Cytotaxonomy of North African species of *Delphinium* L. sect. *Delphinium (Ranunculaceae)*

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Abstract

BLANCHÉ, C., J. MOLERO & J. SIMON (1990). Cytotaxonomy of North African species of *Delphinium* L. sect. *Delphinium (Ranunculaceae)*. Collect. Bot. (Barcelona) 18: 59-74.

Both chromosme numbers and karyotype structure from 15 wild North-African populations of *Delphinium* L. sect. *Delphinium* were studied. *Delphinium balansae* Boiss. & Reuter, with a more symmetrical karyotype, appears as a possible perennial ancestor of the remaining annuals with highly assymetrical and shorter karyotype. A taxonomical reorganization of this section is proposed: two new series (ser. *Macropetala* ser. nova and ser. *Balansae* ser. nova.) and two new nomenclatural combinations *(D. nanum* subsp. *alboliliaceum* and *D. nanum* subsp. *elongatum*) are proposed.

Keywords: *Ranunculaceae, Delphinium,* taxonomy, karyology, North Africa.

Resum

BLANCHÉ, C., J. MOLERO & J. SIMON (1990). Citotaxonomia de les espècies nordafricanes de *Delphinium* L. sect. *Delphinium (Ranunculaceae).* Collect. Bot. (Barcelona) 18: 59-74.

S'han estudiat els nombres cromosòmics i l'estructura dels cariotipus de 15 poblacions nordafricanes de *Delphinium* L. sect. *Delphinium. Delphinium balansae* Boiss. & Reuter, amb cariotipus mès simètric, apareix com a possible ancestre perenne de la resta d'espècies annuals amb cariotipus més asimètric i més curt. Es proposa una reorganització taxonòmica de la secció, d'on es descriuen dues sèries noves (ser. *Macropetala* ser. nova i ser. *Balansae* ser. nova.) i es proposen dues combinacions noves (*D. nanum* subsp. *alboliliaceum* i *D. nanum* subsp. *elongatum*).

Mots clau: *Ranunculaceae, Delphinium,* taxonomia, cariologia, Nordàfrica.

Introduction

The annual species of the genus *Delphinium* are grouped together in the section *Delphinium* (= Sect. *Delphinellum* DC.). Recent works of a general nature dealing with *Delphinium*

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(EWAN, 1945; WANG, 1962; TAMURA, 1967; MALYUTIN, 1973 and 1987) have devoted very little attention to the sect. *Delphinium,* probably on account of its small size in relation to the total number of species in the genus (approximately 5 %, cf. MALYUTIN, 1987) and because of its geographical distribution which is practically limited to the Mediterranean Region *s.l.* (Mediterranean Region, West of the Irano-Turanian Region and parts of the Saharo-Arabian region, sensu TAKHTAJAN, 1986).

On a different level, PAWLOWSKY (1963; 1964), CHOWDHURI, DAVIS & HOSSAIN (1958) and DAVIS (1965) have contributed what in our view are fairly valid criteria for the taxonomic conception of the section *Delphinium* in their research on Europe and Turkey respectively. Of particular note is the treatment given relatively «small» species grouped together in series (cf. PAWLOWSKY, 1963 and 1970, EWAN, *l.c.*), this last category being particularly useful for the *Delphinium* genus which, apart from a few species which are very isolated both taxonomically and geographically, presents a model of variation containing geographically and phylogenetically coherent and well defined natural groups, including a variable number of lesser taxa with a complex network of obvious degrees of relationship. For STEBBINS (1950:56): «In *Delphinium* (...) the pattern is that of closely related homogenous species more or less sharply isolated from each other, as well as of polytypic species, the two tipes occurring with about equal frequence».

This new attempt to resolve this complex group follows upon our earlier works on taxa of the tribe *Delphineae* Warming in the Iberian Península (BLANCHÉ, 1985, BLANCHÉ & MOLERO 1984, 1985 and 1986; BLANCHÉ, MOLERO & SIMON, 1987, etc.). In it we present cytogenetic data on the Nort African species of the section *Delphinium* about which very little is known (only one count by QUÉZEL, 1957). The taxonomic solution by MAIRE (1964) differes substantially from those proposed by Davis and Pawlowsky, followed by MUNZ (1967), and must still be considered provisional. Furthermore the study of the section *Delphinium* in this region (to which *D. balansae* Boiss. & Reuter, the only perennial species in the section, is endemic) may possible provide a clue to the evolution of the genus which cannot be sought elsewhere.

Material and methods

Fixations were performed directly in the field in the locations listed in Table I in the course of two expeditions through Morocco in 1985 (cf.FERNÁNDEZ CASAS & al., 1987) and 1988 (J. Molero, A.M. Romo & A Susanna). Reference sheets are kept in herbariums BCF and BC.

Because of the difficulty in obtaining seeds (most of the populations were still in flower) and in getting them to germinate, the use of root meristems was not considered. The initial material in all cases consisted of flower buds fixed with Carnoy's reagent (absolute ethanol — glacial acetic acid 3:1). After 24 hours, the fixative was renewed and kept in the laboratory at −18° C.

