Delphinium L. Subgen. *Delphinium:* origin and evolutionary trends

CÈSAR BLANCHÉ

Resum

BLANCHÉ, C. (1990) *Delphinium* L. subgen. *Delphinium:* Origen i tendències evolutives. Collect. Bot. (Barcelona), 19: 75-95.

Les característiques avançades de *Delphinium* L. subgèn. *Delphinium* (tàxons anuals) són comparades amb les del subgèn. *Delphinastrum* (DC.) Wang i del subgèn. *Oligophyllon* Dimitrova (tàxons perennes). La morfologia floral mostra un intercanvi de funcions entre els pètals laterals i els pètals superiors i l'estructura de la inflorescència de molts tàxons anuals afavoreix un augment de les taxes de geitonogàmia-autogàmia. L'evolució dels cariotips és basada en una disminució de la longitud total dels cromosomes i en un increment del grau d'asimetria; el nombre cromosòmic roman constant per a totes les espècies anuals (2n = 16). L'eficàcia de la dispersió de les espècies anuals és més gran que no pas la de les espècies perennes, per causa d'un increment en la producció de granes i per l'augment de la flotabilitat, tant a l'aire com a l'aigua. D'altres característiques adaptatives avançades són l'adquisició de noves defenses químiques i l'aparició d'un nou tipus embriogènic. Els nínxols ecològics del subgèn. *Delphinium* corresponen a hàbitats oberts i alterats, en comparació amb els hàbitats estables i relativament tancats dels subgèneres *Delphinastrum* i *Oligophyllon.* Es presenta una hipòtesi global de les tendències evolutives observades en anuals *vs.* perennes en connexió amb consideracions biogeogràfiques, així com un resum taxonòmic final.

Mots clau: *Delphinium,* Evolució, Taxonomia, Biogeografia.

Abstract

BLANCHÉ, C. (1990) *Delphinium* L. subgen. *Delphinium:* origin and evolutionary trends. Collect. Bot. (Barcelona), 19: 75-95.

The advanced features of *Delphinium* L. subgen. *Delphinium* (annual taxa) are compared with those of subgen. *Delphinastrum* (DC.) Wang and subgen. *Oligophyllon* Dimitrova (perennial taxa). Flower morphology shows a functional interchange between lateral petals and upper petals, and inflorescence structure favours geitonogamy-autogamy rates. Karyotype evolution is based on a decrease in the total length of chromosomes and on an increase in the degree of asymmetry: the chromosome number remains constant (2n = 16) in the subgen. *Delphinium.* The dispersal efficiency of the annual species is higher than that of perennials due to seed set increase and improved floatability, both in water and in air. Other advanced adaptive features are the acquisition of new chemical weapons and the emergence of a new embryonogenic type. The ecological niches of subgen. *Delphinium* correspond to open and disturbed habitats in contrast to the stable and relatively closed ones of subgenera *Delphinastum* and *Oligophyllon.* A final hypothesis is made concerning the evolutionary trends observed in annuals *vs.* perennials in connexion with biogeographical considerations, and a final taxonomic summary is given.

Keywords: *Delphinium,* Evolution, Taxonomy, Biogeography.

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INTRODUCTION

According to MALYUTIN's (1987) conception of the genus *Delphinium* L., the subgenus *Delphinium* comprises all the 21 annual species known to date, which are mainly spread over the Mediterranean area. This is only a small part of the whole genus *Delphinium* (the total number of species listed by MALYUTIN *(l.c.)* is 364; see appendix for the list of the taxa considered here).

On the basis of the present state of knowledge and our previous papers (BLANCHÉ, 1985; BLANCHÉ & MOLERO, 1984, 1985 and 1986, and BLANCHÉ & AL., 1985, 1987, 1988, 1990), I will try to outline both the origin of the subgenus and the pylogenetic links within it, as well as the main evolutionary trends in relation to the remaining perennial species.

BIOGEOGRAPHY

Two well distinguished and separate areas of distribution of the representatives of the subgenus *Delphinium* can be recognized, using the phytocoria boundaries proposed by TAKHTAJAN (1986), as showed in figure 1:

a) Sect. *Delphinium.*— Annual species with limb of lateral petals entire. Mediterranean and Irano-Turanian Regions extending marginally into Saharo-Arabian and Circumboreal Regions.

b) Sect. *Anthriscifolium* W. T. Wang.— Annual species with limb of lateral petals bifid. Eastern Asiatic Region.

Thus, there is no actual contact or overlapping between their respective areas and this makes it specially difficult to establish an evolutionary hypothesis. However, if we consider the Eastern Himalayan ranges as the primary focus of diversity of the whole genus *Delphinium* (since it is in this area that the greatest number of species is found as can be seen in Figure 1, and the most primitive perennial species grow as pointed out by WANG, 1962, and MALYUTIN, 1973), it is evident that the sect. *Anthriscifolium* (recorded in Central Chinese, South-Eastern Chinese and Sikang-Yünnan Provinces) occupies a closer position to the primary center than the sect. *Delphinium.*

In contrast, the representatives of the sect. *Delphinium* are mainly distributed in the Tethyan (Ancient Mediterranean Area), from the most western provinces of the Mediterranean Region (Southern Moroccan Province) to the central provinces of the Iranio-Turanian Region (Armeno-Iranian Province) (table 1).

How can this kind of disjunction be explained? Some patterns do not seem to apply to our model. Long-distance dispersal by water, birds or wind is better applied to the colonization of islands and is difficult to accept in *Delphinium* because other species belonging to other sections can be found in the intermediate areas of the hiatus between sect. *Delphinium* and sect. *Anthriscifolium.* Allopatric (polytopic speciation) should be accepted only in certain exceptional cases, as suggested by FAVARGER & KÜPFER (1969): "...la répétition fidèle en deux régions éloignées et peut-être à des époques différentes du même processus évolutif, nous paraît hautement improbable sauf pour des espèces assez proches géographiquement our pour les micromorphes" and this is not the case. However, some evidence seems to support a third possible pattern (fragmentation of a previously continous area):

a) According to present knowledge, no species of sect. *Delphinium* appear within the eastern limits of the Irano-Turanian Region. This is not surprising because of the non-homogeneous diversity of the Irano-Turanian flora, the Iranian Plateau being the richest and Eastern Central Asia the most impoverished area (TAKTHAJAN, 1986).

b) One of the easternmost records (Iran) of sect. *Delphinium* belongs to *D. syncarpum* Freyn., a species whose status is little known and of wich few specimens have been collected

