moral de Sayago, 30TTL56, 19.VI.1981, Sánchez Rodríguez (SALA 32642, SALAF 2472).

subsp. **orientalis** (Boiss. in DC.) Molero & Rovira, *comb. nov.*⁴

Bas. E. virgata Waldst. & Kit. var. *orientalis* Boiss. in DC., Prodr. 15(2):160 (1862). LECTOTYPE in G-DC. (Figure 19): «*Euphorbia lucida* W. et K. / Venue sous le nom d'*Euph. persica* / Jard. bot. Genève / Juillet 1939»; at right, in another label written by Boissier, is indicated: «*E. virgata* W.K. / Var. *Orientalis*».

= *E. virgata* Waldst & Kit. subsp. *orientalis* (Boiss. in DC.) Velenovsky in Fl. Bulg.: 507 (1891).

= *E. waldsteinii* (Soják) Radcliffe-Smith, Kew Bull. 36:216 (1981). = *Tithymalus waldsteini* Sojak, Cas. Nar. Muz. (Praha) 140:177 (1972); based on *E. virgata* Waldst & Kit., Descr. icon. pl. rar. hung. 2:176-177 (1804), non *E. virgata* Desf., Tabl. Ecole Bot. (ed. 1):204 (1804). TYPE: «*Habitat si altiora loca montosa demas, per omnem fere Hungariam, Croatiam et Sclavoniam locis siccis*». LECTOTYPE in PR (KHAN, 1964:115, n.v.).

= *E. sarati* Ardoino, Fl. anal. Alpes-Mar. (ed.1): 335 (1867). TYPE: «Croît à l'Ariane près de Nice, parmi les saules des bords du paillon, où elle a été découverte par M. Sarato». Material type in FI: a sheet labelled in the handwriting of Ardoino «*Euphorbia sarati* Ardoino / L'Ariane, sur rive droite du paillon / juin 1864-65 / C. Sarato».

= *E. esula* L. var. *pseudotenuifolia* Sennen in Bull. Géogr. Bot. 21 (259): 127 (1911). TYPE: «un seul point des olivettes, des coteaux entre Hostalets et Pont de Molins, près Figueres». We have found no sheet bearing a precise reference to this locality. The only material available, prior to the date of publication, corresponds to the exsicc. «Plantes d'Espagne, F. Sennen, n.º 591 / *Euphorbia esula* L./var. *pseudotenuifolia* nova / Catalogne: Llers, olivettes / 1908 V et VI». We choose the sheet BC 755455 as the lectotype.

4. The precise identification of two names which have priority at subspecific level [*E. esula* L. subsp. *pseudocyparissias* (Jordan) Nyman, Consp. fl. eur. 3:652 (1881) and *E. esula* L. subsp. *paradoxa* (Schur) Simonkai, Enum. fl. transsilv.:482 (1887)] requires correct typification of their basionyms. Our view, based on the protologue and references by other authors (we have been unable to study the type material), is that these names should be referred to subsp. *esula*.
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Stems 40-70 cm. Leaves 35-70 x 2-4(5) mm, length 14 to 20 time longer than wider, linear or narrowly linear-lanceolate; base shortly attenuate or cuneate, apex pointed or subobtusely, mucronulate or not; epistomatous, with anisocytic-type stomata on the adaxial surface. Lateral radii 2-4. Pleiochasial radii 6-9.⁵

Distribution in the Iberian Peninsula

Spain (Figure 14): Ge, L.

Ecology

Olive groves. We visited the locality of Llers and the olive groves between Hostalets and Pont de Molins without finding any population of this taxon. It has probably disappeared from the locality.

Localities studied

Spain

GIRONA: Catalogne, Llers, 31TDG98, V/VI.1908, Sennen 591 (MAF 75456); Llers, 31TDG98, V/VI.1908, Elias, BM.

Taxonomical comments on the complex «*E. virgata*» in SW Europe

The variability of *E. esula* subsp. *orientalis* was correctly reflected by BOISSIER (1872:160, under *E. virgata*). Subsp. *orientalis* s. str. (= *E. boissieriana* (Voronov) Prokh.), which has wide, ovate-lanceolate leaves, a developed synflorescence, somewhat larger capsules and seeds, is typical of the eastern area of the species.

E. virgata sensu Waldst. & Kit. s. str., as it occurs in central Europe reaches as far as the western Mediterranean and appears in some points of northeastern France and northwestern Italy, as we observed in the herbaria consulted (BC, BM, FI, G, MA, MPU). The taxon is characterized by its ovate-linear leaves, 3-5(8) mm wide, wider in the lower half of the lamina, with a rounded or cuneate base and a long, attenuate, pointed apex. In northwestern France (and in Holland and Belgium), it presents very narrow leaves (2-4 mm), which are linear, with a cuspidate apex, numerous vegetative branches and a relatively undeveloped synflorescence, identified on the sheets under the binomen *E. esula* subsp. *tommasiniana* var. *angustifolia* Baguet, a taxon which we believe should be assimilated to *E. virgata* var. *uralensis* (Fischer ex Link) Boiss. in DC. (= *E. uralensis* Fischer ex Link), which represents the other extreme of variation. We nevertheless agree with KHAN (1964:115); since there is no clear morphological-geographical or ecological correlation, recognizing these taxa with varietal rank hardly seems justified.

On account of the shape of its leaves and its cuticular microcharacters (see Table 1, n.º 18), *E. tristis* sensu auct. gall. (see KERGUÉLEN, 1987) should be referred to the narrow leafed forms of *E. esula* subsp. *orientalis* (= *E. virgata* Waldst. & Kit.). KERGUÉLEN (l.c.) accepts the combination *E. esula* subsp. *tristis* [(Besser) Rouy in Fl. France 12:164 (1910)], considering this taxon distinct from subsp. *esula* on the basis of the ecological criterion of its calcicolous propensities rather than on morphological grounds; in northwestern Spain, *E. esula* also frequently appears on limestone substrata without any morphological modifications worth mentioning. But the classical locality of the true *E. tristis* [Besser in Cat. jard. bot. Krzemieni-

5. This somewhat restrictive description of the concept of the taxon in its overall area, corresponds solely to the material from Sennen's *exsiccata*, which lacks capsules and seeds.

ce, Suppl. 4:27 (1815)] is «*in collinas ad Tyram*» (south-western Asia?) and its author defines it as having cauline leaves «obovato lanceolatis», which means that this taxon must of necessity be related to *E. esula* subsp. *esula*.

E. sarati Ardoino, from the Alpes Maritimes, should be considered, on account of its morphological characters and leaf surface, included in the synonymy of subsp. *orientalis* (closely related to *E. virgata* Waldst. & Kit.).