Samples were coloured with acetic carmine (boiled for 2 minutes) and then allowed to rest for 24-48 hours at room temperature. They were mounted using acetic acid 45%-glycerol (9:1) and subsequently prepared by means of the «squash» technique. All the specimens come from somatic metaphases of the staminal filaments. They were examined under a Nikon optic microscope where the camera lucida figures are drawn. The metaphasic plates with the most contracted chromosomes were selected for the study of size and morphology of chromosomes, position of the centromere and presence and position of the satellites (10 data for each population).

For the observations regarding meiosis, pollen mother cells (P.M.C.) were used and the same procedure was followed.

The selected divisons were photographed with a Nikon Optiphot microscope. The negati-

TABLE I. - Chromosome numbers of *Delphinium* L. sect. *Delphinium*.
North African populations studied.

Taxon	Locality	Fixation Number	n	2n	Previous counts
D. balansae	Ma, Djebel Tihmadite	CB.220	8	16	Quézel (1957), 2n = 16 (Ma) Galland (com. pers.) n = 8 (Ma)
D. cossonianum	Ma, 20 km S. of Tétouan	CB. 002	8	16	
	Ma, between Fez and Ouezzanne	CB.044	8	16	
	Ma, near Ouezzanne	CB.046	8	16	
	Ma, near Aïn-de-Fali	CB.047	8	16	
D. nanum					
subsp. *nanum*	Hs, Málaga, playa del Golf	–	8	16	Blanché (1985), n = 8, 2n = 16
subsp. *elongatum*	Ma, Plages de Médiyah	CB.003	8	16	
	Ma, near Col de Kerdouss	CB.016	8	16	
	Ma, near Tafraout	CB.018	8	16	
	Ma, between Talbanine and Zaouïa	CB.033	8	16	
	Ma, between Fez and Ouezzanne	CB.045	8	16	
subsp. *albolilaceum*	Ma, between Jorf el Yhoudi and Tnine Riad	CB.005	8	16	
	Ma, 15 km W. of Essaouira	CB.009	8	16	
D. *macropetalum*	Ma, 10 km S. of Safi	CB.010	8	16	
	Ma, Safi vs. Tamanar	CB.012	8	16	
	Ma, Assif Tamri vs. Essaouira	CB.013	8	16	

ves of the photographs and the orignal drawings are deposited at the Botany Laboratory of the Faculty of Pharmacy in Barcelona.

The terminology used to describe the karyotype is that of LEVAN & al. (1964) and from it the chromose formulae have been calculated. The degree of asymmetry of the karyotype is indicated in terms of the classes defined by STEBBINS (1971). In order to facilitate comparisons between different taxa and with data gathered by other authors, the centromeric index has also been calculated (100 x length of short arm / total length of chromosome) as well as the indexes of intrachrosomal asymmetry (A1) and of interchromosmal asymmetry (A2) proposed by ROMERO (1986).

Results

A total of fifteen populations were studied and the corresponding chromosome numbers are shown in Table I. Apart from one previous count of *D. balansae* (QUEZEL, 1957), this is the first time, to our knowledge, that the remaining taxa have been counted

All the populations studied present a diploid level with the same chromosome number ($n = 8$ and $2n = 16$). Only a few meiosis (diakinesis or metaphase I) in *D. balansae* (Fig. 1) show short chromosomes in which the terminalization of the chiasmata had already finished and separation was beginning, while the rest of the complement was still at the equatorial plate. Some seemingly counts of $n = 9$ may appear, as already reported by N. Galland *(com. pers.)* with reference to the same taxon.

The karyotypes of the fifteen populations were studied. Their characteristics are given in Tables II (size) and III (asymmetry) while their respective idiograms appear in Figs. 2 and 3. The majority are fairly asymmetrical karyotypes belonging to STEBBINS' classes 3B and 4B (1971). The average length of the complement is relatively constant, being close to 3 µm, between 3,87 ±0.44 µm for *D. macropetalum* and 3.02 ±0.37 µm for *D. nanum* subsp. *elongatum* ($m \pm SE$, $n = 10$). However, the average length of the chromosomes ranges from 6,64 ± 0,16 µm for pair I of *D. macropetalum* to 1,74 ± 0,06 µm for pair VIII of *D. balansae* ($M \pm SE$, $n = 10$).

Discussion

1.- Our results as to the chromosome number confirm all previous counts of taxa belonging to sect. *Delphinium* ($2n = 16$). On the basis of present data, the section can thus be considered strictly diploid, in accordance with the basic number $x = 8$ proposed by TAMURA (1967) and AL-KELIDAR & RICHARDS (1981). This feature distinguishes the group of annual *Delphinium* from the sections with perennial taxa in which the levels 2 x and 4 x exist side by side (cf. JANKUN, 1973; WARNOCK, 1981 or BLANCHÉ, 1985, among others). With respect to the karyotpe, very clear similarities are also observed (except in the case of *D. balansae*) among North African taxa belonging to the section, and also with Iberian and Balearic representatives (BLANCHÉ, 1985).

These resemblances could give support to MAIRE'S synthetic treatment (1964) in which all the annual species (except for *D. balansae* and *D. cossonianum* which are quite distinct) are grouped together in a single «large» species, *D. peregrinum* s.l., with a great number of dependent lesser taxa. On the other hand, these cytogenetic parallelism, added to the morphological similarities between the taxa studied and between *Delphinium* annuals in general, confirm that this group presents the same model of variation deduced by STEBBINS (1950) from his experiences with perennials, ie. a sort of phenotypic and genotypic «continuum».

