

## DELPHINIUM L. SUBGEN. DELPHINIUM IN THE IBERIAN PENINSULA AND NORTH AFRICA: A NEW TAXONOMIC APPROACH

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### Abstract

Both the microspecies (P.H. Davis, B. Pawlowsky) and macrospecies concepts (R. Maire) were used during the 1960s to obtain a useful taxonomic system for the annual species of the genus *Delphinium* (*Ranunculaceae*). A reappraisal of this group on the basis of new data on breeding systems, pollination ecology, karyotype evolution and isozyme variation is proposed. The annual species as a whole may be considered as a monophyletic group (some gene duplications might indicate a significant evolutionary node), mainly outcrossing and without reproductive barriers (chromosome number, karyotype structure, flower architecture or pollinator behaviour) between species, other than geographic isolation. It forms a continuum around the Mediterranean basin extending to the Irano-Turanian Region. The preliminary electrophoretic results suggest a pattern of very short genetic distances both at species and population levels. A new taxonomical approach involving a degree of nomenclatural renewal and the description of two new North African taxa, *Delphinium favargeri* C. Blanché, Molero & Simon P. and *Delphinium* ser. *Cossoniana* C. Blanché, Molero & Simon P. are presented.

### Introduction

*Delphinium* L. subgen. *Delphinium* includes, following current usage (MALYUTIN, 1987; BLANCHÉ, 1990), a few species of annuals -except the perennial *D. balansae* Boiss. & Reut.- with small (*c.* 1 mm) seeds, grouped in two sections. Sect. *Anthriscifolium* W.T. Wang comprises only 3 species from the subtropical region of China (MUNZ, 1967b and MALYUTIN, *l.c.*) whereas sect. *Delphinium* comprises the remaining ones, which are found in the Mediterranean and Irano-Turanian Regions (BLANCHÉ, *l.c.*). The total number of recognized species belonging to the subgen. *Delphinium* is 28 representing the 8.75 % of the total number of the genus (320 species, *cf.* TAMURA, 1995). The whole group of Mediterranean annual species has been widely recognized as *D. peregrinum* L. *s.l.* (GREUTER & *al.*, 1989).

This group of species can be regarded as a complex of very closely related species distinguished by a small number of morphological characters such as spur length, sepal length and lateral petal shape (PAWLOWSKY, 1963; DAVIS, 1965). The taxonomic organization of such species complex has historically been highly diverse and the range of available names and species described is very large. Both extremes of the species concept have been applied to this group. At one extreme, several authors (including PAWLOWSKY, 1964; DAVIS, 1965 or GREUTER & *al.*, 1989) accepted a narrow species concept, and hence recognized a variable number of species, as shown in Table 1A,



## A. Analytic treatments

*D. peregrinum*  
*D. virgatum*  
*D. venulosum*  
*D. bithynicum*  
*D. cinereum*

P.H. DAVIS (1965)

Flora of Turkey and the East. Aegean Islands 1; 117-119

1964	<i>D. peregrinum</i>	1993	<i>D. peregrinum</i>
	<i>D. hirschfeldianum</i>		<i>D. hirschfeldianum</i>
	<i>D. obcordatum</i>		<i>D. ambiguum</i>
	<i>D. haltearatum</i>		<i>D. halteratum</i>
	<i>D. verdunense</i>		subsp. <i>halteratum</i>
			subsp. <i>verdunense</i>
	<i>D. balcanicum</i>		<i>D. balcanicum</i>
	<i>D. gracile</i>		<i>D. gracile</i>
	<i>D. hellenicum</i>		<i>D. hellenicum</i>

B. PAWLOWSKY (1964, modified 1993)  
 Flora Europaea 1 (2 ed.): 257-260.

## B. Synthetic

*D. balansae*  
*D. cossonianum*  
*D. peregrinum*  
 subsp. *junceum*  
 subsp. *nanum*  
 subsp. *halteratum*  
 var. *cardiopetalum*  
 var. *longipes*  
 var. *confertum*  
 var. *obcordatum*  
 var. *macropetalum*  
 var. *elongatum*  
 f. *tribracteolatum*  
 f. *caeruleum*  
 f. *laxum*  
 f. *rifanum*  
 f. *albolilaceum*  
 f. *pseudogratile*

R. MAIRE (1964)

Flore Afrique du Nord 11: 49-85.

*D. peregrinum*  
 subsp. *verdunense*  
 subsp. *gracile*  
*D. pubescens*  
*D. orientale*

O. BOLÓS & J. VIGO (1984)  
 Flora Països Catalans 1: 225-229

*D. balansae*  
*D. cinereum*  
*D. cossonianum*  
*D. peregrinum* aggr.  
*D. ambiguum*  
*D. balcanicum*  
*D. davisii*  
*D. gracile*  
*D. hellenicum*  
*D. hirschfeldianum*  
*D. macropetalum*  
*D. peregrinum*  
*D. venulosum*  
*D. verdunense*  
*D. virgatum*

GREUTER, BURDET &

LONG (eds.) (1989)

Med-Checklist 4: 404-408.

Table 1. Previous taxonomic arrangements of subgen. *Delphinium* in the Mediterranean Area.



whereas others (including MAIRE, 1964 and BOLÒS & VIGO, 1984) adopted a system based on wider linnaeons, and hence included almost all the diversity under the classic name of *D. peregrinum* L., as shown in Table 1B. In accordance with this second group of authors, the widest concept was proposed by BOLÒS & VIGO (*l.c.*) who continued to include the related annual genus *Consolida* (DC.) Gray within *Delphinium s.l.*, although it is generally accepted as a separate taxonomic entity (TRIFONOVA, 1990; TAMURA, 1995). In the case of the North African taxa, the scheme of MAIRE (1964) made it virtually impossible to determine a sheet through the intricate system of subspecies, varieties and forms (see Table 1B).

In our preparation of *Delphinium* for *Flora Iberica* (BLANCHÉ & MOLERO, 1986), we initially adopted the microspecies concept for the first group of flora, when ever possible. In certain cases, however, the separation between species was not sufficient. The use of the commonly employed characters (*R e/s* = ratio between spur and sepal length; or the lateral petal shape) was unable to distinguish separate units and several intermediate cases occurred, as shown in Fig. 1.

We, therefore, eventually adopted a solution whereby 2 species were considered; *D. halteratum* Sm. in Sibth. & Sm. (with two subspecies, subsp. *halteratum* and subsp. *verdunense* (Balb.) Asch. & Graebn., and *D. gracile* DC. (BLANCHÉ & MOLERO, *l.c.*). Although this solution might be acceptable for general Flora purposes, and although the last edition of *Flora Europaea* (PAWLOWSKY, 1993) also adopted the same option (see also Table 1A), we maintain that these intermediate zones should be interpreted as: a) simple phenotypic plasticity following a general North-South pattern, or b) the result of repeated genetic flows between populations limiting the divergence forces. Finally, we consider what the correct size of the species concept in this group should be and what the biodiversity pattern within subgen. *Delphinium* is.

During the last 10 years, our Laboratory has undertaken field work on populations and experimental work in the greenhouse, enlarging at the same geographical range. The resulting data on species biology, on the survey of variation patterns and on karyotype analysis allow us to consider a more suitable taxonomy for the Ibero-North African species of subgen. *Delphinium*.

## Reproduction biology

### Pollination Ecology

The annual species of *Delphinium*, in common with the whole genus, show flowers which are particularly well adapted to entomophilous pollination (BOSCH, 1993). The general flower structure comprises five external petaloid sepals, one of them extending in spur, and four internal petals, two of them coalesced in a nectariferous tube partially contained within the sepaloid spur and two such clawed and more or less exerted. This flower offers insect rewards such as nectar (range from 1 to 3,5 µl/flower in the annual species, BOSCH unpubl. data) and pollen. Protandry is nearly perfect and the 16 stamens down back before the pistils emergence that, at the end, will open the bifid dry stigmata.