E. tommasiniana Bertol. [= *E. virgata* subsp. *tommasiniana* (Bertol.) Nyman; = *E. virgata* var. *montana* Reich.], described from Monte Spaccato, a locality close to Trieste (Italy), presents intermediate characters between *E. esula* subsp. *orientalis* and *E. graminifolia* Vill. The general shape of the leaf, between linear-oblong and ovate-oblong or ovate-lanceolate, generally wider in the basal zone, with a subtruncate or rounded base, and a large number of pleiochasial radii (7-15), are characters proper to subsp. *orientalis*. However, the leaves which are shiny on both sides owing to continuous wax deposits constitute a character typical of *E. graminifolia*; OUDEJANS (1989) reflects this affinity by combining it at subspecific level [*E. graminifolia* subsp. *tommasiniana* (Bertol.) Oudejans]. Possibly the most appropriate treatment would be to subordinate it to *E. esula* with independent subspecific rank [*E. esula* L. subsp. *tommasiniana* (Bertol.) Kuzmanov in Jordanov].

E. graminifolia Vill. (= *E. tenuifolia* Lam.), considered by some authors (SMITH & TUTIN, l.c.) a synonym of "*E. esula* subsp. *tommasiniana*" should be considered a «genuine» species in the view of some classical authors (COSTE, 1905; FOURNIER, 1961) and other present-day researchers (GREUTER, BURDET & LONG, l.c.; OUDEJANS, l.c.). It is characterized by its thin rhizomes, slender stems, absence of sterile branches, few pleiochasial radii (2-6) and shiny leaves measuring 12-40 x 1-2(3) mm, which are linear, with a subtruncate or rounded base and long, attenuate, pointed apex. It is a taxon very close to *E. nevadensis* subsp. *bolosii*, from which it is difficult to separate on the basis of its morphological traits. Of greater help are its cuticular characters (see Table 1), both species share the same wax type and the continuous deposits on both surfaces lend characteristic shininess to their leaves. This is a differential character with respect to *E. virgata*. The ecology of this taxon endemic to the Provence, which inhabits marshes and wet ground, is also a differential trait with respect to *E. nevadensis* subsp. *bolosii*.

3. *Euphorbia nevadensis* Boiss. & Reuter, Pugill. pl. afr. bor. Hisp.: 110 (1852).

TYPE: «*Hab. in regione alpina Sierra Nevada inter juniperus in parte superiori vallis barranco de San Juan*». LECTOTYPE en G, Hb. Boissier (BURDET, CHARPIN & JACQUEMOUD, 1984: 773; *vidit!*).

= *Tithymalus nevadensis* (Boiss. & Reuter) Klotzsch & Garke ex Klotzsch, Abh. K. Akad. Wiss. Berlin. 1859 (1):90 (1860) = *Esula nevadensis* (Boiss. & Reuter) Gandoger, Fl. Eur. 20:110 (1890).

Procumbent or erect. Rhizome horizontal or oblique, 0.2-0.5 mm in ϕ . Stems 5-45 cm, few or many branches at the base. Sterile branches 0-5. Lateral radii 2-16, 1-2 times dichotomous. Pleiochasial radii 3-9, 1-2(3) times dichotomous. Leaves variable, 5-50 x 2-20 mm, from wide and ovate to linear, entire or slightly serrulate in the apical zone, mucronulate or not; hypoamphistomatic. Pleiochasial bracts similar to the nearest leaves, somewhat shorter and wider. Dichasial bracts 3-14 x 4-20 mm, with denticulate margin in the upper half, usually apiculate or mucronulate. Synflorescence narrow and oblong. Cyathium 1.5-3 x 1.4-2.8 mm, yellowish or reddish when mature; glands 4(5), 1.4-2.3 x 0.6-1.2 mm, yellowish or reddish, of

variable shape, usually emarginate and with two short horns, pointed or broadened, less frequently subtruncate or pectinate. Capsule 2.5-3.5 x 3-4 mm, deeply sulcate, granulate on the back; styles 1-2.5 mm, trifurcate between 1/3-1/2 of the base; stigma with lobes up to 0.4 mm. Seeds 2-2.6(2.9) x 1.3-1.7(1.8) mm, with longitudinal section from ovate-elliptical to oblong, smooth, greyish-white, reddish brown when mature; SCI: 22-32; caruncle 0.4-0.7 x 0.6-1.1 mm, subconical, navicular-truncate in lateral view, slightly stipitate, ventrally emarginate.

Overall distribution

Endemic to the Iberian Peninsula

Key to subspecies

1. Leaves 1.5 to 4 (5) times longer than wide, ovate, elliptical or oblong, not attenuate at the base; greyish-green, not shiny. Sterile branches 0-3 (5) 2
 – Leaves (5)6 to 20 times longer than wide, linear to linear-oblong, base subtruncate, rounded or short and attenuate; dark green, shiny. Sterile branches absent . subsp. *bolosii*
2. Leaves ovate, ovate-triangular, rarely elliptical, with subcordate or truncate base (rarely rounded) and non-truncate apex; subcoriaceous, glaucous subsp. *nevadensis*
 – Leaves elliptical or oblong (rarely ovate-oblong), with rounded base (rarely truncate or cuneate) and apex obtuse, rounded or truncate; herbaceous, subglaucous subsp. *aragonensis*

subsp. *nevadensis*

≡ *E. esula* subsp. *nevadensis* (Boiss. & Reuter) Malagarriga in Las subespecies y la variación geográfica: 5 (1973).

– *E. nevadensis* Boiss. & Reuter var. *carpetana* Pau ex Losa in Anales Inst. Bot. Cavanilles 7:424 (1947), *nom. illeg.*

– *E. nevadensis* Boiss & Reuter var. *granatensis* Ladero & Valdés Bermejo in Sched., *cum descript.* (MAF 98289), *nom. illeg.*

Icon.: Figure 15 A.

Stems 5-45 cm. Sterile branches 0-3(5). Lateral radii (2)4-12(16). Pleiochasial radii (4)5-7(9). Leaves (6)8-22(26) x (4)6-16(20) mm, 1.5-4(5) times longer than wide, ovate, ovate-triangular, rarely ovate-elliptical or elliptical; base subcordate, truncate or rounded; apex pointed or obtuse, rarely rounded; subcoriaceous, greyish-green (28 C4,5; 29 C4; 30 D5), glaucous, often pruinose; anomocytic-type stomata, distributed at regular intervals along the upper surface; discontinuous wax deposits, with crystalloids and platelets. Dichasial bracts 3-13 x 5-20 mm, wide and ovate to oblate-reniform, with subcordate, truncate or rounded base, and rounded or obtuse apex. Scales of the intracyathial septa with laciniae measuring 0.5-2.2 x 0.05-0.3 mm, slightly ciliolate on the upper 1/2-1/3. Capsule 2.8-3.2(3.5) x 3-3.5(4) mm; styles 1.5-2.2 mm, trifurcate at 1/3 of the base. Seeds 2.2-2.6 x 1.4-1.7 mm; SCI: 24-32. 2n = 20,40.