2.- Another aspect of the problem which must be considered is whether the similarities,

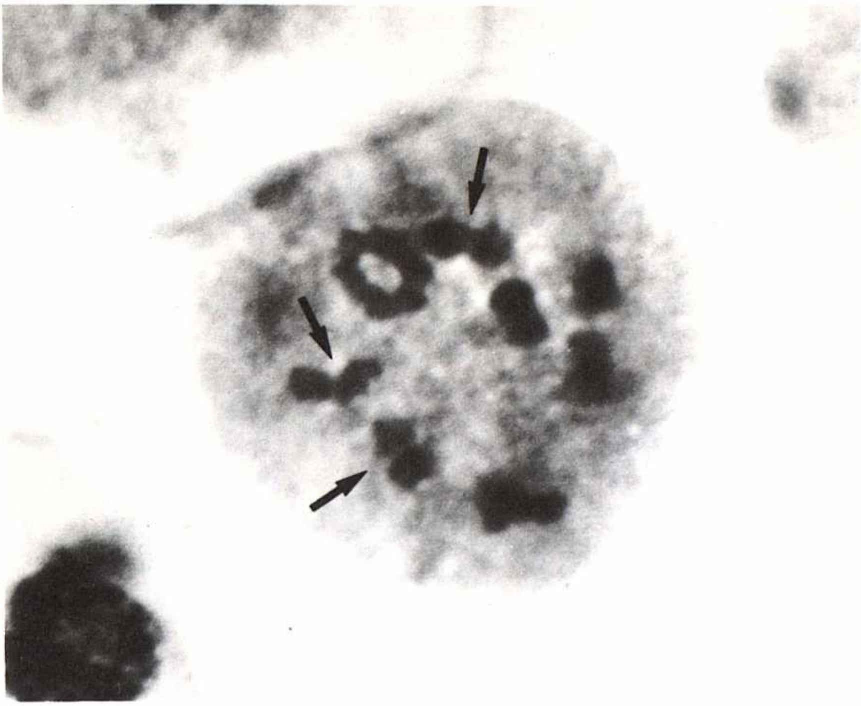

Fig. 1. — Asynchronous meiosis of *D. balansae* (CB. 220, n = 8) in CMP. In metaphase I the presentce of a ring-shaped bivalent corresponding to the long pair (I) is observed. In other bivalents with shorter chromosomes (arrows), the terminalizacion of chiasmas has taken place more rapidly and separation strarts earlier.

the gradual transition between taxa and/or populations and the presence of numerous intermediate phenotypes (cf. MAIRE, l.c. and the revision of North African material from herbariums MPU!, P!, G!, BC! and MA!) can be explained by a possible genetic interchange between populations of the same taxa and even between closely related taxa. In the absence of experimental data (those we have are still very incomplete), it can at least be stated that there ara generally no genetic barriers (level of ploidy, karyotype structure (cf. LEGRO, 1961), phenological impediments (except for the most isolated taxa, *D. balansae* and *D. cossonianum,* cf. BLANCHÉ, 1985) or even obstacles related to the way the corolla is shaped to receive pollinators (BLANCHÉ, Pers. Obs.; but on the other hand cf. the occurrence of neoteny in perennials, GUERRANT, 1982). Though JEANMONOD (1984) considers the homogenizing effect against the selection of genetic flow between populations has been overestimated, this effect is at least possible in annual *Delphinium* species.

3.- To all these factors one must add the role played by geographical and/or phenological isolation in the maintenance of the most clearly differentiated genotypes, in contrast to the possibility of contact between sympatric species with the same phenology. Examples of the first phenomenon are provided by *D. balansae* — an orophyte (s.l.) endemic to the Atlas mountains, between 1800 and 3000 m above sea level, which is absolutely allopatric — and *D. cossonianum,* endemic to North and Central Morocco and possessing ecological specificity (crop fields on black clay lowlands) and phenological isolation from other sympatric species, cf. BLANCHÉ (1985). All the other taxa, including the Iberian and Italian representatives, illustrate the second phenomenon. The mobility of the populations, further increased by man

TABLE II. - Karyotype size of *Delphinium* L. sect. *Delphinium*. North African Populations.