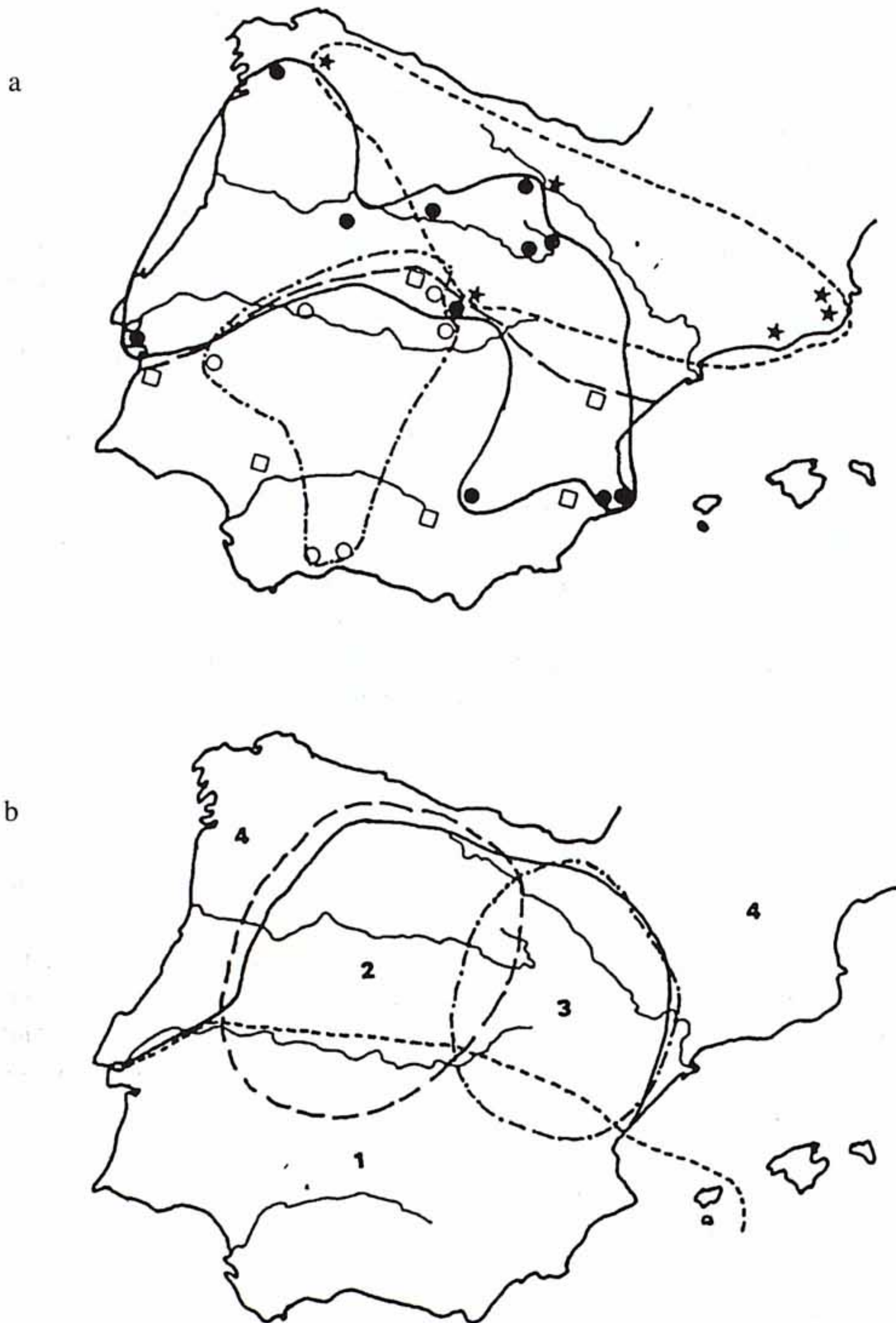


Fig. 1. Geographic distribution of phenotypic plasticity of the pair *D. verdunense* - *D. gracile* in the Iberian Peninsula (from BLANCHÉ, 1991).

a) Distribution of the R e/s character

★ R e/s < 1,5 (type I)

● 1,5 < R e/s < 2 (type II)

○ 2 < R e/s < 2,5 (type III)

□ R e/s > 2,5 (type IV)

(see text for explanation)

b) Distribution of lateral petal typical shape

1. *D. gracile* (3)

2. *D. halteratum* (2)

3. Intermediate between *D. gracile*-*D. verdunense*

4. *D. verdunense* (1)



Corresponding to this general pattern, the principal pollinators of the Western Mediterranean species of subgen. *Delphinium* are Hymenoptera (belonging to the genera *Bombus* or *Amegilla*). The pollen load analysis also confirms the role of these insects as pollinators (see BOSCH & Al., this volume). Some Lepidoptera, however, particularly *Macroglossum stellatarum* L., visited the flowers of the annual species a very much higher proportion than in *Aconitum* L. or *Consolida* Gray species (BOSCH & al., this volume) looking for nectar rewards. The frequency of visits of Lepidoptera may compensate for the low pollen carrying capacity per visit. This result is similar to that presented by WASER & PRICE (1990) when comparing effectivity and effectiveness of bumblebees vs. hummingbirds in the American perennial *Delphinium nelsonii* Greene.

The flight patterns of the principal legitimate pollinators (*Bombus* sp.) depend, among other factors, on the inflorescence architecture (WYATT, 1982; PLEASANTS & ZIMMERMANN, 1990) and the highly ramified open and paniculiform racemes of the subgen. *Delphinium* (BLANCHÉ, 1991). This implies the repeated visit to the flowers of different branches of the same individual and the subsequent promoting of geitonogamy, as recorded in field observations (BOSCH, 1993), although xenogamy has also been observed. Syrphidae and small solitary bees could increase the selfing rates by foraging stamens frequently (BOSCH & al., this volume).

### Breeding systems

To analyse the breeding systems, plants grown from seed were cultivated in pots in the greenhouse and the experimental crosses were carried out following the recommendations of DAFNI (1992). Among the several populations studied (BOSCH, unpubl. data), we present here (Table 2), by way of example, the results concerning one population of *D. verdunense* Balb. (Catalonia: Alt Penedès, St. Llorenç d'Hortons, voucher in BCF) which could be considered as representative as they do not deviate from the remaining populations surveyed for breeding systems. The most relevant data are the following: there is no parthenogenetic seed production after emasculation and bagging of flowers. Bagged entire flowers produced well-developed 35% of the total seed set (ranging in all the populations studied from 25-40%) but the forced hand self-pollination produced the same results, thus contrasting with the seed set obtained in perennials in which insect exclusion prevented the formation of seeds whereas the hand self-pollinated flowers are highly self-compatible for certain species (BOSCH, unpubl. data) and self-incompatible for others (MACIOR, 1975). In subgen. *Delphinium*, geitonogamy, which was one of the systems observed in nature, produced 75% seeds and xenogamy reached 82%.

Interpopulational crossings showed similar results to xenogamy, indicating therefore high compatibility between conspecific populations even when placed in relatively distant localities (see populations D-VER-1 and D-VER-2 in Table 2, which are 180 km apart).

The crossing program continued for the W. Mediterranean species of subgen. *Delphinium* available in our greenhouses and all the interspecific crossings between



Treatment	Developed seeds			Undeveloped seeds			Total seed			
	$n_i$	range	$m \pm SE$ (%)	$n_i$	range	$m \pm SE$ (%)	$n_i$	range	$m \pm SE$	
Free pollination .....	32	470	6-24	14.69±0.88 (70.89)	193	0-24	6.03±1.04 (29.11)	663	14-36	20.72±0.89
Parthenogamy .....	10	0	0	0	-	-	-	-	-	-
Autogamy (passive) .....	15	111	0-24	7.40±1.87 (35.24)	204	3-27	13.60±1.74 (64.76)	315	15-30	21.00±1.11
Autogamy (active) .....	15	111	0-27	7.40±1.86 (36.27)	195	2-21	13.00±1.31 (63.73)	306	14-29	20.40±1.14
Geitonogamy .....	48	616	3-23	12.83±0.76 (74.49)	211	0-20	4.40±0.58 (25.51)	827	9-27	17.23±0.69
Intrapopulational xenogamy .....	26	399	6-21	15.35±0.72 (82.95)	82	0-9	3.15±0.50 (17.05)	481	13-24	18.50±0.52
Interpopulational xenogamy* .....	25	492	13-31	19.68±1.54 (81.59)	111	1-20	4.44±0.88 (18.41)	603	14-33	24.12±0.99
<i>D. verdunense</i> X <i>D. gracile</i> .....	37	566	10-22	15.30±0.51 (69.45)	249	2-17	6.73±0.46 (30.55)	815	15-31	22.03±0.52
<i>D. verdunense</i> X <i>D. cossorianum</i> ..	31	578	6-29	18.65±0.90 (73.35)	210	2-17	6.77±0.66 (26.65)	788	21-32	25.42±0.47
<i>D. verdunense</i> X <i>D. balansae</i> .....	19	255	4-22	13.42±1.16 (64.39)	141	1-24	7.42±1.27 (35.61)	396	12-31	20.84±1.07
<i>D. verdunense</i> X <i>D. obcordatum</i> ...	27	488	12-24	18.07±0.51 (75.43)	159	2-11	5.89±0.38 (24.57)	647	19-32	23.96±0.51
<i>D. verdunense</i> X <i>D. favargerii</i> .....	23	369	7-25	16.04±1.00 (73.36)	134	2-12	5.83±0.60 (26.64)	503	14-31	21.87±0.87

N = Sample size,  $n_i$  = total seed set of each kind;  $m \pm SE$  = mean  $\pm$  standard error of seeds produced per flower; (%) = percentage of developed and undeveloped seeds, respectively. (\* With population VER2, 180 Km far).