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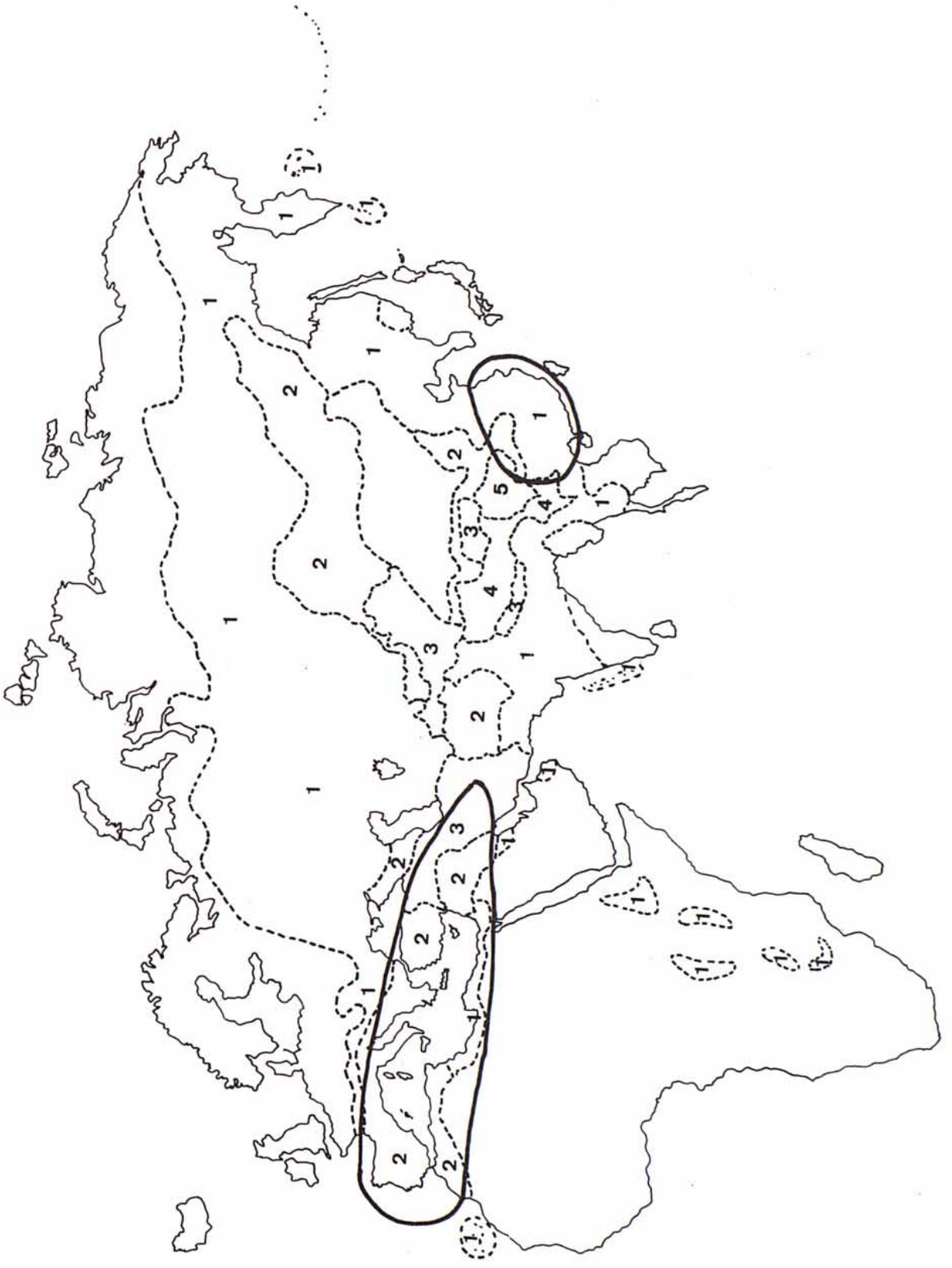

Fig. 1 – Distribution of *Delphinium* species in the Old World. Numbers indicate the species existing in a given area (1: 1-5 species; 2: 6-15 species; 3: 15-25 species; 4: 26-40 species; 5: more than 40 species). Continous areas outline aproximately the distribution of both sections of subgenus *Delphinium*.

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Table 1. Biogeographical analysis of *Delphinium* L. sect. *Delphinium*.

Phytocoria*	Total number** of species	Number of endemic** (or semi-endemic) species
MEDITERRANEAN REGION		
Provinces:		
Southern Moroccan	2	1
Southwestern Mediterranean	4	2
Iberian	3	(1)
Balearic	1	–
South Mediterraean	3	–
Ligurio-Thyrrenian	3	–
Adriatic	2	–
Eastern Mediterranean	6	5
SAHARO-ARABIAN REGION		
Provinces:		
Egyptian-Arabian	1	1
IRANO-TURANIAN REGION		
Provinces:		
Mesopotamian	2	1
Central Anatolian	2	1
Armeno-Iranian	3	2
CIRCUMBOREAL REGION		
Provinces:		
Atlantic-European	1	–
Illyrian or Balkan	1	(1)
Euxine	2	1

* The boundaries adopted are from TAKHTAJAN (1986)
** Data taken from the appendix at the end of the paper

(at least until the completion of Rechinger's *Flora Iranica*). This species shows a deep sinus on the limb of the lateral petals (see MUNZ, 1967:257) which seems to be closely related to the bifid lateral petals of representatives of sect. *Anthriscifolium*.

c) As showed in Table 1, the two main focuses of diversity of the sect. *Delphinium* are to be found at either end of the Mediterranean Region (Greece-Turkey and Western North Africa). In the latter (Atlas Mountains and Aurès-Djudjura Ranges) the only perennial representative of the subgenus (*D. balansae* Boiss. & Reuter) still endures. The fact that the only surviving perennial ancestor of the whole subgenus (perennial habit but floral morphology corresponding to the remaining annual species) grows in the region farthest removed from the hypothetical origin of this group is irrelevant and subject to biogeohistorical constraints. The conservative role of ancient taxa by the North African area is also suggested by EHRENDORFER (1988) with reference to the *Compositae* and by EHRENDORFER (1990) with reference to the *Rubiaceae*.

d) The Eastern Mediterranean Area is the richest region both in the number of species and in the number of endemics (Table 1). The intermediate zones between the Mediterranean and Irano-Turanian Regions or between the Euxine Province and the Irano-Turanian Region have played an important role in the entry of Irano-Turanian elements into the Mediterranean Region, specially in disturbed and transitional areas (DAVIS, 1971). Probably

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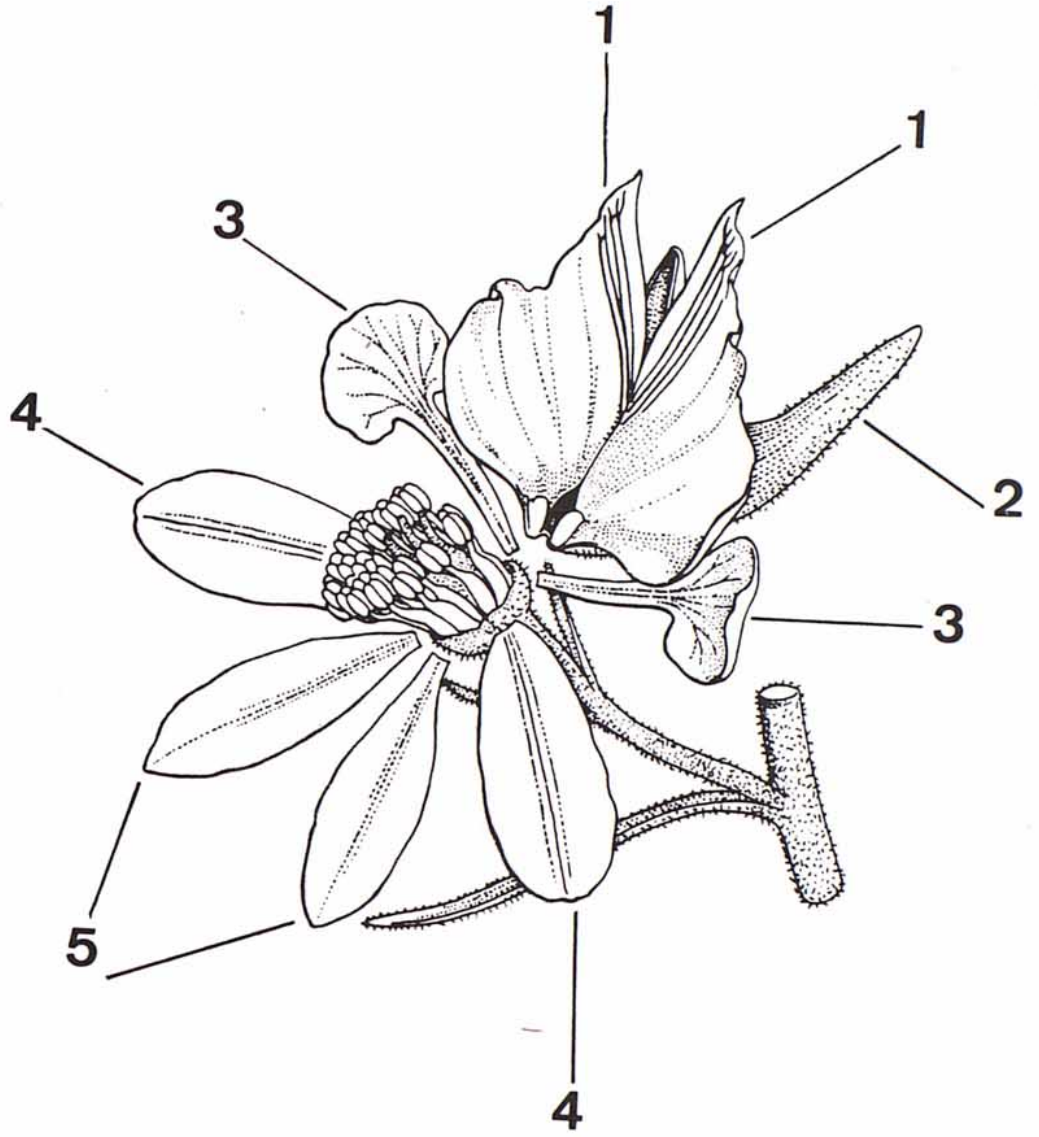