Taxon	**Size of chromosomes** (µm, m ± SE, n = 10)								**Average size** (µm,m ± SE)	**Satellite** (Pair)
Pair Number	I	II	III	IV	V	VI	VII	VIII		
D. balansae										
CB.220	5.62 ± 0.32	5.30 ± 0.41	4.06 ± 0.11	3.80 ± 0.09	3.61 ± 0.16	3.30 ± 0.09	2.96 ± 0.16	1.74 ± 0.06	3.97 ± 0.44	–
D. cossonianum										
CB.002	5.34 ± 0.16	3.68 ± 0.14	3,20 ± 0,14	3.00 ± 0.09	2.98 ± 0.11	2.62 ± 0.07	2.48 ± 0.09	2.22 ± 0.10	3.19 ± 0.34	IV
CB.044	5.62 ± 0.14	3.96 ± 0.15	3.48 ± 0.009	3.28 ± 0.10	3.27 ± 0.09	2.94 ± 0.10	2.62 ± 0.10	2.30 ± 0.08	3.43 ± 0.36	IV
CB.046	5.12 ± 0.12	3.96 ± 0.18	3.56 ± 0.14	3.18 ± 0.10	2.92 ± 0.08	2.66 ± 0.06	2.36 ± 0.08	1.96 ± 0.06	3.21 ± 0.35	V
CB.047	6.30 ± 0.16	3.86 ± 0.08	3.53 ± 0.09	3.31 ± 0.12	3.31 ± 0.08	3.30 ± 0.13	2.82 ± 0.12	2.48 ± 0.15	3.57 ± 0.41	IV
D. nanum subsp. *elongatum*										
CB.003	5.22 ± 0.15	3.66 ± 0.15	3.10 ± 0.12	2.90 ± 0.13	2.72 ± 0.11	2.48 ± 0.09	2.24 ± 0.11	1.82 ± 0.47	3.02 ± 0.37	V, V
CB.016	6.06 ± 0.25	4.20 ± 0.27	3.28 ± 0.28	2.98 ± 0.12	2.80 ± 0.12	2.74 ± 0.10	2.58 ± 0.11	2.34 ± 0.48	3.37 ± 0.47	III, V
CB.018	5.62 ± 0.14	4.18 ± 0.08	3.21 ± 0.10	3.000 ± 0.05	2.90 ± 0.04	2.68 ± 0.06	2.46 ± 0.05	2.04 ± 0.10	3.26 ± 0.40	II
CB.033	5.60 ± 0.16	4.62 ± 0.18	3.62 ± 0.14	3.32 ± 0.13	3.06 ± 0.08	2.86 ± 0.006	2.66 ± 0.06	2.02 ± 0.08	3.47 ± 0.40	–
CB.045	5.70 ± 0.26	3.90 ± 0.13	3.38 ± 0.09	3.20 ± 0.08	3.00 ± 0.06	2.86 ± 0.18	2.74 ± 0.47	2.34 ± 0.11	3.39 ± 0.36	–
D. nanum subsp. *albolilaceum*										
CB.005	5.96 ± 0,22	3.82 ± 0.14	3.46 ± 0.15	3.22 ± 0,11	2.94 ± 0.11	2.66 ± 0.09	2.54 ± 0.03	2.26 ± 0.11	3.35 ± 0.41	VII
CB.009	6.42 ± 0.15	4.60 ± 0.22	3.68 ± 0.06	3.32 ± 0.06	3.32 ± 0.05	3.14 ± 0.07	2.78 ± 0.08	2.14 ± 0.25	3.67 ± 0.46	–
D. macropetalum										
CB.010	6.64 ± 0.16	4.46 ± 0.18	3.98 ± 0.15	3.66 ± 0.13	3.50 ± 0.17	3.24 ± 0.16	3.00 ± 0.15	2.70 ± 0.15	3.87 ± 0.44	–
CB.012	6.50 ± 0.17	4.56 ± 0.28	4.16 ± 0.13	3.72 ± 0.06	3.44 ± 0.15	3.18 ± 0.04	2.92 ± 0.03	2.48 ± 0.06	3.87 ± 0.42	II
CB.013	6.10 ± 0.13	4.12 ± 0.13	3.50 ± 0.05	3.28 ± 0.04	3.10 ± 0.03	2.94 ± 0.06	2.66 ± 0.07	2.44 ± 0.09	3.51 ± 0.41	II

TABLE III. - Karyotype assymmetry of *Delphinium* sect. *Delphinium*. North African populations.

Taxon/ Population	**Degree of asymmetry**	**Centromeric index**								**Chromosome formula**
		I	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	
D. balansae										
CB.220	3B	58.01	28.30	18.71	18.94	37.65	18.18	19.50	31.03	2m + 2sm + 2st
D. cossonianum										
CB.002	3B	37.07	10.32	17.50	26.0	16.77	17.50	11.20	14.40	1sm + 1sm^{sat} + 4st + 2t
CB.044	4B	32.30	15.15	20.10	30.48	16.46	22.40	12.20	10.40	1sm + 1sm^{sat}4st + 2t
CB.046	3B	35.90	19.19	21.30	34.59	11.60	14.28	12.70	14.28	1sm + 1sm^{sat} + 5st + 1t
CB.047	3B	34.90	15.50	12.44	25.68	14.30	10.0	12.14	10.48	1sm + 1sm^{sat} + 3st + 3t
D. nanum subsp. *elongatum*										
CB.003	4B	31.03	22.95	9.67	8.27	9.56	9.67	9.82	10.98	1sm + 1st + 2t^{sat} + 47
CB.016	3B	33.90	23.30	18.90	9.39	11.42	12.40	11.60	11.90	1sm + 1sm^{sat} + 2st + 4t
CB.018	3B	37.30	26.30	10.40	8.60	11.70	14.17	9.75	15.60	1sm + 1sm^{sat} + 2st + 4t
CB.033	3B	36.78	22.07	11.04	10.80	10.40	11.80	13.50	13.80	1sm + 3st + 4t
CB.045	3B	32.63	20.51	10.65	10.0	10.66	9.79	10.21	9.40	1sm + 1st + 6t
D. nanum subsp. *albolilaceum*										
CB.005	3B	33.22	17.27	15.02	18.63	14.96	12.78	14.17	15.48	1sm + 1sm^{sat} + 6st
CB.009	4B	32.08	18.26	12.50	12.60	13.15	19.10	15.10	14.90	1sm + 7st
D. macropetalum										
CB.010	3B	35.50	12.50	11.50	11.50	10.28	10.40	13.30	17.30	1sm + 3st + 4t
CB.012	4B	29.84	25.0	12.01	10.09	11.04	11.94	10.95	13.71	1sm + 1st^{sat} + 1st + 5t
CB.013	3B	33.40	14.07	12.57	13.41	11.61	14.28	12.03	15,57	1sm + 1st^{sat} + 4st + 2t