Distribution in the Iberian Peninsula

Spain: Sierra Nevada, Central System, Levantine coastal ranges, Moncayo (Figure 16). A,

Ab, Al, Ay, Gr, I, M?, Sg, Z.

Ecology

Rocky places, screes, rock crevices, pastures; sometimes in reforested pine woods and heliophilous scrub. Mainly on acid, schist and granite substrata; also on calcareous, partly decarbonated soils. From the montane to the alpine zone, 1200-1300 m. In the Sierra Nevada, characteristic of the alliance *Holcicion caespitosi*; in the Central System, in communities of *Jasionio sessiliflorae*-*Koelerietalia crassipedis*.

Localities studied

Spain

ALBACETE: Sierra de Alcaraz, 1500-1600 m, 30SWH47, VII.1890, Porta & Rigo 642 (BM, G, MPU). ALICANTE: Sierra de Aitana, 31SYN38, 15.VI.1923, Gros (BC 99287); Sierra de Mariola, 1200 m, 31SYN18, 11.VI.1991, Porta & Rigo (MA 75426). ALMERIA: Sierra de los Filabres, 30SWG62, 14.VI.1929, Gros (BC 99288). AVILA: Hoyocasero, 1260 m, 30TUK37, 20.VI.1983, Luceño (MA 260025); Hoyocasero, Cueva del Maragato, 30TUK27, 18.VII.1983, E. Rico (MA 292294); Hoyocasero, 1350 m, 30TUK37, 28.VII.1984, Sánchez Mata & V. de la Fuente (MAF 121624); Hoyocasero, Monte Navalvillon, Cueva del Maragato, 1420 m, 30TUK27, 29.VII.1985, Sánchez Mata (MAF 121622); Hoyocasero, Monte de Navalvillar, Cueva del Maragato, 30TUK27, 20.VI.1989, Molero & Rovira (BCF 35128); Pto. de la Menga, La Conchera, 30TUK38, 7.VIII.1984, Sánchez Mata (MAF 121626); Pto. de Villatoro, Valle de Amblés, 1300 m, 30TUK19, 21.VI.1977, Fuertes & Ladero (GDA 4089, MA 213640, 250487, MAF, SALA 20277, SALAF 1134); Puerto de Villatoro, 30TUK19, 2.VII.1968, Fuertes & Ladero (SALAF 20277); Sierra de Guadarrama, Canencia, El Hornillo, 30TVL00, VI.1916, C. Vicioso (MA 75430, 75431); El Hornillo, «El Pocito», 1250 m, 30TVL00, 31.VIII.1984, Sánchez Mata (MAF 121623); Sierra de Guadarrama, Peñarcon, 30TVL00, 7.VII.1914, C. Vicioso (MA 75429); GRANADA: Sierra de Baza, 30SWG12, 18.VII.1971, Ladero & Valdés Bermejo (MAF 98289); Sierra Nevada, Panderon de Veleta, 30SVG60, 24.VII.1851, Bourgeau 1481 (G); Sierra Nevada, Cueva de Panderones, 30SVG60, VI-1889, P. del Campo (MA 75428); Sierra Nevada, Laguna de las Yeguas, 30SYG60, 21.VI.1852, López-Seoane (MA 74964); Sierra Nevada, Peñones de San Francisco, 2600 m, 30SVG60, VIII.1879, Huter, Porta & Rigo 447 (G, MPU); Sierra Nevada, Minas de Beires, 30SVG81, 23.VI.1926, A.J. Willmott (BM); Sierra Nevada, Cerro del Royo (near C. Almirez), 30SVG60, 25.VI.1926, Willmott & Lofthouse (BM); Sierra Nevada, Dornajo, 2050 m, 30SVG60, 8.VII.1971, M.^a Luisa López (MAF 88869); Sierra Nevada, Peñas de San Juan, 2600 m, 30SVG80, 6.VII.1971, Molero (BCF 35179); Sierra Nevada, barranco del río San Juan, 2600 m, 30SVG60, 22.VII.1989, Molero Mesa & Pérez Raya (BCF); Sierra Nevada, Puerto de la Ragua, 30SVG90, 17.VII.1973, Ladero & Valdés (MAF 94426); Sierra Nevada, Prados de Otero, 30SVG60, 9.VII.1980, Ladero, López Guadalupe & Molero Mesa (SALA 23300, SALAF 1135); Sierra Nevada, Veleta, 3000 m, 30SVG60, 21.VI.1980, Pérez Raya (GDA 17234); Sierra Nevada, Veleta, 2600 m, 30SVG60, 17.VII.1988, G. Montserrat & J.M. Montserrat 453 (JACA); Sierra Nevada, Mulhacen, 3300 m, 30SVG70, 23.VII.1987, Cabezudo, Nieto & Flores (MGC 21743); Sierra Nevada, Trevelez, Loma de La Alcazaba, 3200 m, VG70, 7.VIII.1979, Molero Mesa (GDA 6959); SEGOVIA: Grado del Pico, 1060-1300 m, 30TUL87, 5.VII.1984, Rico & Romero (SALA 34031); El Valle del Tabladillo, 30TVL37, 11.VI.1985, T. Romero (SALA 37217); Sepúlveda, 30TVL37, 1.VI.1986, Giráldez & Romero (SALA 41323). ZARAGOZA: Moncayo, Peñas de Herrera, 1450 m, 30TXM02, 29.V.1990, Molero, Rovira & Vallés (BCF 35125); Pujurosa, Peñas de Herrera, 1520-1550 m, 30TXM02, 21.VI.1988, Gómez, A. Martínez & L. Villar (JACA 190189).