Table 2. Breeding systems in *D. verdunense* (VER1, Hs: Barcelona; St. Llorenç d'Hortons).



*D. gracile*, *D. balansae*, *D. cossonianum* Batt., *D. obcordatum* DC. and *D. favargerii* gave notable reproductive success (around 65-75 % of the seed set) (BOSCH, unpubl. data).

The P/O ratio of CRUDEN (1977) ranged from 2300-3000 (one exception: 4700 for *D. balansae*, the single perennial species of subgen. *Delphinium*) (BOSCH, 1993). These values lie just along the boundary between facultative xenogamy and obliged xenogamy and as such confirm the experimental results.

The reproduction results which should be taken in to consideration for a final taxonomic proposal are, thus:

- Autogamy is possible (species are not self-incompatible and seed set can be obtained), but limited (and one of the modes of genetic isolation in Mediterranean annuals discussed by Prof. M. Zohary at this meeting is not yet fully available).
- Geitonogamy offer good results but xenogamy show better seed set.
- Annual species are highly self-compatible and interpopulational crosses in the same species are also permitted (whereas there is no descendance when crossed with species belonging to other subgenera of *Delphinium*).

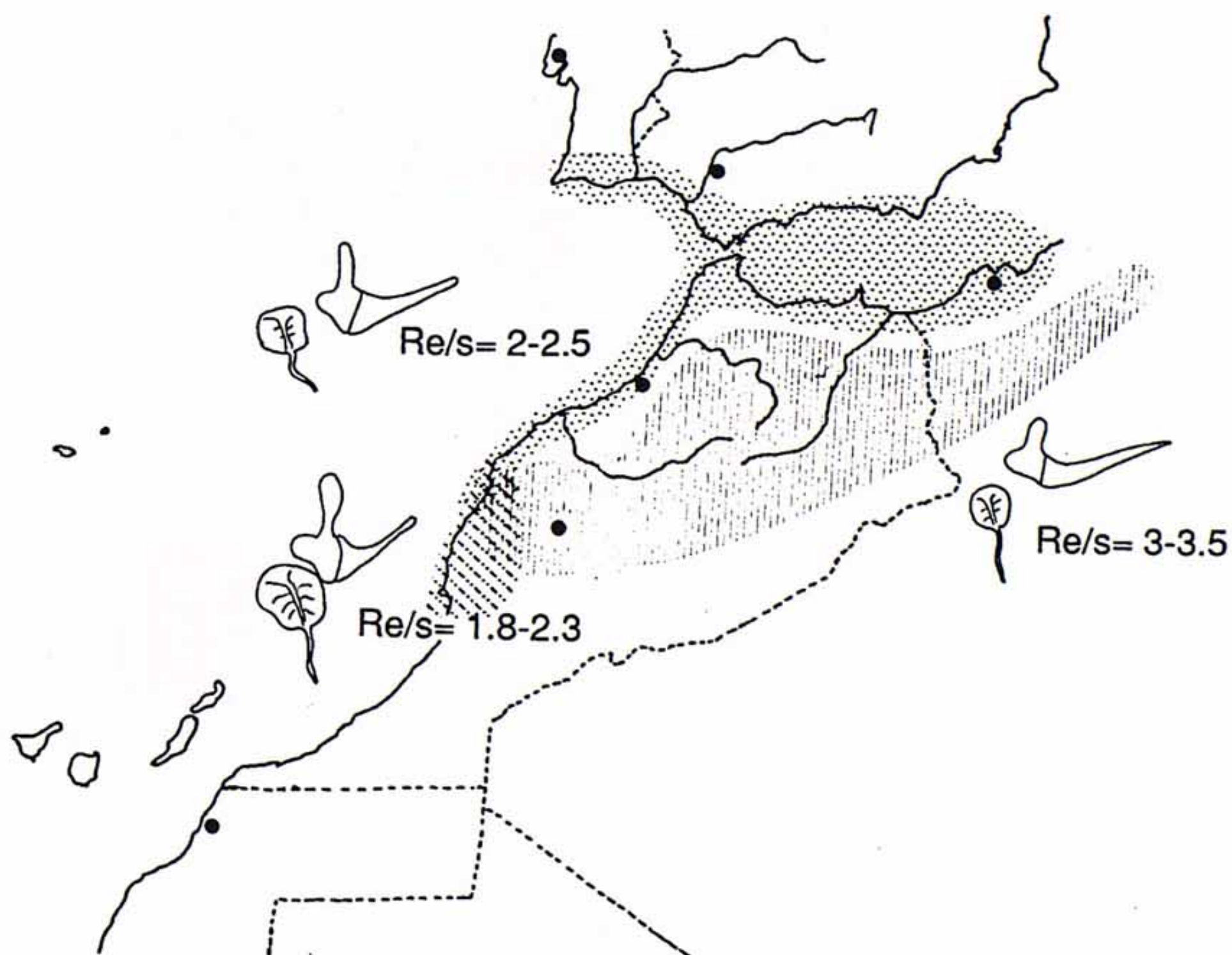


Fig. 2. Geographic distribution of  $R e/s$  and petal shape of the *D. macropetalum* grown in Morocco and S. Spain.



The absence of genetic barriers leads to a high probability of interpopulation genetic flow, both between sympatric species as well as along the boundaries of adjacent distribution areas. Thus, the presence of numerous intermediate forms is perfectly predictable, in agreement with the peripatric clinal speciation model of WHITE (1978) and corresponds to the pattern presented above for the pair *D. verdunense*-*D. gracile* in the Iberian Peninsula (Fig. 1). When we examined the variability of the group of *D. macropetalum* DC. (lateral petals of rounded limb, not cordate at base) in Western North Africa, the same pattern was observed (see Fig. 2.). In this map, 3 taxonomic units were clear, by distinguishable, following the examination of many of herbarium sheets and the conducting of field observations: first, a southern and eastern area with

TAXA	n	2n	ORIGIN	REFERENCE
<i>D. balansae</i>		16	Ma	QUÉZEL (1957)
	8		Ma	GALLAND (1990 in litt.)
	8	16	Ma	BLANCHÉ & al. (1990)
<i>D. balcanicum</i>		16	Gr	LOON & SNELDERS (1979)
		16	Gr	STRID & FRAZEN (1981)
		16	Bu	KOEVA-TODOROVSKA (1985)
<i>D. cossonianum</i>		16	Ma	BLANCHÉ & al. (1990)
<i>D. davisii</i>		16	An	GIMÉNEZ (1995)
<i>D. favargerii</i>		16	Ma	BLANCHÉ & al. (1990)
		16	Ma	BOSCH & al. (ined.)
<i>D. gracile</i>	8		Hs	PASTOR & al. (1984)
	8		Hs	GALLEGO & APARICIO (1990)
	8	16	Hs	BLANCHÉ (1991)
<i>D. halteratum</i>		16	Si	CAMPO & ROMANO (1995)
<i>D. macropetalum</i>		16	Ma	BLANCHÉ & al. (1990)
<i>D. obcordatum</i>	8		Hs	BLANCHÉ & MOLERO (1984)
		16	Ma	BLANCHÉ & al. (1990)
		16	Ma	BOSCH & al. (ined.)
		16	?	GREGORY (1941)
<i>D. peregrinum</i>		16	An	DEMIRIZ (1980)
		16	Bu	KOEVA-TODOROVSKA (1985)
		16	An	GIMÉNEZ (1995)
		16	?	TJEBBES (1928)
<i>D. verdunense</i>		16	?	LEWITSKY (1931)
	8		?	MEHRA & RAMANANDAN (1972)
		16	?	AL-KELIDAR & RICHARDS (1981)
	8		Hs	BLANCHÉ & al. (1985)
		16	Lu	QUEIRÓS (1990)
	8	16	Hs	BLANCHÉ (1991)
	8	16	Hs	BOSCH (1993)
		16	Hs	SIMON & al. (1995)
<i>D. virgatum</i>		16	An	GIMÉNEZ (1995)

Table 3. Chromosome numbers in *Delphinium* subgen. *Delphinium*.



purple flowers and yellowish gorge showing long spurs and shorter sepals (R e/s= 3-3.5) and a short upper lobe of the upper petals, as well as smaller lateral petals; a second group of populations with flowers lilac-deep blue with longer upper lobe of petals and R e/s= 2-2.5; and a third group, strictly restricted to sandy littoral areas, with the longest upper lobes and R e/s= 1.8-2.3. Numerous intermediate forms, however, have been found among the three groups, both in the field as well as among herbarium samples.