in the process of crop expansion, seed mixing and the colonization of new arable land, provides far more frequent contact between populations with a close geographical relationship. The possible entry of new genotypes into a particular population may explain the existence of intermediate forms, the fading of differences and finally a «mosaic» type model for the distribution of phenotypes.

4.- Despite the strong resemblance of the karyotypes studied, more or less noteworthy differences can be observed with a variety of meanings. When associated to variations in morphology and/or ecological preference, these make it possible to establish correlations of systematic value.

5.- *D. balansae* must be singled out first and foremost on account of the special characteristic of its karyotype. The average length of the complement is among the greatest in the taxa under study (cf. Table II) and the presence of submetacentric chromosomes in pairs II and V, together with the relatively long short arms of the rest of the complement, set it clearly apart. These characteristics can be interpreted in the light of data relating to sect. *Delphinastrum* DC. which includes the perennial taxa of the Western Mediterranean (Table IV). In fact, *D. balansae* (the only perennial species of sect. *Delphinium*) occupies an intermediate position between annuals and perennials: the chromosomes are similar in size to those of the annuals, but the karyotype structure, is practically identical, in terms of asymmetry (centromeric index), to that of the perennials. This evidence is of great interest since, up to now, no possible link had been discovered between annual and perennial *Delphinium* species and this intermediate position makes *D. balansae* into a possible relictual ancestor of the annuals.

Analysis of Table IV reveals on the one hand an increase in asymmetry in the annual species (sect. *Delphinium*), illustrated by a decreasing centromeric index (average position of the centromeres closer to the end of the chromosomes, or, in other words, chromosome arms of more unequal size), and on the other a tendency for the size of annual karyotypes to decrease with respect to perennials. This reduction in length must be associated with a loss of genetic material, a hypothesis which is confimed by AL-KELIDAR & RICHARDS (1981) who evaluate the loss nuclear contents of DNA in annual *Delphinium* species at about 30 % less than in perennials, a figure approximately the same as the decrease in length reported here.

6.- In the various populations of *D. cossonianum* studied, there is little variation in the karyotype (cf. Tables II and III and Fig. 3). The main characteristics are one submetacentric pair (pair I) and another between submetacentric and acrocentric (pair V and, accidentally, pair IV on account of the very small differences in their respective size in population CB. 046), together with the constant presence of satellites on the long arm of the chromosmes of pair IV (pair V in CB. 046 for the reason stated above). The centromeric index of pair IV (between 25.68 and 34.59, cf. Table III) is much closer to that of *D. balansae* (pair V, IC = 37.67) than to the remaining taxa (pair V, IC betwen 8.27 and 13.41). Taxonomically *D. cossonianum* is an extremely isolated species (it is the only annual with five carpels, the rest having three, and the seeds and structure of the inflorescence are clearly differenciated) and it is endemic to the N and NW of Morocco.

7.- In contrast, analysis of the results of *D. macropetalum* and *D. nanum* (subsp. *elongatum* and subsp. *albolilaceum*), two taxa with great phenotypic affinities which are included by MAIRE (1964) in various combinations in his concept of *D. peregrinum* s.l., reveals other characteristic traits. Thus while the karyotypes of *D. balansae* and *D. cossonianum* display great constance and stability, these species display minor variations in karyotype structure which are apparently not correlated to other factors. Of significance for instance is the variability observed in the number and position of the satellites. In certain populations of all three taxa (CB. 010, CB. 033, CB.045 and CB.009), no satellites were detected in any of the metaphases studied (Figs. 2 and 3). Other populations, however, have a pair of satellite-bearing chromosomes (pair II in CB.012, CB.013 and CB.018; pair VII in CB.005) or even two pairs (populations CB.016, pairs III and V; CB.003, pairs V and VII). Though satellites tend to some

TABLE IV. - Characteristics of the karyotypes of species of sect. *Delphinium* compared with those of perennial species of sect. *Delphinastrum* DC.

Taxon	**Size of chromosomes (µm)**	**Assymetry (Centromeric index)**
Sect. *Delphinastrum* *	4.98 ± 0.16	28.29 ± 3.89
D. *balansae*	3.89 ± 0.44	28.80 ± 4.88
Sect. *Delphinium* **	3.44 ± 0.39	16.95 ± 3.13

The results are expressed as the mean ± the standard error (m ± SE)
* Average of the data corresponding to perennial species studied in Blanché, 1985.
** Average of the data presented in the present study (Tables II and III).