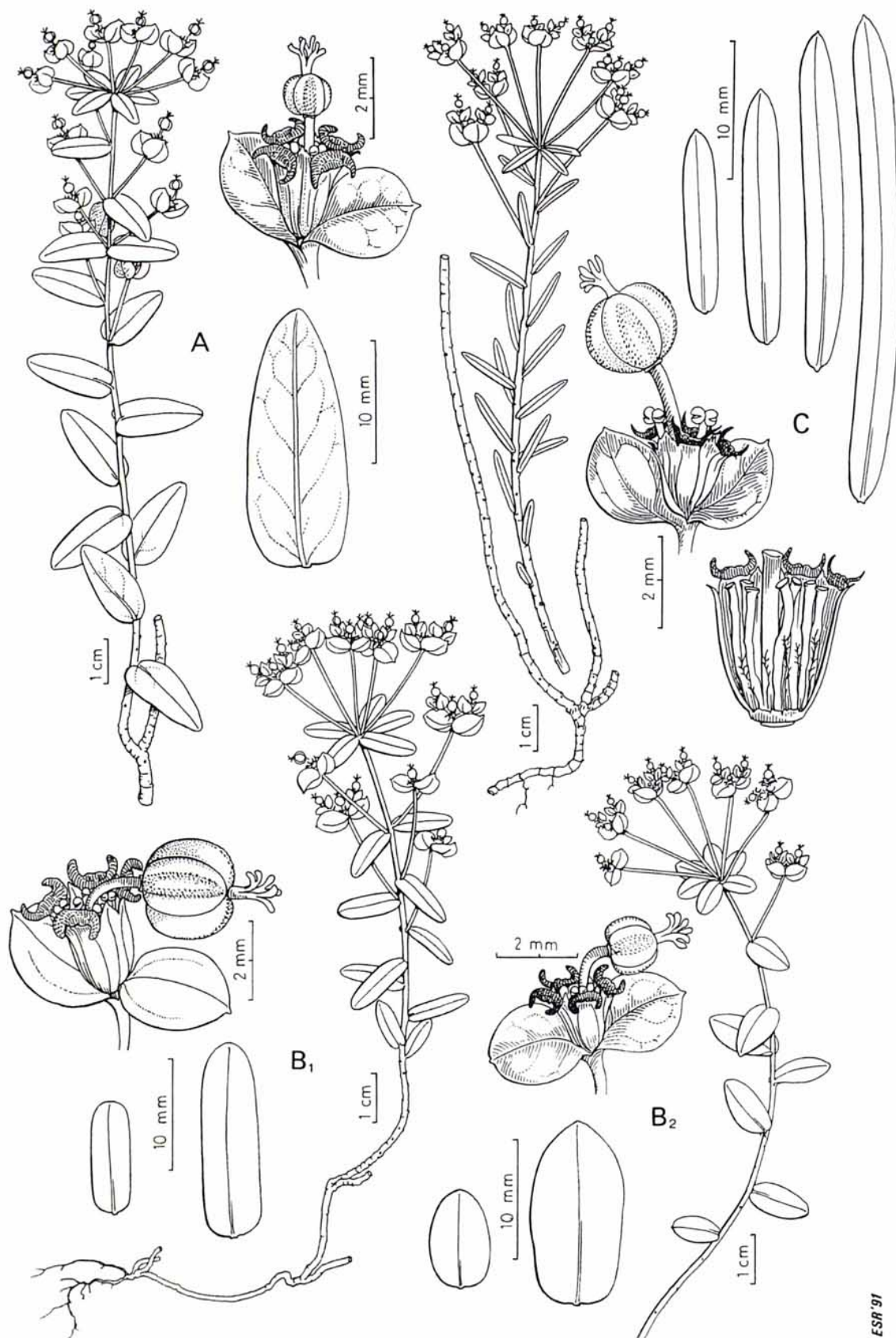


Fig. 15 — A) *E. nevadensis* subsp. *nevadensis* (Hs: Av, Hoyocasero, MA 292294): habit, leaf and cyathium. B) *E. nevadensis* subsp. *aragonensis*: B₁ (Hs: T, Ports de Tortosa, Caro, BC 75452), habit, leaves and cyathium; B₂ (Hs: Bu, Valverde, BCF 36893), habit, leaves and cyathium. C) *E. nevadensis* subsp. *bolosii* (Hs: T, La Pena, BCF 36707): habit, cyathium, leaf gradient.

subsp. **aragonensis** (Loscós & Pardo) O. Bolòs & J. Vigo in Butll. Inst. Cat. Hist. Nat. 38:84 (1974).

Bas. Euphorbia aragonensis Loscos & Pardo in Willkomm, Ser. inconf. pl. Aragon: 95 (1863), *pro parte*, excl. syntype Masada de la Manzaneda. TYPE: «*Hab. in Aragonia australi in monte Sierra de Torrelilla, circa Belmonte*». LECTOTYPE in COI Hb. Willkomm (Figure 20). Sheet containing 3 specimens; the lectotype chosen is the middle specimen, the stem of which bears a label in Loscos' handwriting: «*Euphorbia de / hojas cuadradas / Belmonte*». In the bottom left-hand corner is another label in Willkomm's handwriting: «*Herbarium willkommii / Euphorbia aragonensis L.P. / in Aragonia australis circa Belmonte / legit Loscos junio 1860*».

≡ *Euphorbia nevadensis* var. *aragonensis* (Loscós & Pardo) Boiss. in DC., Prodr. 15(2):1268 (1866) ≡ *Esula aragonensis* (Loscós & Pardo in Willkomm) Gandoger, Fl. Eur. 20:110 (1890) ≡ *E. esula* L. subsp. *aragonensis* (Loscós & Pardo) Malagarriga in Sinops. Fl. ibér.: 209 (1975).

= *E. sennenii* Pau in Boletín soc. Arag. cienc. nat. 6:29 (1907). TYPE: «*Valverde, Cellorigo (Sennen et Elías)*». LECTOTYPE in MA (n.º 75053). Sheet containing 9 specimens and 2 fragments. The second complete specimen from the right of the sheet is chosen as the lectotype. The label accompanying the sheet says: «*Euphorbia castellana* Pau (in the handwriting of Pau) / Castille: Valverde, Montagnes / 1906-2-6 Fres. Sennen et Elías (in the handwriting of Sennen)». It seems obvious that Pau originally intended to call the new taxon «*castellana*»; but on publishing it, decided to call it «*sennenii*». There is no other herbarium material consulted by Pau which may be related to type material.

Icon: Figure 15 B.

Stems 12-35 cm, slightly branched (1-3 branches) at the base. Sterile branches 0(2). Lateral radii 0-7. Pleiochasial radii 3-8. Leaves (5)8-20(24) x (3)5-8(10) mm, 1.5-4(5) times longer than wide, elliptical, oblong or ovate-oblong, with subtruncate or rounded base, apex truncate or broad and obtuse, rarely rounded or subobtus; herbaceous, greyish-green (28 C4,5; 29 C4), dull or slightly satin; anisocytic-type, irregularly distributed stomata on the adaxial surface; crystalloid-type wax deposits. Dichasial bracts 2-12 x 13-14 mm, between oval-triangular and oblate-subreniform, truncate or rounded at the base, apex obtuse or rounded. Scales of the intracyathial septa as in subsp. *nevadensis*. Capsule 2.5-3.2 x 3-3.8 mm; styles 1-1.5 mm, trifurcate between 1/3-1/2 of the base. Seeds 2.2-2.7 x 1.4-1.6 mm; SCI:23-32. 2n=20.