Fig. 2 – Flower structure of *Delphinium verdunense* Balbis. 1: Upper petals; 2: Spur; 3: Lateral petals; 4: Lateral sepals; 5: Lower sepals.

the ancestors of the present sect. *Delphinium* arrived in these areas in relatively remote times (the Irano-Turanian flora moved into E. Anatolia from Iran during the Pliocene when the East Anatolian climate increased in aridity (DAVIS, *l.c.*). Its arrival in the W. Mediterranean is necessarily of more recent origin, as can be inferred from the total absence of sect. *Delphinium* (even nowadays, under man's influence) from Corsica and the Balearic Islands (BLANCHÉ, 1985; GAMISANS, 1985) except Eivissa Island which was formerly linked to the Iberian Peninsula. In this group of islands, however, the paleoendemic group of *D. staphisagria* L.-*D. pictum* Willd. - *D. requienii* DC. can be found. Thus, the genus *Delphinium* could have arrived in the Western Mediterranean in two waves, the first (*D. staphisagria* group) occuring in more ancient times (during the Miocene, before the islands were cut off from the mainland, cf. GAMISANS, *l.c.*) and the second (involving the annuals of sect. *Delphinium*) taking place more recently, after the formation of the islands.

In addition to the development of an annual life cycle, it is possible to identify a series of advanced features, which can be regarded as a set of new adaptive strategies and which differentiate the subgen. *Delphinium* from the remaining perennial taxa. The following are worthy of mention:

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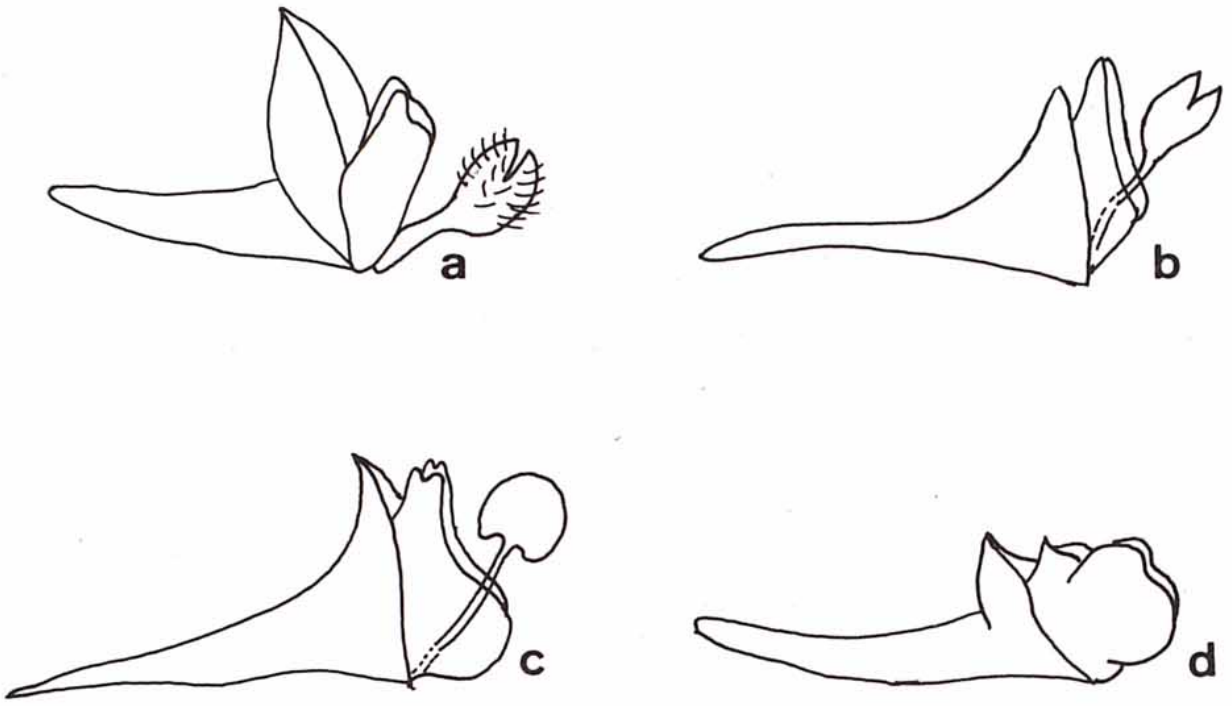

Fig. 3 – Flower schemes of a) *Delphinium fissum* (perennial); b) *D. anthriscifolium*; c) *D. cossonianum* and d) *Consolida mauritanica*.

POLLINATION MECHANISM

1. Flower Morphology

The flowers of *Delphinium* are well known as an example of the "bee-flowers syndrome" (FAEGRI & van der PIJL, 1980), although some other animals can pollinate them efficiently (e.g., hummingbirds cf. GUERRANT, 1982; WASER & PRICE this volume). The flower consists of 5 petaloid sepals, one of them with a long spur, and four petals, the two upper nectariferous ones extending into the spur sepal, and the two lateral ones, usually exsert, placed just in front of the entrance of the spur (Figure 2).

Up to now, the only legitimate pollinators observed in the subgenus *Delphinium* belong to the genus *Bombus* (bumble-bees) although some butterflies have been seen sucking on the flowers and a lot of small insects can produce holes of c. 0,5 mm at the end of the spur, thus removing nectar without pollen transfer (MÜLLER, 1899, BLANCHÉ, 1985).

Besides flower structure, other mechanisms of reproductive adaptation to pollination by insects include protandry, which begins with the emergence and subsequent downwards movements of the anther (after dehiscence) and ends with the emergence of the pistils and the opening of the stigmata.

Thus, flower characteristics must be of vital importance to the reproductive behaviour of the *Delphinium* species, and their modifications should have far-reaching biological significance. By studying the general arrangement and shape of the flower in *Delphinium,* the following evolutionary pattern can be traced (Figure 3): from subgen. *Delphinastrum* to the

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sect. *Delphinium* through the sect. *Anthriscifolium,* the relative surface area and appearance of both kinds of petals are interchanged. The function of the big lateral ciliate, bifid petals which, in subgen. *Delphinastrum,* serve as mark to attract and guide pollinators (MÜLLER, 1895), is progressively assumed by the enlarged lateral lobes of the upper petals in the subgen. *Delphinium.* Simultaneously, the lateral petals of subgen. *Delphinium* lose their limb size and modify their position in comparison with those of *subgen. Delphinastrum.* This evolutionary trend reaches its farthest point in the related genus *Consolida* (DC.) S.F. Gray where the lateral petals dissapear completely and the lateral lobes of the upper petals show greatest development [BLANCHÉ, 1985].

This pattern places the sect. *Anthriscifolium* in an intermediate position between the perennials and the sect. *Delphinium.* Their lateral petals are not ciliate but they retain the 2-lobed shape (Figure 3).

2. Inflorescence structure

In contrast to the more or less simple racemose inflorescences with few lateral branches that characterize the great majority of perennials, the species of subgen. *Delphinium* have compound racemes with many more branches in the majority of species (BLANCHÉ, 1985), as showed in Figure 4.