Fig. 2. – Idiograms of *Delphinium* sect. *Delphinium*. (I) North African populations. A, B, *D. macropetalum* (A: CB. 010; B: CB. 012). C, *D. balansae* (CB. 220).

extent to be present in particular chromosomes (II, III, V, and VII) and absent from the others, there is no obvious correlation with ecology or geographical distribution. Populations only 20-50 km apart and with practically identical phenotypes reveal differences in the number and position of the satllites. In a previous work (Blanché, Molero & Simon, 1987) we suggested on the basis of data referring to the genus *Consolida* that this variability of satellites might have some geographical significance. That hypothesis must now be reconsidered in the light of the present data, as already pointed out to us by Prof. C. Favarger (com. pers.). This variability in the position of the satellites must therefore be interpreted as characteristic at population level only and indicative of a certain karyotype instability which may well be linked to adaptation processes.

8.- Turning now to another topic, no significant differences are observed between the average lengths of the chromosomes of *D. macropetalum* and *D. nanum* (both subspecies). Their respective chromosome formulae always consist of lsm and only the proportion of st/t varies (and even with the values very close on either side to the numeric limit between them established by Levan & al., 1964). The asymmetry corresponds to 3B and 4B, using the classes defined by Stebbins (1971). In an endeavour to obtain greater resolution, we have calculated indexes A1 and A2 as established by Romero (1986) (see Fig. 4), together with data on perennial species (Blanché, 1985). *D. cossonianum* here appears to be highly individualized while *D. balansae* occupies a position of transition between annual and perennial taxa, as observed above, though it also falls into Stebbins's class 3B (l.c.). In contrast, the populations

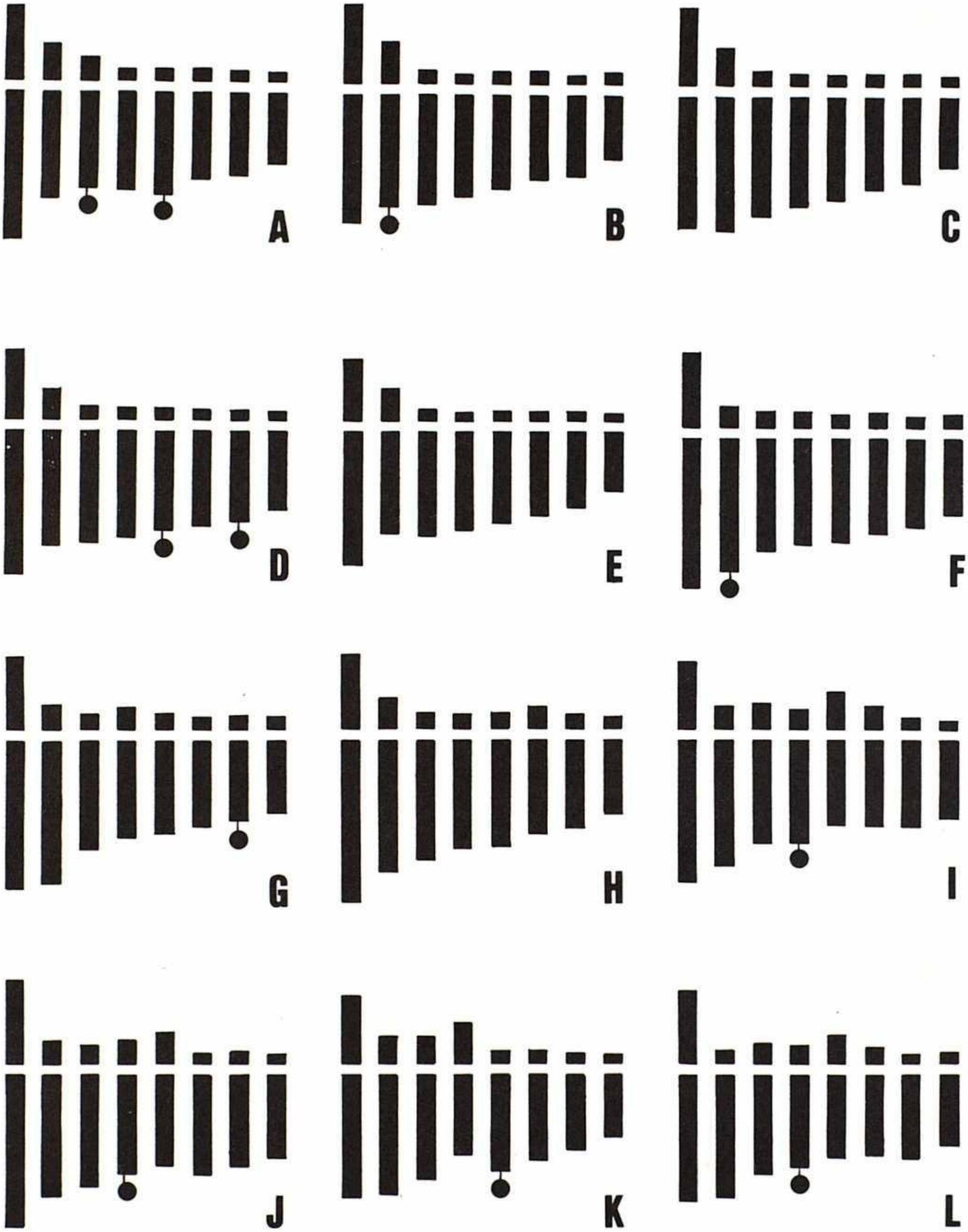

Fig. 3. — Idiograms of *Delphinium* sect. *Delphinium* (II). North African populations. A-E, *D. nanum* subsp. *elongatum* (A: CB.016; B: CB.018; C: CB.033; D: CB.003; E: CB.045). F, *D. macropetalum* (CB. 013); G, H, *D. nanum* subsp. *albolilaceum* (G: CB.005; H: CB.009). I-L, *D. cossonianum* (I: CB.044; J: CB.002; K: CB.046; L: CB.047).