### Karyology

The karyological studies are in agreement with the apparent absence of genetic interspecific barriers. The chromosome number of all the species of subgen. *Delphinium* counted were found to be  $2n=16$  (Table 3). This constant diploid number is remarkably different from the polyploidy or increasing dispoloidy found in the perennial *Delphinium* or *Aconitum* species or from the increasing and decreasing dispoloidy reported from the remaining annual genera of the tribe, as *Consolida* or *Aconitella* Spach (see BLANCHÉ & *al.*, in press and GIMÉNEZ, 1995).

The karyotypes are also very similar between species and generally constant between populations, both in the Iberian Peninsula (BLANCHÉ, 1991) as in North Africa (BLANCHÉ & *al.*, 1990). There are bimodal and very asymmetric karyotypes (Fig. 3 and Table 4) clearly shorter than in perennials. The shortening of the mean chromosome length averaged 30% and it should be pointed out that this figure is of the same order (*c.* 30%) of decrease of DNA amount reported by AL-KELIDAR & RICHARDS (1981) for annuals with respect to perennials.

The typical karyotype (Fig. 3) of subgen. *Delphinium* consists of a single long, generally metacentric chromosome pair, seven pairs which gradually become shorter and acrocentric chromosomes (see also Table 4). Following a general survey scanning the variability of karyotypes of annual Mediterranean *Delphineae*, GIMÉNEZ (1995) concluded that the most significant source of karyotype diversity in such species is the second pair (Fig. 4) and, thus, the constant length and arm ratio of this pair in subgen.

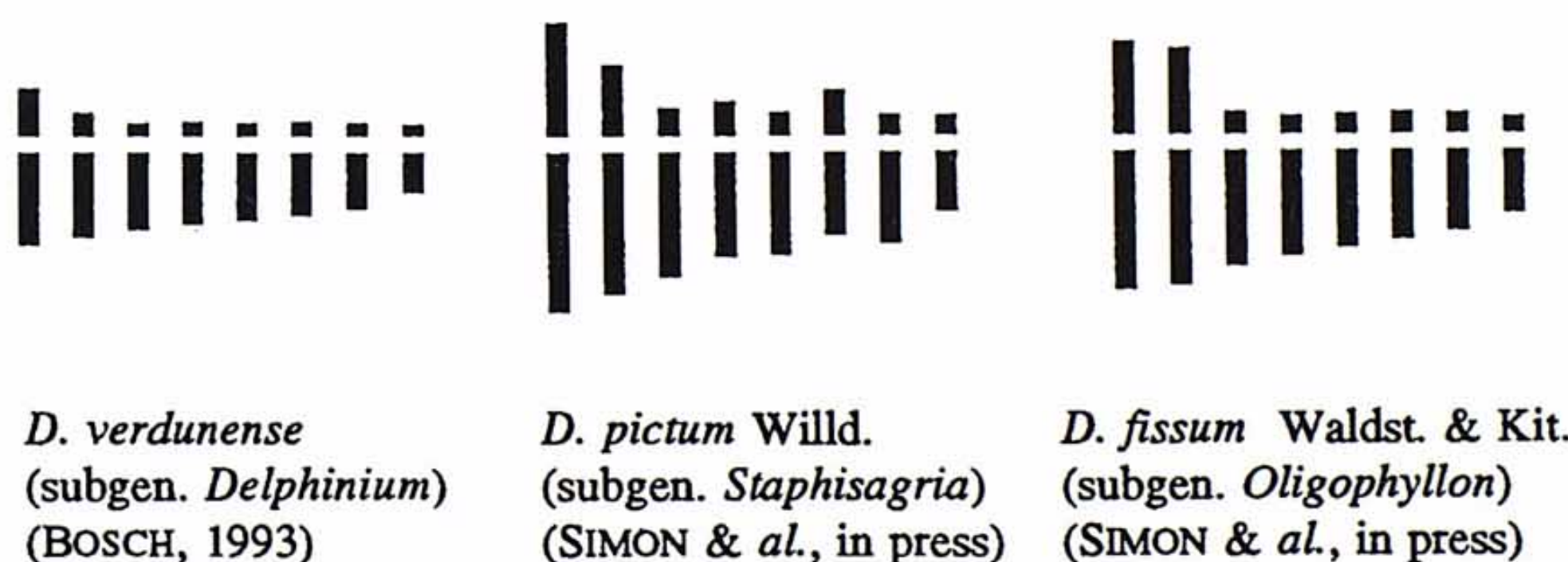


Fig. 3. Typical karyotype of subgen. *Delphinium* compared with those of subgen. *Staphisagria* and subgen. *Oligophyllon*. All 3 idiograms were drawn at the same magnification (1cm = 8  $\mu$ m).



TAXA	FORMULA*	REFERENCE
<i>D. balansae</i>	2m + 2sm + 4st	BLANCHÉ & <i>al.</i> (1990)
<i>D. cossonianum</i>	1sm + 1sm <sup>sat</sup> + 4st + 2t	BLANCHÉ & <i>al.</i> (1990)
<i>D. davisii</i>	1m + 1sm + 6st	GIMÉNEZ (1995)
<i>D. favargerii</i>	1sm + 7st	BOSCH & <i>al.</i> (ined.)
<i>D. gracile</i>	1sm + 5st + 2t	BLANCHÉ (1991)
<i>D. halteratum</i>	1sm + 1st <sup>sat</sup> + 6st	CAMPO & ROMANO (1995)
<i>D. macropetalum</i>	1sm + 3st + 4t	BLANCHÉ & <i>al.</i> (1990)
<i>D. obcordatum</i>	1sm + 7st	BOSCH & <i>al.</i> (ined.)
<i>D. verdunense</i>	1sm + 7st	BOSCH (1993)
<i>D. peregrinum</i>	1m + 7st	GIMÉNEZ (1995)
<i>D. virgatum</i>	1m + 2sm + 5st	GIMÉNEZ (1995)

\* Following the chromosome classification of LEVAN & *al.* (1964).

Table 4. Chromosomic formulae of *Delphinium* subgen. *Delphinium*.