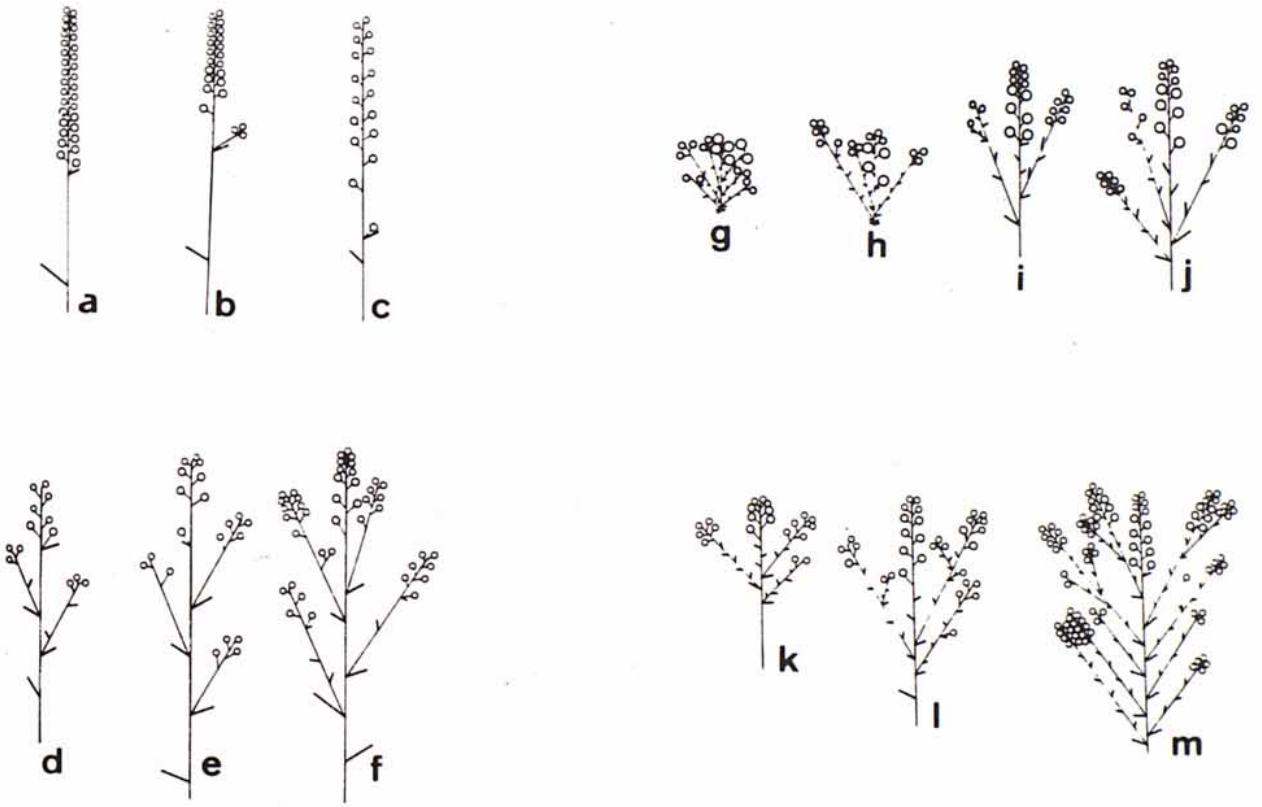

Fig. 4 – Inflorescences of subgenus *Delphinastrum* (a: *D. fissum*, subsp. *fissum* Hungary, BC 1796; b: *D. fissum* subsp. *sordidum*, Spain BCF s/n; c: *D. bolosii*, Catalonia, BCF 30643; d: *D. pentagynum*, Spain, MAF 47034; e: íd., Spain, LY-Rouy s/n; f: id., Spain, MAF 94365) and subgenus *Delphinium* (g: *D. nanum*, Morocco, BC 139213; h: *D. nanum*, Spain, BC 1841; i: *D. verdunense*, Spain, BCF s/n; k: *D. verdunense*, Catalonia, BCF s/n; l: *D. verdunense*, Spain, BCF s/n; m: *D. verdunense*, Catalonia, BCF s/n)

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This fact is of great importance in relation to the pollinator behaviour, because bumblebees can easily visit consecutive branches of the same individual (BLANCHÉ, unpubl. data), this favouring improvement of the autogamy-geitonogamy rates or, at least, a decrease in the chance of cross pollination.

KARYOTYPE EVOLUTION

All the species of the subgenus *Delphinium* investigated up to now are strictly diploid with 2n = 16 chromosomes (x = 8), in contrast with the subgenus *Delphinastrum* where other basic numbers (x = 9, BLANCHÉ & MOLERO, 1983; x = 10, AK-SARKAR, 1982) and other ploidy levels (3x, 4x, see among others FEDOROV, 1974) have been found. This absence of polyploids can be interpreted as a characteristic feature of more recent origin of subgen. *Delphinium*. The presently known chromosome numbers of subgenus *Delphinium* are listed in Table 2.

The karyotypes of the annual species are highly asymmetrical and bimodal, with 1 or 2 long, submetacentric chromosomes, the remaining ones being shorter (progressively decreasing in size) and nearly acrocentric (BLANCHÉ, 1985; BLANCHÉ & AL., 1990). If we compare the known karyotypes of subgen. *Delphinium* with those of the perennial subgen. *Delphinastrum* (Table 3 and Figure 5), we can assume that:

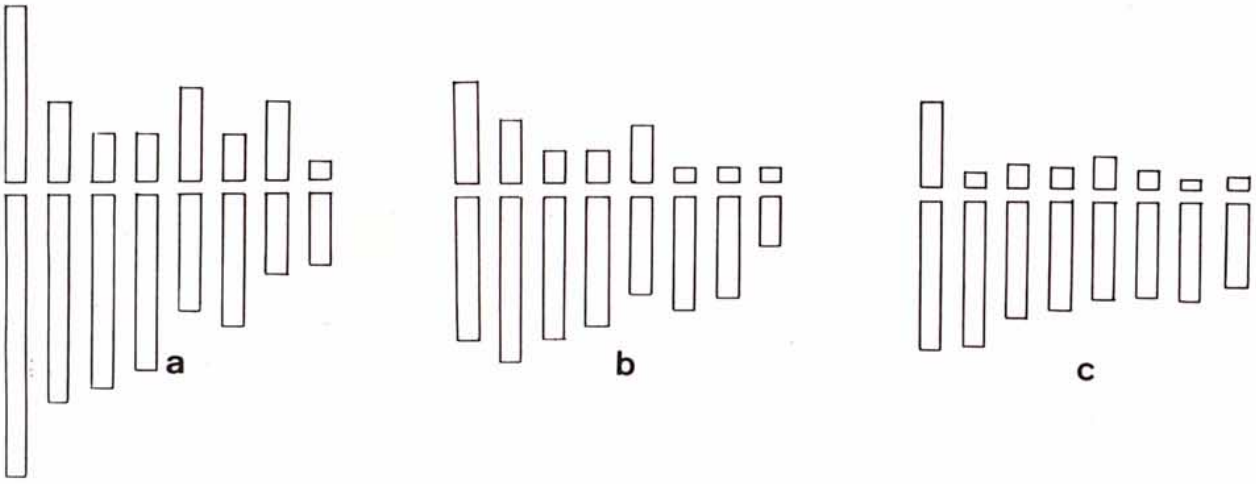

Fig. 5 – Idiograms of a) *Delphinium pentagynum* (Perennial, Subg. *Delphinastrum*) b) *D. balansae* (Perennial, Subg. *Delphinium*) and c) *D. cossonianum* (*Annual*, Subg. *Delphinium*). Data from BLANCHÉ (1985) and BLANCHÉ & AL, (1990).

a) There has been a progressive reduction in chromosome size, closely related to the increase in intrachromosomal asymmetry (decrease in the centromeric index).

b) The loss of genetic material in such plants with smaller chromosomes may have resulted from loss of acentric fragments because of the conservation of the same number of centromeres.

c) We can consider those species with small chromosomes and a higher proportion of acrocentric and/or telocentric chromosomes (subgen. *Delphinium*) as derived from those having long chromosomes and a higher proportion of metacentric and/or submetacentric chromosomes (subgen. *Delphinastrum*).