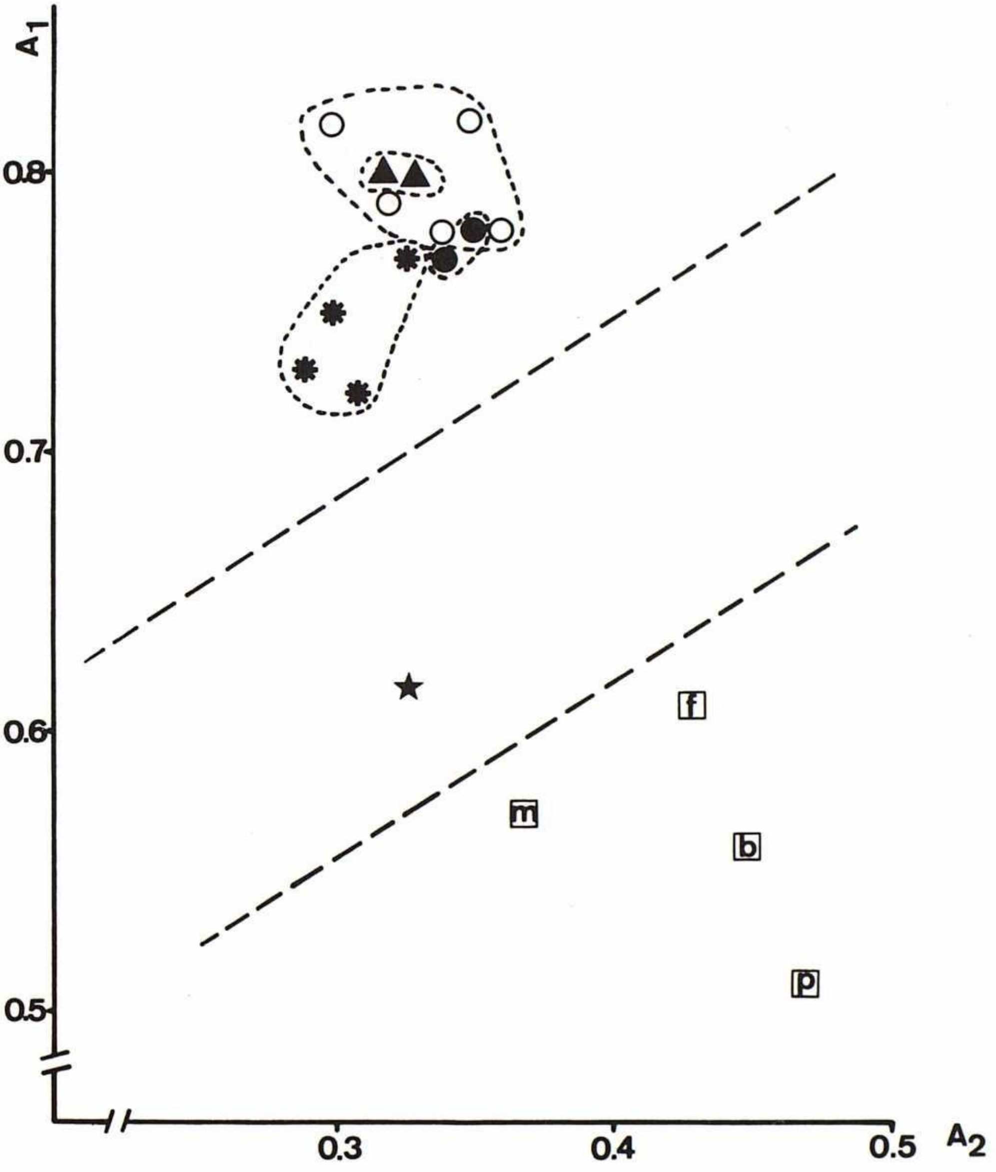

Fig. 4. — Diagram showing assymetry of karyotypes from Romero (1986). Annual taxa belonging to sect. *Delphinium:* ✱ *D. cossonianum,* ○ *D. nanum* subsp. *elongatum,* ● *D. nanum* subsp. *albolilaceum,* ▲ *D. macropetalum.* Perennial taxa belonging to sect. *Delphinium:* ★ *D. balansae.* Perennial taxa belonging to sect. *Delphinastrum* (data from the Iberian Peninsula, according to Blanché, 1985), □ m, *D. montanum,* f, *D. fissum* subsp. *sordidum,* b, *D. bolosii,* p, *D. pentagynum.*

of *D. macropetalum* and *D. nanum* form interconnecting clusters of points, thus confirming the proximity of these two taxa.