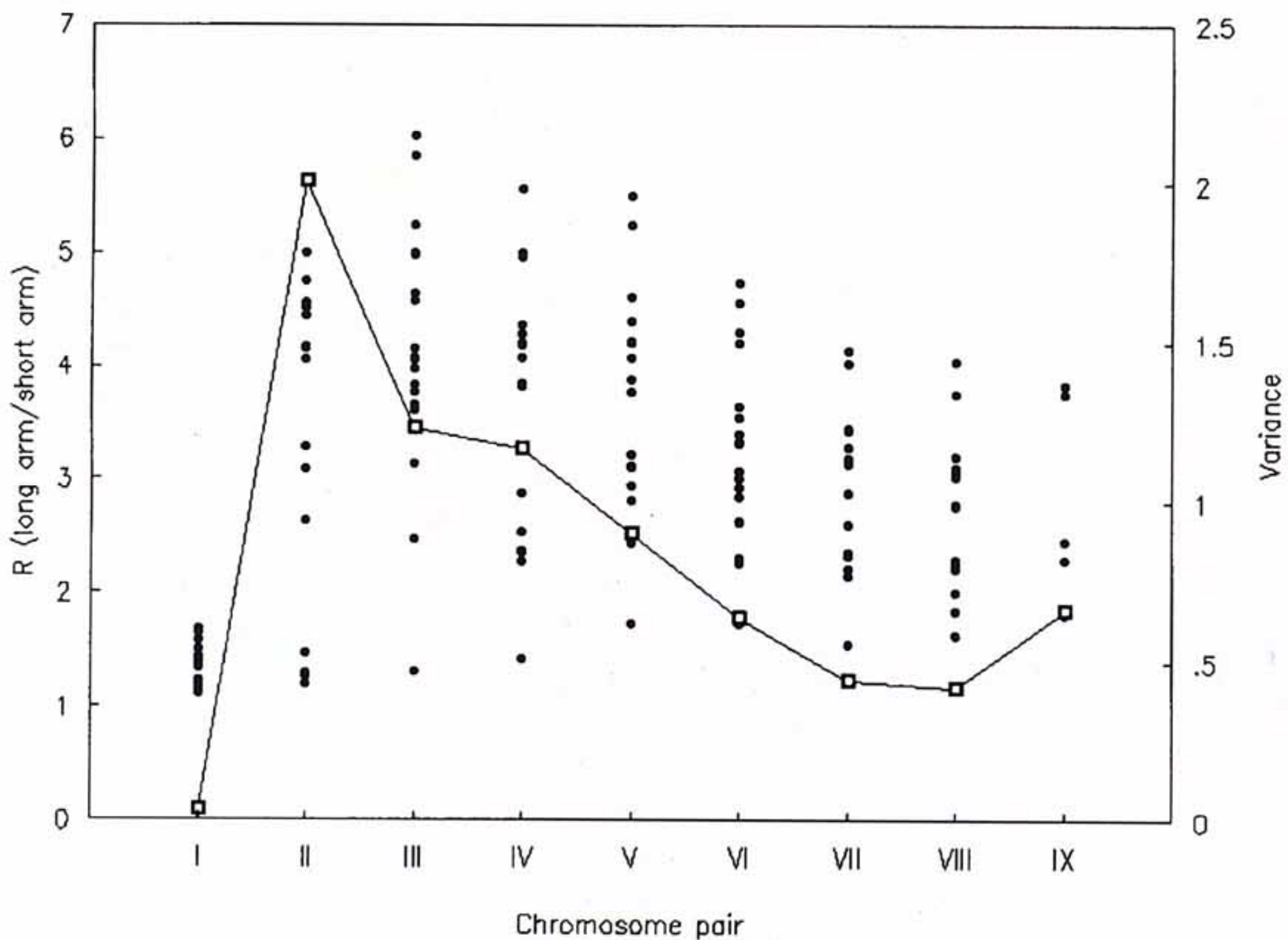


Fig. 4. Comparison of chromosome ratio (R) and variance for each chromosome pair on 19 populations belonging to 12 annual species of *Delphineae* (from GIMÉNEZ, 1995).



*Delphinium* has to be interpreted -in evolutionary terms- a sign of monophyly and of low divergence or adaptive radiation during karyotype evolution. Considering the great similarity with karyotypes of species coming from regions as far apart as Turkey, North Africa and the Iberian Peninsula, it is evident that, at least at the chromosome level, there are no reasons to avoid interspecific crossing contributing to a further genetic homogenization. But, the question remains as to whether these species are as genetically close as has previously been supposed?

### Isozyme analysis

The following step was, logically, to determine the extent of genetic variability within the chosen group (subgen. *Delphinium*). In order to do this we used isozyme electrophoresis on starch gels which gives good results in perennial species of *Delphinium*, both in the literature (WASER, 1987; RICHTER & *al.*, 1994) and in our previous research (BLANCHÉ & *al.*, in press). The general technical conditions were as described in SOLTIS & SOLTIS (1989) with the specifications of SOLTIS & *al.* (1983) concerning buffer prescriptions.

In this preliminary study, we surveyed 15 populations of the annuals complex, coming from the populations stock available in our greenhouse (see list in Table 5). The data presented here concern 11 isozyme loci: ACO-1, ACO-2, 6-PGD-1, 6-PGD-3, PGM-1, PGM-2, AAT/GOT-1, ME, MDH-1, MDH-2 and MDH-3 which were well interpreted; whereas, some enzymatic systems which were assayed were not sufficiently well resolved and, therefore, provisionally rejected (as LAP, PRX, LDH, SkDH, FDH, GDH, EST, CAT and IDH).

Other systems, including AAT/GOT-2, presented very soft colorations in some plants making interpretation of all the gels difficult. The 6-PGD-2 showed an excess of bands which proved difficult to interpret and which might indicate a possible duplication of this gene, but progeny tests are still being carried out before definitive interpretations can be made. Similarly both PGI and ADH systems, were well resolved but we have as yet been unable to offer genetic interpretations.

In the case of PGM-1 an abnormally high presence of bands is also present, in contrast to the normal monomeric behaviour of PGM-2. The only genetic interpretation of PGM-1 compatible with the results of the perennial species -presenting the simplest pattern- is that of tetrasomic segregation and, then, of genetic duplication, in a situation very similar to that of the *Ulmus* species surveyed by MACHON & *al.* (1995). This duplication, together with the possible 6-PGD-2 duplication could be interpreted as indications of the monophyletic group, as they are not found in any other species reported by the literature or studied in our laboratory (all of them perennials) and belonging to the remaining subgenera of *Delphinium*.

The general characteristics of the isozyme variation patterns were calculated from individual allele frequencies and processed in a personal PC compatible computer with the BIOSYS-1, version 1.7. (SWOFFORD & SELANDER, 1989) software. The results are presented in Table 5 and include 7 North African, 5 Iberian and 3 Turkish populations of the sect. *Delphinium*-complex.



POPULATION	N	A	P	Ho	He
<i>D. favargeri</i> – Ma: FAV1	30	2.4 (0.5)	63.6	0.157 (0.064)	0.210 (0.060)
<i>D. favargeri</i> – Ma: FAV2	30	2.5 (0.6)	72.7	0.151 (0.084)	0.196 (0.062)
<i>D. favargeri</i> – Ma: FAV3	30	2.2 (0.3)	63.6	0.112 (0.051)	0.134 (0.040)
<i>D. obcordatum</i> – Ma: OBC1	30	2.1 (0.4)	54.5	0.167 (0.083)	0.166 (0.058)
<i>D. macropetalum</i> – Ma: MAC1	5	1.6 (0.2)	54.5	0.200 (0.089)	0.178 (0.060)
<i>D. cossonianum</i> – Ma: COS1	30	2.0 (0.3)	45.5	0.130 (0.079)	0.168 (0.070)
<i>D. balansae</i> – Ma: BAL1	30	1.7 (0.2)	45.5	0.127 (0.076)	0.098 (0.036)
<i>D. verdunense</i> – Hs: VER1	29	1.8 (0.4)	36.4	0.147 (0.084)	0.172 (0.079)
<i>D. verdunense</i> – Hs: VER2	30	2.5 (0.4)	45.5	0.161 (0.64)	0.238 (0.077)
<i>D. gracile</i> – Hs: GRA1	30	1.7 (0.3)	45.5	0.212 (0.102)	0.162 (0.068)
<i>D. gracile</i> – Hs: GRA2	30	1.7 (0.3)	36.4	0.182 (0.086)	0.147 (0.067)
<i>D. gracile</i> – Hs: GRA3	28	1.9 (0.2)	54.5	0.201 (0.087)	0.168 (0.047)
<i>D. davisii</i> – An: DAV1	30	1.6 (0.3)	36.4	0.142 (0.087)	0.138 (0.065)
<i>D. peregrinum</i> – An: PER1	15	2.4 (0.3)	72.7	0.242 (0.094)	0.292 (0.064)
<i>D. virgatum</i> – An: VIR1	15	2.2 (0.3)	72.7	0.303 (0.119)	0.262 (0.071)

N= sample size; A= mean number of alleles per locus; P= percentage of loci polymorphic, (0.95 criterion); Ho= observed heterozygosity; He= expected heterozygosity. (Values in parentheses corresponding to standard error).

Table 5. Genetic variability at 11 loci in 15 populations of mediterranean *Delphinium* subgen. *Delphinium*.



Locus	$F_{IS}$	$F_{ST}$	$F_{IT}$
ACO-1	- 0.044	0.035	- 0.007
ACO-2	0.180	0.745	0.791
GOT-1	0.160	0.555	0.626
MDH-1	- 0.363	0.235	- 0.043
MDH-2	0.113	0.508	0.563
MDH-3	0.456	0.706	0.840
ME	1.000	0.086	1.000
6PGD-1	0.262	0.036	0.288
6PGD-2	0.346	0.289	0.535
PGM-2	0.218	0.499	0.608
Mean	0.280	0.516	0.652

Table 6. Summary of F-statistics at all polymorphic loci of mediterranean *Delphinium* subgen. *Delphinium*.