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Table 2. Chromosome numbers of *Delphinium* L. subgen. *Delphinium*

Taxon	Origin	n	2n	Source reference
D. balansae	Morocco		16	QUÉZEL, 1957
	Morocco	8	16	BLANCHÉ & AL., 1990
D. balcanicum	Greece		16	LÖVE, 1979
D. cossonianum	Morocco	8	16	BLANCHÉ & AL., 1990
D. gracile	Spain	8		PASTOR & AL., 1984
	Spain	8	16	BLANCHÉ, 1985
D. nanum				
subsp. *nanum*	Spain	8	16	BLANCHÉ & AL., 1985
subsp. *elongatum*	Morocco	8	16	BLANCHÉ & AL., 1990
subsp. *albolilaceum*	Morocco	8	16	BLANCHÉ & AL., 1990
D. peregrinum	–	8		GREGORY, 1941
	Turkey		16	LÖVE, 1980
D. verdunense	France		16	LEVITSKY, 1931
	–	8		MEHRA & RAMANDAN, 1972
	–		16	AL-KELIDAR & RICHARDS, 1981
	Spain	8		BLANCHÉ & AL., 1985
	Spain	8	16	BLANCHÉ, 1985

At this point, looking at the data listed in Table 3, it is interesting to point out that *D. balansae* occupies a clearly intermediate position between annuals and perennials. As stated above and earlier (BLANCHÉ & AL., 1990), *D. balansae* is a relict endemic of the Atlas Mountains in N. W. Africa belonging to the sect. *Delphinium* which has even retained a perennial life cycle. Because of its strategic phylogenetic position, it is noteworthy that its karyotype characteristics are a precious living testimony of how the evolution of this group may have taken place. That is: first step (e.g. *D. balansae*), loss of chromosome parts more or less equally in all arms; second step (e.g. *D. cossonianum,* and the remaining annuals) unequal loss of chromosome parts resulting in increased asymmetry.

Table 3. Karyotype evolution in *Delphinium* L. (subgen. *Delphinastrum* (DC.) Wang and subgen. *Delphinium*)

	Mean Chromosome Size (µm, Mean ±SE)	Centromeric Index (Mean ± SE)
Subgen. *Delphinastrum* (Perennials, 2x)	4,98 ± 0,16	28,27 ± 1,20
D. balansae (Perennial, 2x)	3,69 ± 0,44	28,80 ± 4,80
Subgen. *Delphinium* (Annuals, 2x)	3,43 ± 0,01	17,43 ± 0,51

* Data from BLANCHÉ & AL., 1990.

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DISPERSAL EFFICIENCY

No detailed comparative study of the respective seed dispersal mechanisms of the subgenus *Delphinium* and the subgenera *Delphinastrum* and *Oligophyllon* has yet been undertaken, but some general considerations can be made. *Delphinium* fruits are follicles, 3-5(7) in number. Their general dehiscence and seed expulsion mechanism is explained by CRONIN & NIELSEN (1978). In short, the general dispersal mechanism is anemochory; the follicles being shaken by the wind and the seeds carried a short distance from the mother plant (up to 5 m, CRONIN & NIELSEN, l.c.). These events have been observed both in perennials and annuals (BLANCHÉ, unpubl. data). The distances reached may be increased by a "catapult effect" produced by the feed of cattle or wild animals. Secondary myrmecochory has occasionally been reported in some species (TURNBULL & AL., 1983).

In fact, the seed structure seems to be perfectly adapted to aerial dispersal mechanisms. The most primitive perennial species of *Delphinium* (HUTH, 1895; MALYUTIN, 1973; BLANCHÉ, 1985) have subpyramidal seeds, longitudinally winged at their edges (Figure 6a), and therefore present an obvious anemochory syndrome. Most advanced groups of perennials have acquired new transversal scales arranged in more or less helicoidal series, and simultaneously have lost their longitudinal wings (Figure 6 b, c). This phenomenon is already reported in the related genus *Aconitum* (see MOLERO & PUIG, this volume) as well as in the annual *Consolida* (J. SIMON, pers. comm.). The presence of transversal scales has been transferred to the subgen. *Delphinium* (Figure 6 d, e), where a considerable reduction in size can be observed (see Table 4).

Table 4. Seed characteristics of *Delphinium* L. subgen. *Delphinium vs.* subgen. *Delphinastrum* (DC.) Wang

	subgen. *Delphinastrum*	subgen. *Delphinium*
1. FLOTABILITY IMPROVEMENT		
a) Size	2-3 mm	1-1,5 mm
b) Form	Subpyramidal	Subspheroidal
c) Suspension mechanism	3 longitudinal wings or 20-40 longitudinal scales	5-9 continous rings of transversal, concrescent scales
d) Weight-Volume ratio	dense seeds small umbilical orifice	soft seeds umbilical orifice occupying 1/2-1/3 of the total seed volume
2. SEED SET INCREASE		
a) Mean theoretical seed production/ individual (Mean ± S.D.)	741 ± 100,1	1274 ± 215,0

Data compiled from BLANCHÉ (1985) and unpublished data.

After being expelled from the follicle and falling to the ground, the seeds of *Delphinium* can be moved by the action of ecological agents, specially rolling over the surface of the snow (in perennials, cf. CRONIN & NIELSEN, 1978) or that of the soil, if it is relatively smooth. In annuals, they can even be carried to long distances by flowing water after autumn rainfalls just when fruits and seeds are mature and/or primarily dispersed (BLANCHÉ, unpubl. data).

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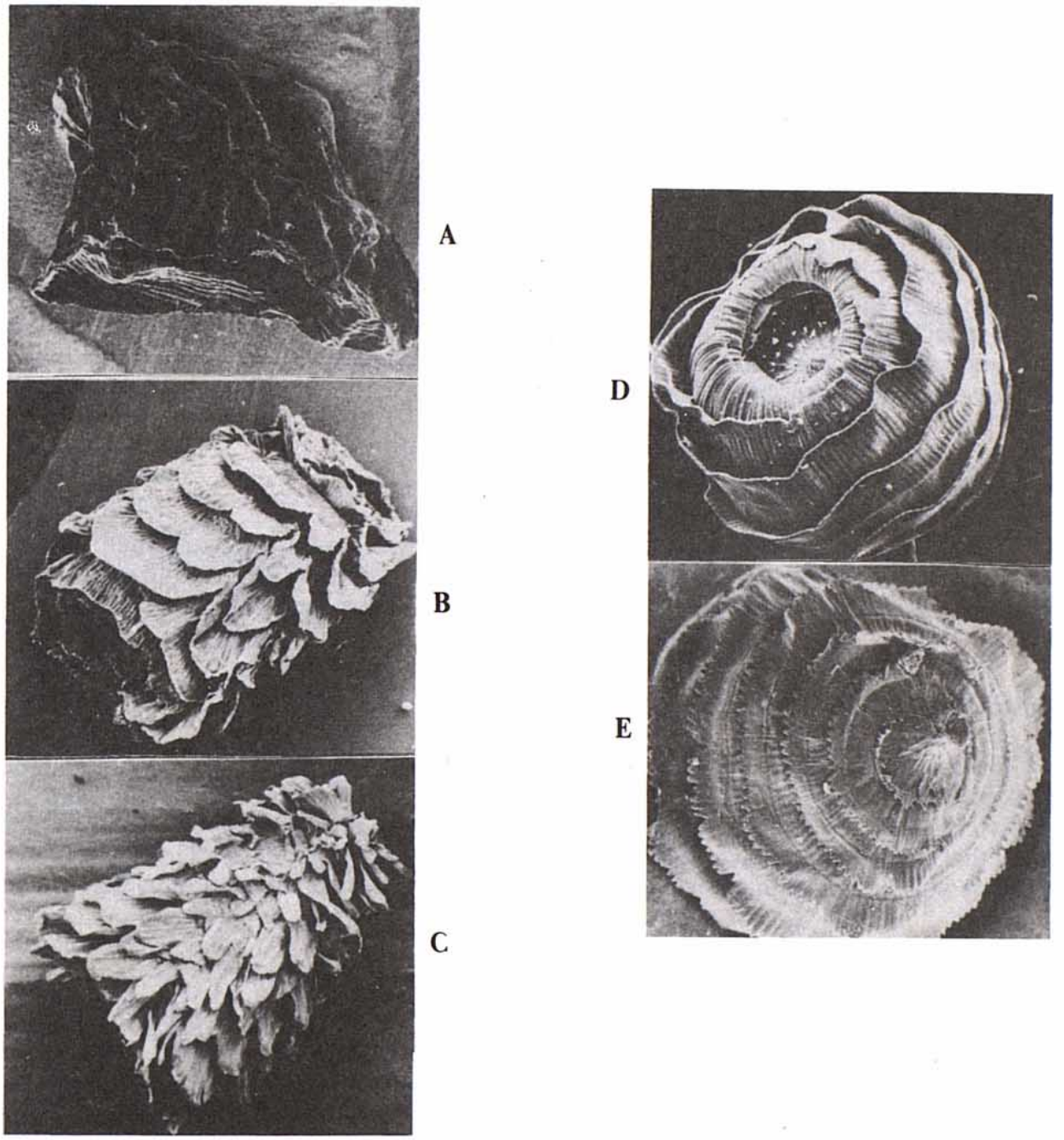