Notes

E. aragonensis Loscos & Pardo was described from the mountains of southern Aragon and Ports de Beseit, in a controversial area where two taxonomical entities coexist under the same name. In the protologue, the Aragonese authors attribute great variability to the new species: «*Variat foliis lanceolato-linearibus lanceolatisque acutis, obtusisve mucronatis et foliis oblongis v. oblongo-quadratis latis, retusis vel emarginatis...*». In fact, this fragment of the description corresponds to a synthesis of two differentiated forms from different localities. The form described as «*foliis lanceolato-linearibus lanceolatisque acutis*» corresponds to the sheet collected by Loscos in the Masada de la Manzaneda, deposited in the COI-Willkomm herbarium; this sheet includes a series of specimens whose leaf morphology is practically exclusive to this locality (Figure 18,B), but which must be assimilated as an extreme variation to subsp. *bolosii*. The same sheet was subsequently used by Lange (1877) to describe *E. esula* var. *acutifolia* Lange.

The form described as «*foliis oblongis v. oblongo - quadratis latis, retusis vel emarginatis*» corresponds to the material collected by Loscos from Belmonte and probably (though no herbarium sheet has been preserved) from Castellote. The sheet from Belmonte, which is conserved in the COI-Willkomm herbarium and is used here to typify *E. aragonensis* (Figure 15,A), contains a number of specimens which fit the restrictive definition of the taxon. We are in agreement with BOLOS & VIGO (1974, 1989), who combined it at the subspecific level.

The populations from Belmonte and from the Ports de Tortosa grow on stony ground and grassy slopes in the culminal zone, above 1100 m, in the mesothermic environment of pinewoods of *P. sylvestris* with *Buxus sempervirens*. In the Els Ports range, they are found at altitudes somewhat above those occupied by subsp. *bolosii* (500-1100 m); the latter colonizes drier environments, on marly and stony ground belonging to the domain of holm oaks or pinewoods of *P. salzmanii*. Certain transitional forms which are difficult to attribute to either subspecies appear in the contact zone.

These eastern populations of the ranges of Teruel and Els Ports usually present oblong leaves with a truncate apex which are not found in western populations. But even in Els Ports de Tortosa individuals with elliptical or elliptical-oblong leaves and an obtuse apex, identical to the populations from Burgos described as *E. sennenii*, can be differentiated.

With respect to *E. sennenii*, in the protologue Pau established the hypothetical affinities of this taxon with *E. gayii* Salisb. endemic to Sardinia and Corsica, and this opinion is shared by LOSA ESPAÑA (1947) and other present-day authors. There are obvious similarities between the two taxa in terms of the cyathium, capsule and seed; but the habit, leaf morphology and structure of the synflorescence are clearly distinct.

Subsp. *aragonensis* presents greater affinity with subsp. *nevadensis*, in terms of leaf morphology and habit and it shares with subsp. *bolosii* certain cuticular microcharacters, with the exception of the waxes.

Distribution in the Iberian Peninsula

Mountains around the northwestern side of the Ebro basin, Ports de Tortosa and mountains of SE Teruel (Figure 16). **Spain:** Bu, Lo, Na, Te, T, VI.

Ecology

Scres, grassy places at the foot of cliffs («*Seslerietea*»), dry, stony meadows, heliophilous scrub (of rosemary, kermes oaks and box), edges of woods and clearings, in the domain of submediterranean oak and holm oak woods. Between 300 and 1350 m. Calcicolous.

Localities studied

Spain

BURGOS: Pancorbo, 30TVN92, 9.VIII.1972, P. Montserrat (JACA 560372); Pancorbo, 650 m, 30TVN92, 18.V.1974, P. Montserrat (JACA 82274); Valverde, 30TWN02, 12.VI.1906, Sennen & Elías (MA 75053); Valverde, Cillorigo, Obarenes, 30TWN02, VI/VII.1908/9, Hno. Elías & Sennen 915 (MA 75719); Valverde, 30TWN02, 27.V.1912, Hno. Elías (BM); Miranda de Ebro, montes de Valverde, 550 m, 30TWN02, 27.V.1990, Molero, Rovira & Vallés (BCF); Bujedo, 460 m, 30TVN92, 27.V.1990, Molero, Rovira & Vallés (BCF 36895). NAVARRA: La Población, El León dormido, 1100 m, 30TWN41, 18.VIII.1973, P. Montserrat & Luis Villar (JACA 484373); La Población, El León dormido, 30TWN41, 16.VI.1989, J. Molero & A. Rovira (BCF 35126); Burgui, Bardipeña, 1000-1350 m, 30TXN63, 7.VI.1975, L. Villar (JACA); Nazar, Peñagallet, 950 m, 30TWN52, 16.VI.1987, Uribe-Echebarría (MA 477721). TARRAGONA: Tortosa, Monte Caro, 31TBF72, 15.VI.1915, Font Quer (BC 57222, BC 75452); Beseit, 1050 m, 31TBF72, C. Baiges, 22.VIII.1989 (BCF 35129). TERUEL: Belmonte, 1860 m,

30TYL42, w.d., Loscos (COI- Herb. Willkomm). VITORIA: Lagrain, 1200 m, 30TWN31, 17.VIII.1973 (JACA 469073).

subsp. **bolosii** Molero & Rovira, *subsp. nova*.

Caules graciles, (10)15-34(42) cm alti, ramis sterilibus orbat. Folia (6)10-45(52) x (1,5)2-4(7) mm, 5-20-ies longiora quam lata, linearia vel lineari-oblonga, basi rotundata, subtruncata vel breviter attenuata et apice obtusa — raro acuta — sed aliquando mucronata, una cum bracteis fere coriacea, nitida, viridi-flavescentia, sed saturate viridia post exsiccationem. Bractee dichasiales 5-14 x 4-13 mm, ita longae quam latae vel vix longiores. Laciniae septales inflorescentiarum masceularum 0,6-2 x 0,05-0,2 mm, paulo divisae atque parce apice pubescentes. Capsula 3-3,5(4) x 3,5-4(4,5) mm. Stylus 1,2-2,5 mm, a medio trifurcatus. Semina 2-2,5 x 1,4-1,8 mm, ovato-oblonga.

Subspecies clarissimo magistro Oriol de Bolòs observatione maxima dicata.

TYPE: Montsant, 900 m, 25.VI.1918, *Font Quer*. Holotype in BC (n.º 103280).