The mean number of alleles per locus is 1.6-2.5, with more than half many values higher than 2. This results are relatively high, if compared with the values around 1.3-1.5 obtained in other Mediterranean perennial species (BLANCHÉ & *al.*, in press). The percentage of polymorphic loci is also high, although clearly lower in European than in African or Anatolian populations. The F-statistic calculations are shown in Table 6, where the mean total diversity ( $F_{IT}$ ) is 0.652, again these results are relatively high it compared to the summary presented by HAMRICK & GODT (1989). The diversity among populations ( $F_{ST}$ ) is 0.516 and this contributes more to total diversity than intra-population diversity ( $F_{IS}$ )= 0.280.

Analysis of the data obtained from the isozyme systems investigated, would seem to indicate that there are high levels of similarity between populations. To verify these findings, the unbiased genetic identities and distances of NEI (1978) were calculated, so as to avoid the bias caused by small sample sizes (see Table 5). The values of genetic identity measure the similarity of allelic frequencies between pairs of populations and, as stated by WASER (1987), range from 0 (where there are no common allele between populations) to 1 (where both populations share the same alleles at the same frequencies). Following the construction of the corresponding matrix, the most significant data could be observed (see Table 7). The averaging identity between populations is 0.814, which is relatively high, and ranges from 0.522 to 0.998. The greatest similarities were found between populations relatively close to each other, whereas least similarities were found between the most geographically distant populations. We compared the genetic distance data matrix with the geographical distance data matrix but a very poorly significant correlation of 0.233 was obtained, suggesting a not geographical basis to the observed genetic variation.

In spite of the possible use of certain loci (including ACO-2 or AAT/GOT-1) as molecular markers at the specific level, the genetic distances as a whole when compared with the taxonomic distances (built upon the 20 most useful morphological characters) are virtually uncorrelated (0.181).



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 AVERAGING IDENTITY BETWEEN POPULATIONS

$$X = 0.814 \quad (n = 105, SD = 0.098, SE = 0.010)$$

## HIGHEST GENETIC SIMILARITY

			Km
0.998	between	<i>D. gracile-1</i> & <i>D. gracile-2</i>	315
0.995	between	<i>D. obcordatum-1</i> & <i>D. balansae-1</i>	265
0.993	between	<i>D. verdunense-1</i> & <i>D. verdunense-2</i>	120
0.991	between	<i>D. favarger-1</i> & <i>D. favarger-3</i>	130
0.990	between	<i>D. favarger-1</i> & <i>D. favarger-2</i>	125

## LOWEST GENETIC SIMILARITY

			Km
0.522	between	<i>D. davisii-1</i> & <i>D. gracile-3</i>	2760
0.565	between	<i>D. davisii-1</i> & <i>D. gracile-2</i>	2765
0.584	between	<i>D. davisii-1</i> & <i>D. gracile-1</i>	2660
0.607	between	<i>D. cossonianum-1</i> & <i>D. gracile-3</i>	750
0.636	between	<i>D. balansae-1</i> & <i>D. gracile-3</i>	650

## CORRELATION BETWEEN GENETIC DISTANCES MATRIX (NEI, 1978) AND GEOGRAPHIC DISTANCES

$$r = 0.233$$

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 Table 7. Genetic identity measures in 15 populations of mediterranean *Delphinium* subgen. *Delphinium*.

In conclusion, the isozyme survey suggests a pattern of populations containing a high genetic intra-population variability but with relatively close genetic distances (with the only exception of *D. davisii* Munz, a highly isolated Anatolian endemic species).

**Taxonomic implications**

In accordance with the preceding data, and following the analysis of typical morphometric parameters, we can consider the group of species of subgen. *Delphinium* as:

- a) A monophyletic group (based on evidence of karyotype and isozyme duplication).
- b) With soft morphological or karyological differentiation.



- c) Very close genetically, with a partial, geographically-based pattern of variation.
- d) Limited self-pollination but with functional geitonogamy and cross-pollination.
- e) Where the morphological diversity lies mainly in the floral features (colour, shape and size of flower pieces) in spite of the low correlation between flower structure and actual pollinator diversity (both species and behaviour), at least at the level of the present survey.

This general pattern is described before outlining a particular taxonomic arrangement. Also, the previous taxonomic history of such groups (more than a hundred names are available for all possible combinations) has to be taken in to account because of the abundance of intermediate forms and the insufficient quantity number of herbarium materials collected at the time of some taxa descriptions, particularly in the case of North African representatives according to MAIRE (1964).

Although a more detailed framework will be published once the total herbarium material has been examined, we include here the 3 main taxonomic conclusions available for current projects on the floristics of the W. Mediterranean area.

*1. Generic nomenclature.*- Two typifications of the genus *Delphinium* are already known and are cited as examples in the ICBN (GREUTER & *al.*, 1994). The first is based on *Delphinium consolida* L. (BRITTON *in* BRITTON & BROWN, 1913) following the automatic typification of the American Code and the second is based on *Delphinium peregrinum* L. (NIEUWLAND, 1914; GREEN, 1929). The choice of first name implies the use of the name *Delphinium* for those plants actually known as *Consolida*, the name of a segregate genus which implies the need to change all names for the more than 300 *Delphinium s. str.* species. In an attempt to avoid this source of conflict, two proposals are suggested which conserve the generic name with its usual sense.

The first proposal is based on *D. peregrinum* L. (*typ. cons. prop.* by JARVIS, 1992) and was accepted by the relevant Subcommittee 3C (votes 6:0:0), but, finally, was not adopted by the Tokyo Code. The nomenclatural consequences for the plants studied here are negligible.

The second proposal is based on *D. elatum* L. (*typ. cons. prop.* by WARNOCK, 1993), which is also correctly used for the Linnaean species, but this proposal considers the possibility of restoring (to the rank of separate genus) the annual species of *Delphinium* under the name of the genus *Phledinium* Spach. In this case, the type species of the new genus should be *D. peregrinum* and, thus, that species could not be considered as being type of another genus. This would imply the need to change most perennial species to another available name. This possibility, however, is largely improbable, because no modern authors have proposed the segregation of this subgenus into a separate genus exclusively formed by annuals. This new proposal was not evaluated by the corresponding subcommittee. If approved, the nomenclatural consequences for our group would necessitate the use of another name for the subgenus or the section (because the autonym would have to be reserved for the taxa containing the new type, *D. elatum*). The alternative could be the name employed by CANDOLLE (1817) as the name for his section (*Delphinellum* DC.) and subsequent combinations at the needed ranks (subgenus, section, series, etc.). For the moment, we continue to use the



traditional typification considering *D. peregrinum* as type species (following JARVIS, 1992) and then name our group as the autonym containing the type, subgen. *Delphinium*.

2. *Two names to avoid.*- In considering the available names for the Iberian and North African species, two names have had to be rejected because of the confusion they create and because they have been widely applied to Moroccan plants, a country where floristic projects are currently being undertaken.

***Delphinium ambiguum* L. *Sp. Pl.* 2nd. Ed. : 749 (1762)**

Two basic reference floras -Flora Europaea (PAWLOWSKY, 1993) and Med-Checklist (GREUTER & *al.*, 1989)- include *D. ambiguum* L. as an accepted name for a plant belonging to the group of *D. nanum* DC.- *D. obcordatum* DC., that is, annuals with a relatively large, rounded limb of lateral petals mostly grown in sandy soils. In BLANCHÉ & MOLERO (1993), we reviewed this nomenclatural problem and we concluded that there are two available typifications (CANDOLLE'S, 1817: 343 and MUNZ'S, 1967a: 177) both based on the same herbarium sheet (LINN 694.4). This sheet clearly belongs to a plant from the genus *Consolida* but not to the genus *Delphinium s. str.* and, thus, it should not be applied to any plant of the *D. nanum-obcordatum*-group.

The cause for conflict lies in the origin of the Linnaean plant, which consists of a garden form of the plant usually known as *Consolida ajacis* (L.) Schur with multiplied flowers and a variable number of carpels. This fact led Linnaeus to doubt (hence "*ambiguum*") between the true *Delphinium* ("*tricapsulares*" in Linnaeus own words) and the *Consolida* ("*unicapsulares*") when assigning plants and, finally, he decided to put a 1 carpel plant (but having 3 carpels after garden modification) among the wild plants with 3 carpels (*cf.* LINNAEUS, 1762). Thus, it seems, that any wild *Delphinium s. str.* (with 3 true carpels) might be identified as *D. ambiguum*, a name which, therefore should be rejected.