Fig. 6 – Seeds of a) *Delphinium montanum*; b) *D. fissum*; c) *D. emarginatum*; d) *D. verdunense*; e) *D. cossonianum*. (a, b, c: perennials; d, e: annuals).

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In view of these general mechanisms, both water and air floatability should be considered as important limiting factors to the success of dispersal. In addition to the new transversal scaly system, the species belonging to the subgen. *Delphinium* have acquired new features which substantially improve suspension capacity as compared with perennials. Both air and water floatability (whether primary or secondary dispersal mechanisms are predominant) are already enhanced in annuals by a decrease in size, a better adapted spheroidal shape, acquisition of a larger suspension surface (by arrangement of scales in transversal rings) and a better wheight-volume ratio (deep umbilical cavity).

Seed set production is a less clear parameter because of the great range of variation introduced by consideration of a large number of individuals of very different species. It also depends on the total number of flowers produced in a given year, pollination efficiency, etc, such factors beeing difficult to estimate in an overview. However, taking the data from near 700 herbarium specimens studied in BLANCHÉ (1985), a first approach can be considered as "theoretical" seed set production (Table 4). These data show greater production in annuals than in perennials. The more ramified inflorescences (higher flower number) and the lower seed size can help us to understand these results.

STRATEGICAL INNOVATIONS

The successful expansion of sect. *Delphinium* in the Mediterranean Region where annual species cover much larger areas than perennials must be correlated to other adaptive strategies, besides the annual cycle itself, of wich the following are two:

1. Acquisition of new chemical weapons

The most biologically active repellents found in the genus *Delphinium* are diterpenoid alkaloids (TAMURA, 1966) wich possess a well documented efficiency as a defense against herbivores (BENN & JACYNO, 1983). Although little extensive research has so far been carried out in this field, according to present knowledge (Table 5), 10 of the 25 (40 %) of diterpenoid alkaloids isolated from annual species of *Delphinium* are exclusive. Furthermore, this kind of

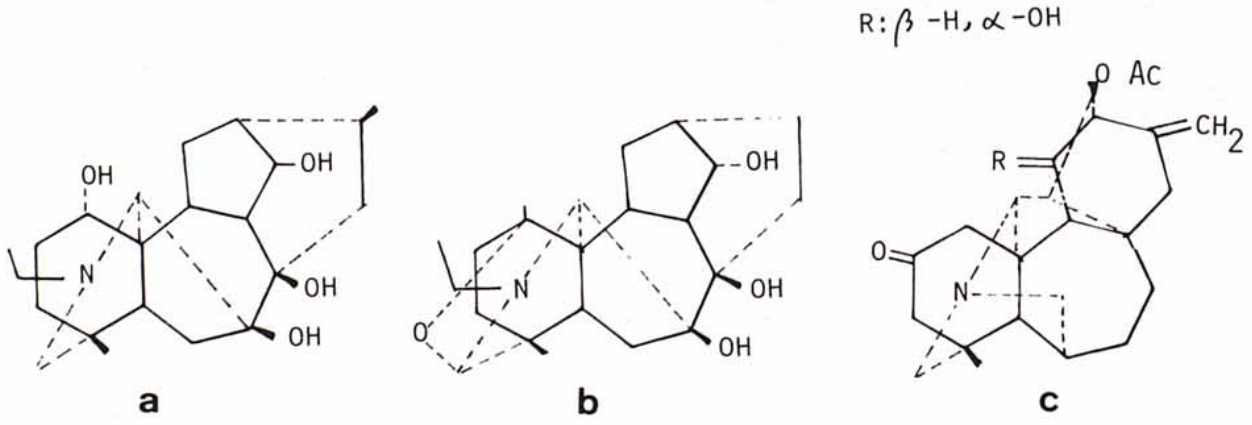

Fig. 7 – Diterpenoid alkaloids isolated from subgen. *Delphinium*: a) Cardiopetalidine (C-19); b) Graciline (C-19) and c) 13-Acetylhetisinone (C-20).

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"chemical endemisn" can be observed in the different types of recorded alkaloids: 30 % of Lycoctonine-type, 50 % of Hetisine-subtype and 50 % of Aconitine-type are exclusive of annuals. Some inusual functionalizations are also reported by DE LA FUENTE & REINA (this volume) in annual species.

This results can be interpreted as deep genetic changes involving several enzyme systems (several metabolic pathways corresponding to several alkaloid-types) better than the expression of a single mutation. Thus, in the subgen. *Delphinium,* an important innovation in the arsenal of chemical weapons has taken place (see also Figure 7).

Table 5. Diterpenoid alkaloids isolated from *Delphinium* L. subgen. *Delphinium*

Alkaloid*	Type**	Species
Graciline*	L	*D. gracile*
Gracinine*	L	*D. gracile*
Gadesine	L	*D. gracile*
Dihydrogadesine	L	*D. gracile, D. verdunense, D. nanum*
Nudicaulidine	L	*D. gracile, D. verdunense, D. nanum*
Cardiopetalidine*	L	*D. verdunense*
14-beenzoyldihydrogadesine	L	*D. verdunense*
14-acetyldihydrogadesine	L	*D. verdunense*
14-acetylnudicaulidine	L	*D. verdunense*
14-benzoylnudicaulidine	L	*D. verdunense*
Hetisinone	A-H	*D. gracile, D. verdunense*
13-acetylhetisinone	A-H	*D. gracile, D. verdunense, D. nanum*
Cardiopetamine*	A-H	*D. gracile, D. verdunense*
15-acetylcardiopetamine*	A-H	*D. verdunense*
11-acetylcardionine*	A-H	*D. gracile*
Hetisine	A-H	*D. verdunense*
Cardionine*	A-H	*D. verdunense*
13-acetylhetisine	A-H	*D. verdunense*
Sanyonamine	A-H	*D. verdunense*
Peregrinine*	Aco	*D. nanum*
Cardiopetaline*	Aco	*D. verdunense*
Karakoline	Aco	*D. verdunense*
Bicoloridine	Aco	*D. nanum*
Atisinum chloride	Ati	*D. verdunense*

* Alkaloids exclusive of subgen. *Delphinium.*
** L = Lycoctonine-Type; A-H = Atisine-Type subtype hetisine; Aco = Aconitine-Type; Ati = Atisine-Type subtype atisine.

Data from: DE LA FUENTE & AL. (1988, 1990) and GONZÁLEZ & AL. (1980, 1981, 1983, 1984, 1986 a, b).

2. New embryogenic type

Changes in the orientation of the cell walls in the first divisions of the zygote (proembryo stages) can result in important changes in subsequent embryo development. This field has been throughly investigated by BABIS (1974, 1976, 1980 a, b, c) who showed that unlike other plant genera, embryo development in *Delphinium* is nearly species-specific (BABIS, 1980 a).