= *E. esula* L. var. *acutifolia* Lange in Willk. & Lange, Prodr. Fl. Hisp. 3:503 (1877). TYPE: «in *Arag. austr. (ad Masada de Manzaneda, Loscos!)*». LECTOTYPE in COI Hb. Willkomm (Figure 21). Sheet containing five fragments, as well as five labels of different origins; we chose as the lectotype the second specimen from the right. Among the labels two are of interest; one is blue, in the handwriting of Loscos, and says: «*Euphorbia/Masada de La Manzaneda*»; the other is in the handwriting of Willkomm: «*Euphorbia aragonensis L.P./var. lanceolatifolia / in aragonia australis en la Masada de la Manzanera / legit Loscos mayo-julio 1860-62*».

= *E. nevadensis* Boiss. & Reuter subsp. *aragonensis* (Loscos & Pardo) O. Bolòs & Vigo var. *acutifolia* (Lange) O. Bolòs & Vigo in Butll. Inst. Cat. Hist. Nat., 38:84 (1974) = *E. nevadensis* Boiss. & Reuter var. *aragonensis* (Loscos & Pardo) Boiss. in DC. forma *acutifolia* (Lange) A. & O. Bolòs, Miscel·lània Fontseré: 92 (1961).

— *E. aragonensis* Loscos & Pardo var. *lanceolatifolia* Loscos & Pardo ex Lange in Willkomm & Lange, l. c., *nom illeg.*

Icon.: Figure 15C.

Stems (10)15-34(42) cm, solitary or 2-3. Sterile branches absent. Lateral radii 0-14. Pleiochasial radii (4)5-8(9). Leaves (6)10-45(52) x (1,5)2-4(7) mm, 5-20 times longer than wide, from linear to linear-oblong, exceptionally wide or narrow and oval-triangular; base subtruncate, rounded or shortly attenuate; apex obtuse, rarely pointed, mucronulate or not; yellowish-green, dark green (29 E8) through drying, shiny; ano- or anisocytic-type stomata, irregularly distributed on the adaxial surface; continuous wax deposits, without crystalloids. Dichasial bracts 5-12 x 4-13 mm, length equal to or greater than width, ovate-lanceolate, ovate-rhombic, ovate or suborbicular, with truncate, rounded or widely cuneate base and obtuse apex. Scales of the intracyathial septa with laciniae of 0.6-2 x 0.05-0.2 mm, glabrous or with few cilia on the apex. Capsules 3-3.5(4) x 3.5-4(4.5) mm; styles 1.-2.1(2.5) mm, trifurcate at the middle; stigmas with lobes 0.2-0.7 mm. Seeds 2-2.5(2.7) x 1.3-1.6(1.8) mm; SCI:20(22)-30. 2n=20,60.

Notes

This taxon would undoubtedly deserve specific rank if no transitional forms toward subsp. *aragonensis* existed in the contact areas, as occurs in Els Ports de Tortosa and some enclaves in Logroño and Navarre.

Distribution in the Iberian Peninsula

Outer ranges bordering on the eastern area of the Ebro basin (Figure 16). **Spain:** B, Cs, Hu, L, Lo, Na, T, Te.

Ecology

Mediterranean orophyte occurring in screes, stony places, marly soils, stony clearings in shady pine woods, mesoxerophilous scrub, between 500 and 1200(1400) m. Calcicolous. In communities of *Thlaspietea* (a species characteristic of *Kentrantho-Euphorbietum bolosii*) and *Rosmarinetalia* (especially in the alliance *Aphyllanthion*).

Localities studied

Spain

BARCELONA: Anoia, La Pobla de Claramunt, 490 m, 31TCG90, 4.VI.1978, J. Nuet Badia (BC 631117); Bages, Castellfollit del Boix, 31TCG91, 5.VI.1977, O. de Bolòs (BC 622894);

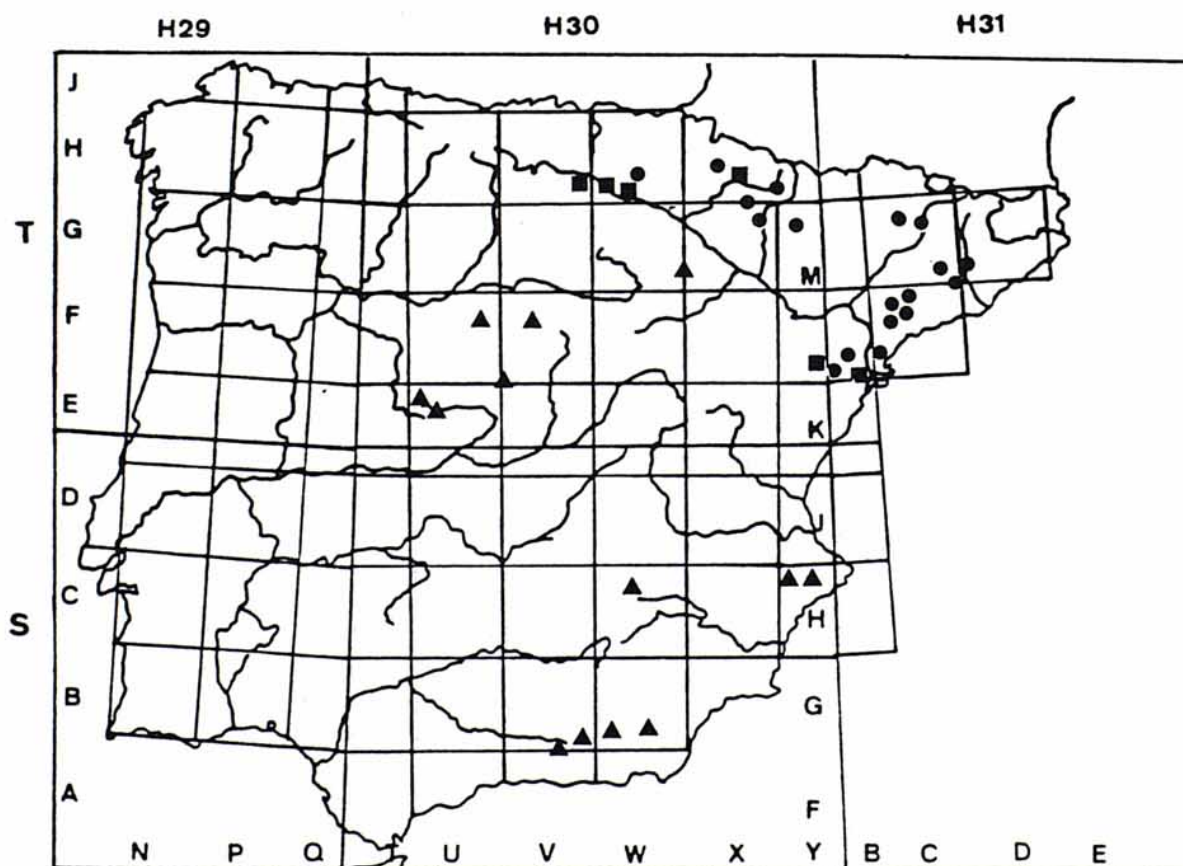


Fig. 16 — Distribution map of *E. nevadensis* Boiss & Reuter subsp. *nevadensis* (▲); subsp. *aragonensis* (Loscos & Pardo) Bolòs & Vigo (■); subsp. *bolosii* Molero & Rovira (●).