***Delphinium peregrinum* L. var. *elongatum* Boiss. *Voy. Bot.* 2: 13 (1839)**

Following the system of MAIRE (1964), this name would be applied to a number of North African plants (including nomenclatural combinations of subordinate forms such as f. *tribraceolatum*, *caeruleum*, *laxum*, *rifanum*, *albolilaceum* and *pseudogratile*). In fact, however, a typification of this name is available (BURDET & *al.*, 1989) which is based on true specimens of Boissier and, following examination, it is clearly a plant which belongs to the taxon *D. gracile* DC., described by CANDOLLE (1817), that is, an early synonym and (according to the ICBN) a priority name for the plant described later (BOISSIER, 1839) .

3. *A new annual species.*- In accordance with the experimental results for annual species variation patterns, it would appear that a new taxonomic entity should be



recognized at the specific level (which, while being unable to discriminate among an intricate network of intermediate forms, needs to produce a useful taxonomic answer) to name the strain of populations of nearly purple flowers and yellow gorge easily recognized in the field in C. & S. Morocco. Various early collections of this plant were identified in the herbaria as *D. peregrinum* var. *elongatum* (a name rejected for this use in point 2 above) but most remain unidentified as *Delphinium* sp., indicating the unsuitability of MAIRE's (1964) system.

***Delphinium favargeri* C. Blanché, Molero & Simon P. sp. nova**

Floribus (21) 24-27 (29) mm. Sepalis (5)6-7(8) mm, extus purpureis calcaris (18)19-21(22) mm. Petalis discoloribus, albicantis, fauce lutescentibus; lateralibus exsertis; limbo suborbiculare, 4-5 mm, basi non cordato nec decurrente; lobis superioribus 3-4 (5) mm.

*Typus*: "Beni-Mellal, 5 km cap a Kénifra, marges espinosos amb Ziziphus, 440 m. 20-VI-1994. C. Blanché, M. Bosch, J. Molero, A. Rovira & J. Simon legerunt". *Holotypus* in BCF 39583. *Iconography*: Fig. 5

Flowers of (21)24-27(29) mm. Sepals usually dust purple (although sometimes more bluish or pinky flowers are observed); spur (18)19-21(22) mm, lower sepals (5)6-7(8) mm. Petals discolour (lateral whitish, gorge yellowish). Lateral petals exert with limb of 4-5 mm, suborbicular and with base neither cordate nor decurrent. Upper lobe of upper petal 3-4 (5) mm. This species is dedicated by the authors to Prof. Claude Favarger of the Université de Neuchâtel (Switzerland).

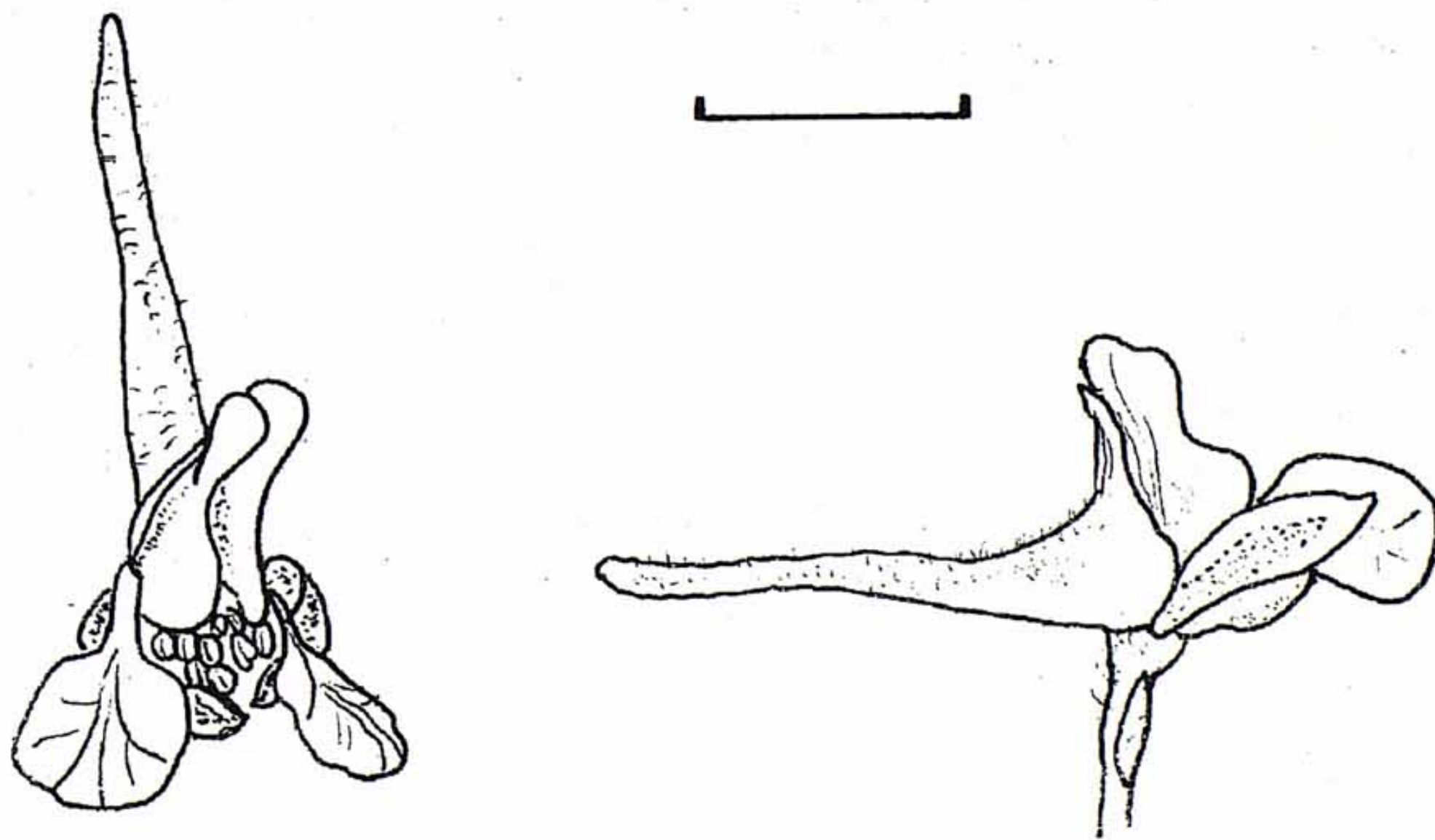


Figure 5. Flowers of *D. favargeri*. a, front view; b, side view. Scale bar, 10 mm.



This species belongs to the ser. *Macropetala* C. Blanché, Molero & Simon P. by its relatively exsert, rounded lateral petals and it is closely related to the pair of species *D. obcordatum*-*D. macropetalum*, from which it differs in the length of the upper lobe of its upper petals, in the length of spurs and sepals and in the general colour in the field (a certain absence of this character is observed in herbarium material). A summary of these differences is presented in the following taxonomic approach.

The minor taxonomic entities combined under *D. peregrinum* var. *elongatum* Boiss. by MAIRE (1964) cannot be applied to our species for several reasons (f. *tribracteolatum* (DC.) Huth has been used at the specific level to describe anomalous forms with 3 bracteoles; f. *caeruleum* Maire is, in fact, the type of the variety as MAIRE (*l.c.*: 79) himself states and, thus, an illegitimate name that should be replaced by the autonym f. *elongatum* if needed; and f. *laxum* Gatt. & Maire, with lateral petals attenuated has to refer to plants belonging to the group of *D. peregrinum* but not to ser. *Macropetala*). The forms of the second group of Maire's Key (*l.c.*: 80), although closer to our species concept (mainly identified by discoloured appearance) are also not applicable to our taxon because they are described as presenting lateral petals cordate (f. *albolilaceum* Maire and f. *pseudogratile* Maire), a feature very rare in *D. favargerii*.

This new species is distributed in C. and S. Morocco, from 100 to 1500 m, in open areas, field and road margins and dry meadows mainly in inner regions. Exceptionally it reaches the Atlantic belt near Essaouira or in Cap Bedouzza, favoured by field extension but absent in strictly littoral communities (sand dunes, etc.). Some populations belonging to this new species were studied karyologically previously (BLANCHÉ & *al.*, 1990 under the name *D. peregrinum* var. *elongatum*) and presented  $2n=16$  chromosomes in all cases.