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This author recognized four embryonomic groups within the genus, according to the first transverse division of the zygote (BABIS, 1976):

a) Type "T": The zygote divides transversely *(D. staphisagria, D. elatum).*

b) Type "O": The zygote makes oblique divisions *(D. tricolor, D. cashmirianum, D. grandiflorum, D. nudicaule, D. zalil, D. belladonna).*

c) Type "S": There is a notable slanting division of the zygote *(D. verdunense).*

d) Type "L" or "V": Almost longitudinal or vertical division of the zygote occurs *(D. tatsienense).*

Type "S", found in the only annual species investigated, belongs to a new type of embryo development in Angiosperms called "Ranunculad Type" by BABIS (1976:108). We can assume that the divison of the zygote depends on more than a single genetic factor and no one of the four types of divisions found in *Delphinium* is intermediate, as BABIS (1980a) pointed out. Thus, this new type of embryo development belonging to the most derived groups (Types "L" and "V" are regarded as the most primitive by LEBÈQUE, 1952 and BABIS, 1976) might be regarded as a new acquisiton by the annual species, not previously recorded in other groups and resulting from a new particular genetic combination.

ECOLOGY

The ecological niches of perennial and annual species of *Delphinium* are more or less sharply distinct, at least when sympatric species occur. Their relative ecological specificity can be summarized as follows:

1. Population structure

a) Perennials. – They colonize fairly stable, closed habitat (megaphorbs, mountain meadows, forests, rocks, ravines, etc.), forming dense colonies. In open habitats (steppe, shrubbery, dry slopes) the population densities decrease notably. Low self-fertilization rates (0-1 %, JANKUN, 1973; MACIOR, 1975) with vegetative propagation playing an important role in some cases (BLANCHÉ, 1985). Long-lasting independent establishments with their own ressources. Population modification by entry of new genotypes occurs only in very rare occasions (EPLING & LEWIS, 1952).

b) Annuals. – They colonize very unstable, open habitats (dry meadows, steppes, field crops, open shrubbery, sandy dunes, rocky slopes, etc.). Vegetative multiplication absent (except in the case of *D. balansae*) and higher germination rate (BLANCHÉ, 1985; ALIAS & BLANCHÉ, unpubl. data). Very plastic populations with very variable demography year to year (BLANCHÉ, 1985) but usually with a great number of individuals/population (hundreds of individuals, BLANCHÉ field observ.).

2. Phenology

In the Western Mediterranean Area we studied the phenology of a dozen more or less sympatric (s.l.) species (within the boundaries of the Iberian Peninsula) from more than 700 herbarium specimens and the results are showed in Figure 8.

An obvious extension of the flowering period in the annual species can permit:

a) an increase in pollination efficiency (nearly 4 months of permanent exposition to pollinator insects). Since *Bombus* is the most frequently observed pollinator, its activity extends from March to October (PRYS-JONES & CORBET, 1987:9).

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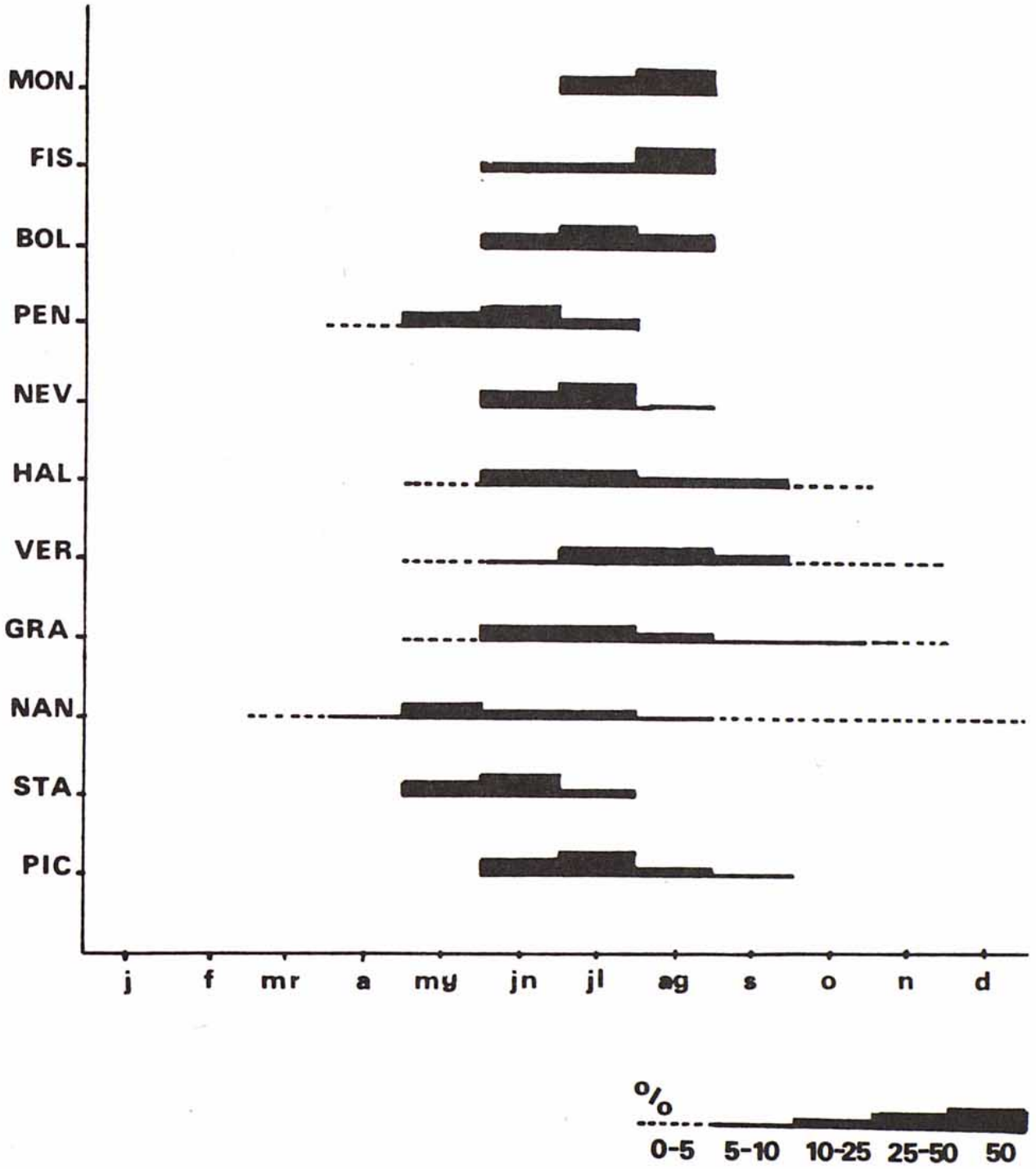

Fig. 8 – Phenology of W. Mediterranean species of *Delphinium*. (Data from BLANCHÉ, 1985. Iberian and Balearic sympatric species: MON: *D. montanum* DC.; FIS: *D. fissum* subsp. *sordidum* (Cuatrc.) Amich & al.; BOL: *D. bolosii* Blanché & Molero; PEN: *D. pentagynum* Lam.; NEV: *D. emarginatum* C.B. Presl. subsp. *nevadense* (Kunze) Blanché & Molero; HAL: *D. halteratum* Sm.; VER: *D. verdunense* Balbis; GRA: *D. gracile* DC.; NAN: *D. nanum* DC. subsp. *nanum*; STA: *D. staphisagria* L.; PIC: *D. pictum* Willd.) (% of flowering individuals/month, recorded from herbarium specimens)

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Table 6. Phenological field observations of sympatric populations of *Delphinium* L.

Species "A"	State *	Species "B"	State *	Species "C"	State *	Locality	Date
D. staphisagria	f, F	*D. pictum*	B-2	–	–	Sa Calobra (Mallorca, Balearic Islands)	VI. 1984
D. fissum	B-1	*D. gracile*	f	–	–	Riofrío (Salamanca, Spain)	VII. 1984
D. pentagynum	f, F	*D. nanum*	B-1	–	–	Touama (Marrakech, Morocco)	V. 1985
D. cossonianum	F	*D. nanum*	B-1	–	–	Ouezanne (Fès, Morocco)	V. 1985
C. mauritanica	f, F	*D. nanum*	B-1	*D. balansae*	V	Itzer (Atlas, Morocco)	V. 1985

* Key to the phenological states: V, vegetative; B.1, young buds; B-2: 1st flower opening only; f, flowering; F: ripe follicles.
** Field observations of the author.