9.- In the light of these results and of the analysis of phenotypical and ecological characteristics, what might be the most valid taxonomic outline for the section? MAIRE (1964), probably the only author who has dealt with North African *Delphinium* and had direct knowledge of the annual species, proposed an integrating conception suggested by field experience which brought to light very subtle differences and numerous intermediate forms. The outline we propone below endorses this view while taking into account both the criteria established by DAVIS (1965) and PAWLOWSKY (1963) and the geographic distribution of the section throughout the Mediterranean region.

Taxonomic outline for north African *Delphinium* sect. *Delphinium*

Delphinium L. sect. **Delphinium** (= sect. *Delphinellum* DC.)

Series **Halterata** Pawl. - Limb of lateral petals cordate at base. Crop fields and dry meadows. W and C Mediterranean.

D. halteratum Sibth. & Sm. (Ga, It, Sa, Si). Introduced into North Africa (Morocco, Algeria).

D. verdunense Balb. (Ga, Hs, Lu). Absent from North Africa.

D. gracile DC. (Hs, Lu, Bl (Eivissa)). Introduced into North Africa (Algeria).

D. cossonianum Batt. Endemic to Morocco.

Series **Macropetala** Blanché, Molero & Simon, *ser. nova*. - *Petalorum lateralium limbus pro portione magnus, suborbicularis, subtrapezoidalis vel suborbiculari-obcordatus, basi truncatus non cordatus, saepius manifeste exertus. Hispania, Lusitania, Africa boreo-occidentalis.* SERIEI TYPUS: *D. macropetalum* DC. Limb of lateral petals large, exert, suborbiculate, subtrapezoidal to obcordate; base of limb truncate, not cordate. Dry meadows, crop fields, dunes. Preference for sandy soils. W. Mediterranean, especially near the coast.

D. macropetalum DC. Endemic to SW Morocco.

D. nanum DC. (= *D. obcordatum* DC., cf. BLANCHÉ & MOLERO, 1984).

subsp. *nanum*. (Hs, Lu, as far as Si). Morocco, Algeria.

subsp. *elongatum* (Boiss.) Blanché, Molero & Simon, comb. et stat.
nov. (= *D. peregrinum* L. *var. elongatum* Boiss., Voyage bot.
Midi. Espagne; 2: 12, 1939). Exclusively North African:
Morocco, Algeria, Tunisia, Lybia.

subsp. *albolilaceum* (Maire) Blanché, Molero & Simon, *comb. et stat. nov.* (= *D. peregrinum* L. var. *elongatum* Boiss. fa. *albolilaceum* Maire *in* Jahandiez et Maire, Cat. Pl. Maroc, 3:879, 1934).

Series **Balansae,** Blanché, Molero & Simon, *ser. nov.* - *Plantae perennes. Africa boreo-occidentalis.* SERIEI TYPUS: *D. balansae* Boiss. & Reuter.

D. balansae Boiss. & Reuter. Endemic to Morocco and Algeria.

Series **Peregrina** Pawl. - Limb of lateral petals gently decurrent towards the base of the claw. Eastern Mediterranean.

D. peregrinum L. - Absent from North Africa (cf. also BLANCHÉ & MOLERO, 1985).

Conclusions

1.- Cytogenetic analysis reveals a growing tendency towards karyotype asymmetry in annual species of *Delphinium*. In the light of the suggestions made by STEBBINS (1971:92) this phenomenon must be considered a «secondary» evolutionary characteristic, since it is superimposed over the already high «primary»asymmetry of the perennial *Delphinium* species due to the specialization of the floral structure.

STEBBINS (l.c.) explains the mechanism governing this increase in karyotype asymmetry as the result of pericentric inversions and unequal translocations of fragments of chromosome arms which occur without any change in the number of centromeres or of independent chromosomes. This process is not detected in long-living perennial species occupying relatively stable habitats. On the other hand, it is usually associated with the colonization of new, open habitats and the transition to annual cycles ocurring at the same time as continued allogamy which is often rendered necessary by floral structure. This model indeed matches our observations perfectly and is an alternative to the fairly well known strategies of autogamy, polyploidy or apomixis.

2.- In addition to this overall mechanism there is the role played by geographical, ecological and/or phenological isolation which have facilitated (in the case of *D. balansae* and *D. cossonianum*) or hindered (in the case of *D. macropetalum* or *D. nanum*) the processes of differentiation and indeed of speciation in populations with few genetic barriers to separate them (LEGRO, 1961, indicates the existence of over 4000 cultivars of *Delphinium* for horticultural use which were obtained from 211 hybridations).

3.- Finally, the biogeographical analysis of the whole of section *Delphinium* reveals the existence of two major focusses of speciation in the Mediterranean Region:

a) a first centre of diversity in the Eastern Mediterranean (Turkey-Greece) which presents a high degree of endemism, characteristic of explosions of annuals caused by the arrival of Irano-Turanian elements in the Mediterranean Region (cf. DAVIS, 1971).

b) a secondary focus of diversity in the Western Mediterranean, with its centre in the Atlas mountains, where *D. balansae* has been conserved as a relictual element, the only surviving perennial ancestor of this section. There are also a large number of endemisms.

This model is analogous to that reported by EHRENDORFER (1988) for the *Achillea*-group *(Anthemideae, Compositae),* which includes both centres of diversity, but in which the ancestral groups are also conserved in the region of the North West Africa (the monotypic perennial genus *Heliocauta* and the greater diversity of the circum-Mediterranean genus *Anacylus*).

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