### **Taxonomical approach to the moroccan representatives of subgen. *Delphinium***

Thus, we suggest the following check-list for the Moroccan taxa of the subgen. *Delphinium*, with the updated taxonomy, prior to publication of a complete monograph.

#### **Subgenus *Delphinium***

#### **Sectio *Delphinium***

*Typus: Delphinium peregrinum* L. (TAMURA, 1995)

#### **Ser. *Cossoniana* C. Blanché, Molero & P. Simon ser. nova.**

Petalorum lateralium basi cordatus cum ser. Halterata congruens, sed differt carpellis 5 non 3.

*Typus: Delphinium cossonianum* Batt.

This new series is described to include the annual species of W. Mediterranean and Macaronesian distribution with 5 carpels, a characteristic not found (excluding



occasional mutations) in other plants of subgen. *Delphinium*. The lateral petals are cordate at base, and as such resemble ser. *Halterata*, but other features, such as the narrowly divided leaflets and the usually multiflowered racemes found in ser. *Cossoniana*, are also of diagnostic value.

This series includes *D. cossonianum*, endemic of N. and C. Morocco and *D. maderense* C. Blanché, endemic of the island of Madeira (BLANCHÉ, 1992) (Fig. 6a).

Ser. **Balansae** C. Blanché, Molero & P. Simon

Perennial plants.

It comprises the only perennial species of subgen. *Delphinium*, previously recognized as a possible relict (BLANCHÉ, 1990) of an ancient group of ancestors bearing a closely similar flower structure to that of the remaining annual species.

The only species of this series is a North African endemic, *D. balansae* Boiss. & Reuter, a montane plant (not strictly orophyte in the sense of GALLAND, 1988) recorded in the Atlas System (from the Anti-Atlas in Morocco to the Aurès in Algeria, including the Grand Atlas and Middle Atlas and Tlemcen mountains near Oran), absent from low altitudes generally under 1000 m (Fig. 6b)

Ser. **Macropetala** C. Blanché, Molero & P. Simon

Lateral petals more or less exserted, with rounded limb, not cordate at base.

Species included: *D. macropetalum* DC., *D. obcordatum* DC. and *D. favargerii* sp. nova. (Fig. 6c).

This series includes a group of forms which are very closely related and where a "practical" -and some artificially produced- system should be applied. The name *D. nanum* DC. should be reserved for the dwarf like forms coming from sandy regions in Egypt showing lateral petals subtrapezoidal and, thus, the name *D. obcordatum* DC. (following the concept of PAWLOWSKY, 1964 and the typification by BLANCHÉ & MOLERO, 1984 to ensure its correct use), should be restored for the plants of the littoral or sublittoral sandy regions of W. Portugal, S. Spain, N. and W. Morocco having deep blue-lilac flowers, spur 2-2.5 longer than sepals and upper lobes of the upper petals of 5-8 mm. Related to *D. obcordatum*, but with distinctly bigger lateral petals (limb more than 9 x 9 mm), spur 1.8-2.3 longer than sepals and upper lobes much longer (more than 9 mm) are the also lilac-flowered *D. macropetalum*, endemic of the littoral dunes of the Atlantic coast of Morocco between Safi and Agadir, having its classical type locality near Essaouira. Finally, *D. favargerii* sp. nova described in this paper represents an inland vicariant of this group, progressively much ramified and with distinctly coloured floral pieces (more dust purple in the sepals and a visible yellow gorge), as well as shorter upper lobes of upper petals (up to 4.0-4.5 mm). To date, this species has been endemic to C. and S. Morocco.

Ser. **Halterata** B. Pawl.

3 carpels. Lateral petals cordate at base.

A series found in the northern W. Mediterranean side (*D. verdunense* Balb. cited at some Moroccan localities under the name *D. cardiopetalum* DC. but we have not seen any voucher of North African origin typically belonging to this species. *D.*



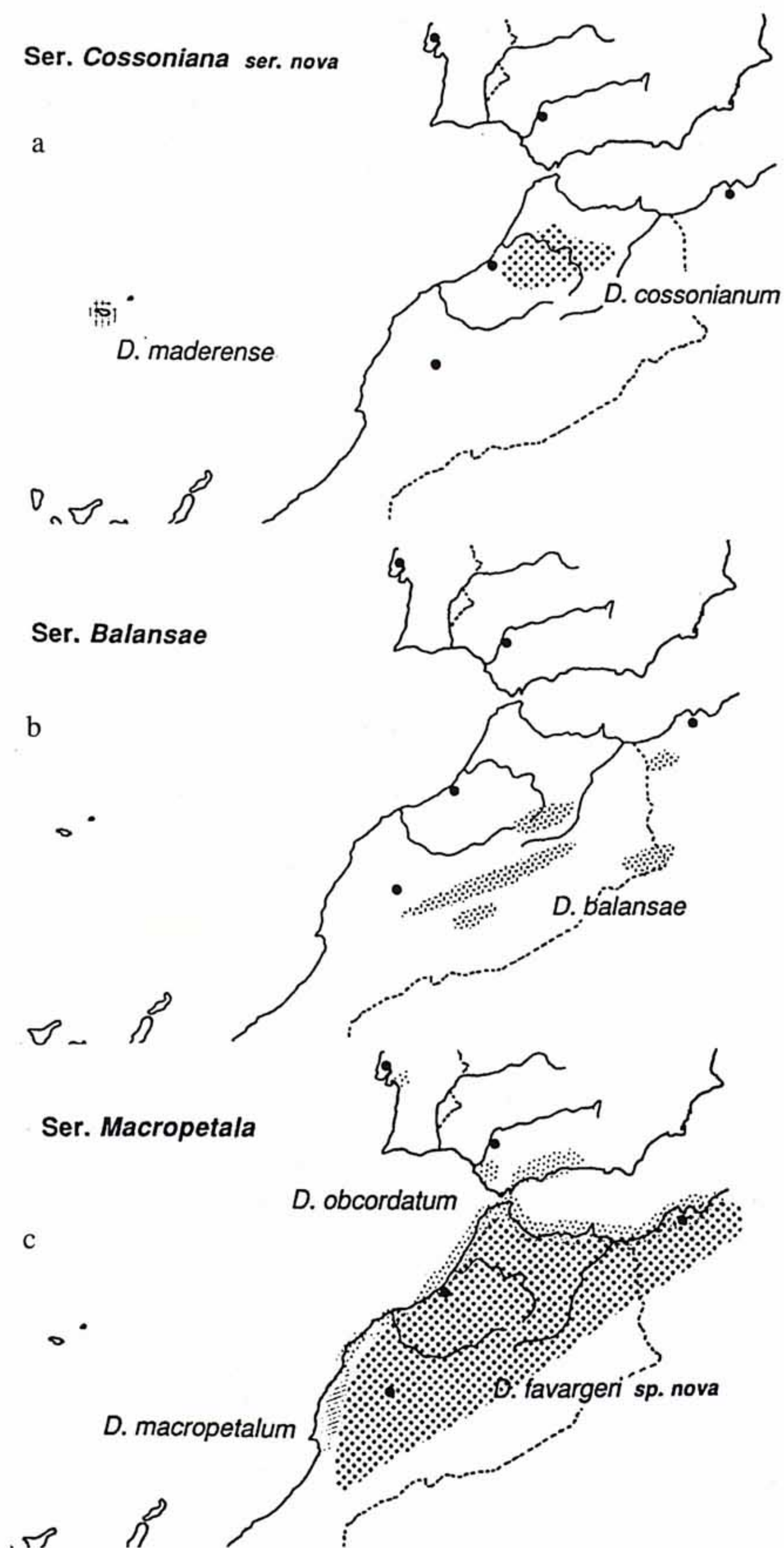


Fig. 6. Geographic distribution in the W Mediterranean Area and Macaronesia of: a, Ser. *Cossoniana*; b, Ser. *Balansae*; c, Ser. *Macropetala*.



*halteratum* Sm. in Sibth & Sm. has been observed by the authors in Tunisia and forms reliable to *D. gracile* DC. are available in herbaria from Algeria. In all cases, citations come from disturbed and humanized places, such as cereal fields, railways, road margins, etc. We think that there are no native plants of ser. *Halterata* in Western N. Africa, although new citations could be added in the future from disturbed habitats, even in Morocco).

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