Bages, Santa Cecilia de Montserrat, 675 m, 31TCG90, 25.IV.1983, Nuet & Panareda (BC 673345); Bages, Monistrol de Montserrat, 285 m, 31TDG00, 20.V.1987, Nuet & Panareda (BC 673415); Manresa, Servitge, 31TDG02, V.1910, Font Quer (BC 57227); CASTELLON: Port de Morella, vall del Salt, Viver de Terralles, 500 m, 31TBF60, 18.VI.1956, A. & O. de Bolòs (BC 150914). HUESCA: Biel, Sto. Domingo, 1400 m, 30TXN70, 23.V.1975, P. Montserrat & L. Villar (JACA 1139/75); Ena, Pico Alto, 900 m, 30TXM89, 28.V.1973, P. Montserrat (JACA 137373); Guara, La Paul-La Espátula, 1100-1200 m, 30TYM28, 11.VII.1974, P. Montserrat (JACA 3916); Jaca, Oroel, La Cruz, 1800 m, 30TYN01, 4.VI.1943, A. de Bolòs (BC 136765); Collado de Oroel, 1080 m, 30TYN01, 7.VII.1971, L. Villar & P. Montserrat (JACA 426271); Pto. de Oroel, stony marles, 1200 m, 30TYN01, 15.IV.1991, J. Molero & al. (BCF 35127); Jaca, Oroel W, 1400-1500 m, 30TYN01, 9.VI.1986, P. Montserrat (JACA 479286); Jaca, Torre del Moro, 900 m, 30TXN91, 12.V.1967, Puigdefabregas & P. Montserrat (JACA 395067). LLEIDA: Organyà, Els Tres Ponts, 31TCG67, 4.VI.1932, Font Quer (BC 99285); Les Garrigues, 31TCF28, 24.IV.1973, J.M.^a Masalles (BCC); Pallars Jussà, Senterada, 31TCG38, 3.VII.1973, O. Bolòs, Folch, Marganedes & Sierra (BC 610582). LOGROÑO: «Lucronio», 30TWN40, V.1876, Zubia (BC 649296, 57219). NAVARRA: Aoiz, entre Aoiz y Gorriz, 570 m, 30TXN34, 8.VI.1971, P. Montserrat & L. Villar (JACA 249671); Srra. de Codes, 1100 m, 30TWN52, 18.VI.1973, L. Villar (JACA 210973). TARRAGONA: Albarca, 31TCF27, 28.V.1975, Fdez. Casas & Molero (MA 329180); Conca de Barberà, Blancafort, 675 m, 31TCF49, 21.VI.1973, J.M. Masalles (BCC); Cornudella, 31TCF27, 22.IV.1972, J. Molero (BCF 111491); Montsant, 900 m, 31TCF27, 25.VI.1918, Font Quer (BC 103280); Montsant, pr. Font del Navàs, 850 m, 31TCF27, 29.V.1957, A. et O. de Bolòs & P. Seró (BC 144952); Montsant, Albarca, marly soil, 740 m, 31TCF27, 20.IV.1991, J. Molero (BCF 36894); La Pena, Pic de l'Aguila, 31TCF37, 16.V.1976, Molero & Pujadas (BCF 35178); Muntanyes de Prades, La Pena, cap el Mirador, 950 m, 31TCF37, 4.VII.1989, Molero (BCF 35124); Muntanyes de Prades, La Pena cap el Mirador, 950 m, 31TCF37, 3.VI.1990, J. Molero (BCF 36707); Ports d'Horta, Les Eres, 700 m, 31TBF73, 23.V.1984, J. Molero & A. Rovira (BCF 72954, 71739); Ports de Tortosa, Els Pons, 1000 m, 31TBF72, 18.VI.1935, Font Quer & Rothm. (BC 84358); Ports de Tortosa, Font del Teix, de Almescar hacia Vallcanera, 31TBF72, 3.VII.1962, A. et O. de Bolòs, L. de Torres & J. Vigo (BC 149101); Serra de Llaveria, la Miranda, 760 m, 31TCF15, 19.VI.1973, R. Folch (BC 631227); Serra la Llena, 31TCF27, 10.III.1974, A. Boldú (BCF 18114); TERUEL: Masada de la Manzaneda, 1860-62, Loscos, COI, herb. Willkomm; Toza de Peñarroya, 31TBF51, 2.VII.1918, C. Pau (MA 75453).

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Fig. 17 — Type of *E. pinifolia* Lam.

Fig. 18 – Type of *E. androsaemifolia* Willd. ex Schlecht.



Fig. 19 – Type of *E. esula* L. subsp. *orientalis* (Boiss. in DC.) Molero & Rovira.

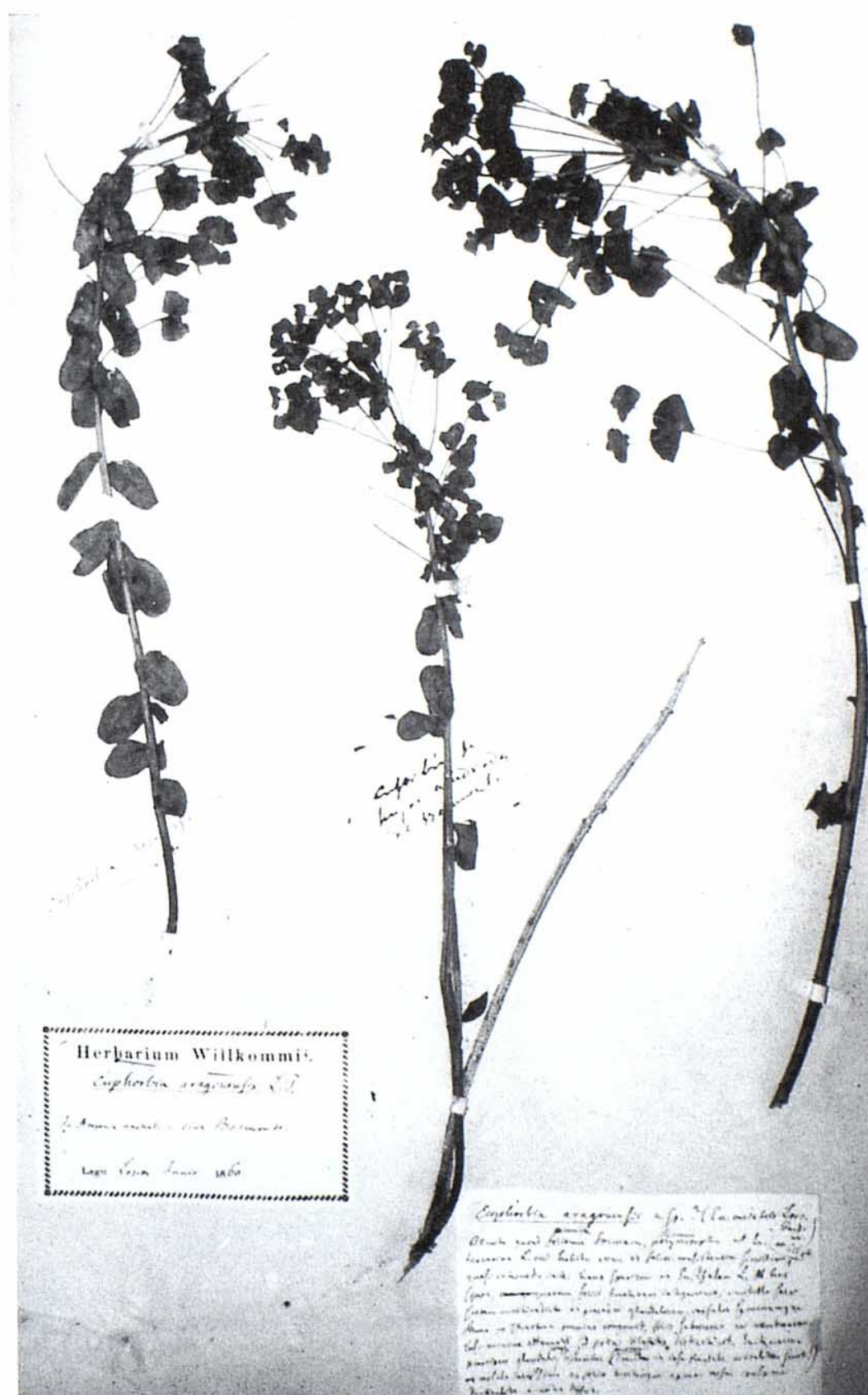


Fig. 20 — Type of *E. aragonensis* Loscos & Pardo in Willk.

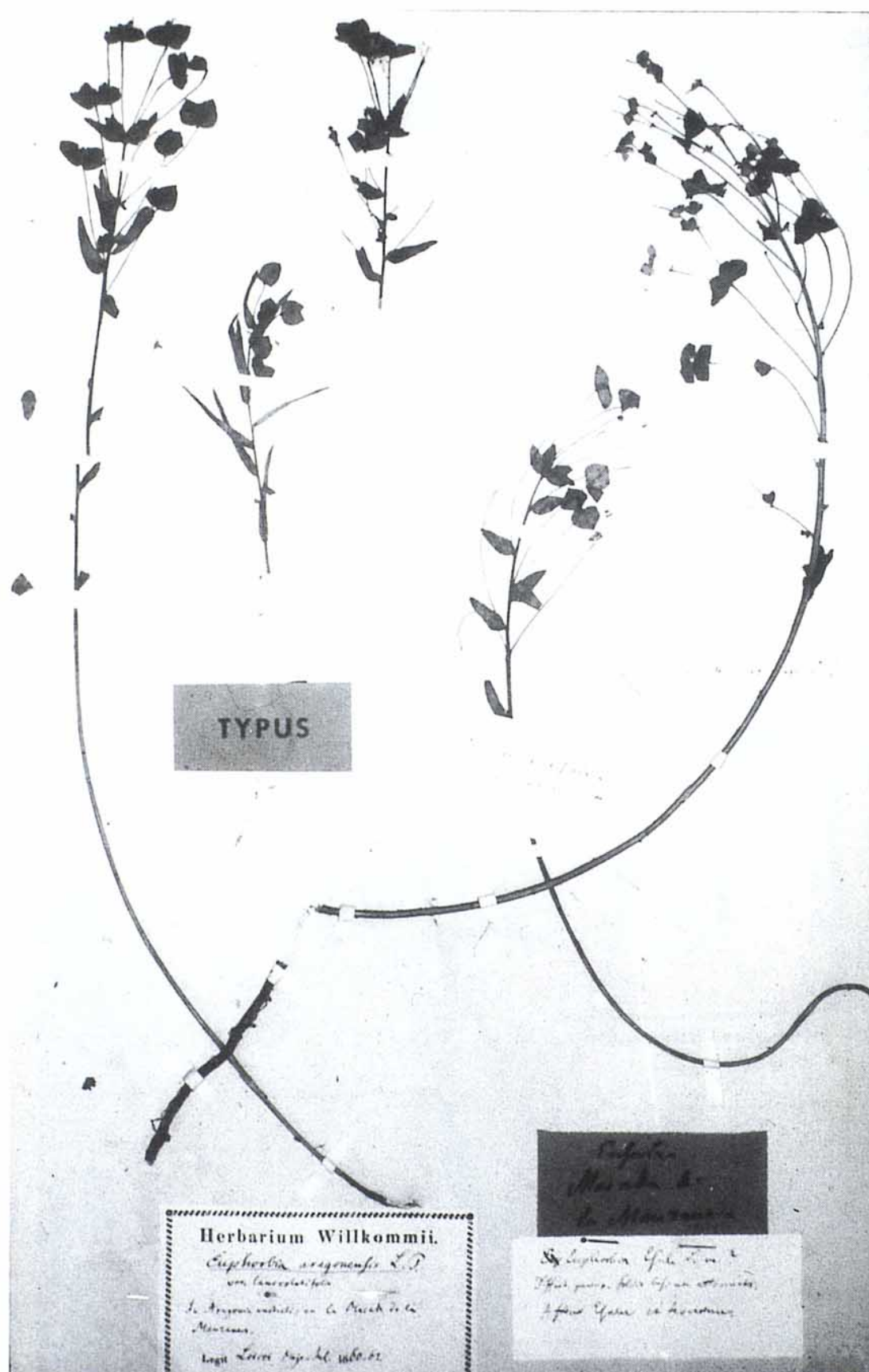


Fig. 21 — Type of *E. esula* var. *acutifolia* Lange.

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