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b) completion of the anthesis period at a slower pace (lower energy consumption per time unit). This may agree with the lower DNA values expected from the shorter chromosomes (in annuals *vs.* perennials) (but see *contra* AL-KELIDAR & RICHARDS, 1981).

According to my personal field experience, the phenologic isolation of sympatric (s. str.) species in given locality can be used as a reproductive barrier both within annuals and between annuals and perennials (Table 6).

CONCLUSIONS

There is a relatively small amount of information about the annual species of *Delphinium*. Furthermore, this poor knowledge is restricted to certain geographic areas (Iberian Peninsula, Western North Africa, Turkey) whereas some important representatives of China or Iran need still new investigations. This makes difficult to understand the phylogeny of subgen. *Delphinium* in its whole area of distribution. Thus, further research in fields such as taxonomy, cytogenetics and reproductive biology has to be done.

However, to the present state of knowledge summarized above, an evolutionary hypothesis is presented in Figure 9, as a first approach.

The origin of subgen. *Delphinium* must be investigated among the perennial gene pool related with the most primitive sect. *Anthriscifolium* (among *D. grandiflorum* or *D. tatsiense,* cf. MALYUTIN, 1973; among sect. *Pogonanthus,* cf. WANG, 1962). From these possible ancestors, a flower-reduced *Delphinium* (flower smaller, lateral petals not ciliate) may have arisen, retaining however a perennial life cycle and belonging to an hypothetical *"protoanthriscifolium"* -group. From it, and after dramatic changes leading to the annual cycle, the present sect.

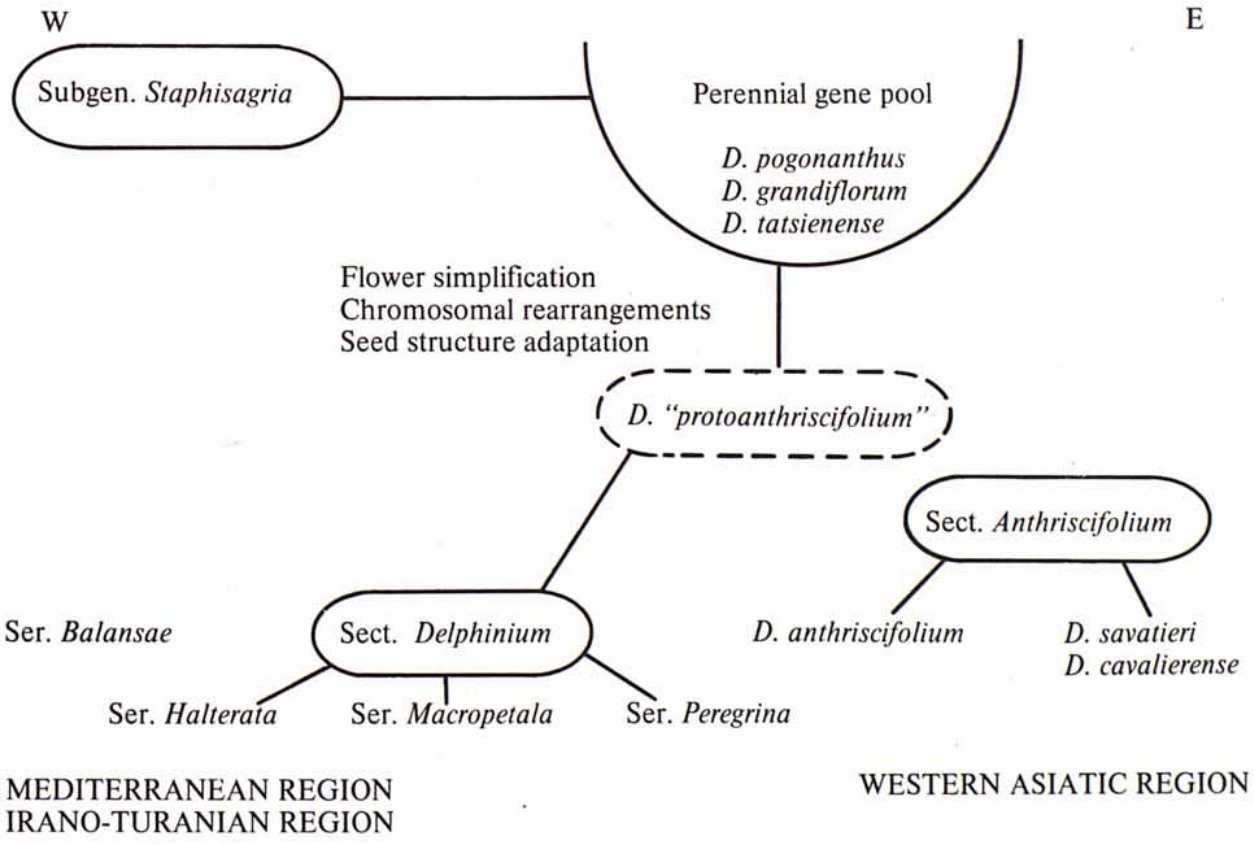

Fig. 9 – Phylogenetic hypothesis of subgen. *Delphinium vs.* Perennial species.

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Anthriscifolium may have evolved, being preserved under subtropical conditions (TAMURA, 1967) in Southern China and Indo-China.

The western populations of the *"protoanthriscifolium"*-group migrate to the West, giving origin to even more flower-simplified *Delphinium* from wich *D. balansae* is the only present relict, having a perennial life cycle. This old group, under dry climatic conditions, acquired the annual condition, beginning its diversification from the Middle East (Irano-Turanian Region) to the West (Mediterranean Region), adapted to open habitats of steppes and lowlands of semi-arid territories.

The actual representatives of the subgenus *Delphinium* can be arranged as in the following attempt of synopsis:

TAXONOMIC SUMMARY

Although we are not able to complete an accurate taxonomic revision of the subgenus *Delphinium* at present, we present a synopsis of the actual knowledge of this grup including the nomenclatural information of the taxa cited below:

Genus Delphinium L., Sp. Pl. 530, 1753
TYPUS: *D. peregrinum* L.

Subgenus Delphinium
TYPUS: *D. peregrinum* L.

Sect. Anthriscifolium W.T. Wang, Acta Bot. Sinica 10: 277, 1962
TYPUS: *D. anthriscifolium* Hance
Sp. incl:

1. *D. anthriscifolium* Hance, J. Bot. 6: 207, 1868. (China)
2. *D. savatieri* Franchet, Bull. Soc. Linn. Paris 1:329, 1882 (China)
3. *D. cavaleriense* Leveillé & Vaniot, Bull. Acad. intern. Géogr. bot: 49, 1902 (China).

Sect. Delphinium
(= Sect. *Delphinellum* DC.)
TYPUS: *D. peregrinum* L.

Ser. *Peregrina* B. Pawl., Fragm. Flor. Geobot. 9:438, 1963
TYPUS: *D. peregrinum* L.
Sp. Incl.:

4. *D. peregrinum* L., Sp.Pl.: 531, 1753 (Turkey, Syria, Lebanon, Cyprus, Iraq, Greece, Italy, Sicily, Albany, Palestina, Iran, Jordan, Israel, Lybia)
5. *D. sheilae* Kit Tan, Notes Roy. Bot. Gard. Edinburgh 42:17, 1984. (Arabia-Jabal Dabbah)
6. *D. virgatum* Poir. in Lam., Encycl. Suppl. 2: 458, 1812 (Turkey, Siria, Palestine, Jordan)
7. *D. hirschfeldianum* Boiss., Fl. Orient. Suppl.: 19, 1888 (Greece - Islands of Aegina and Cythnos.)

Ser. *Balansae* Blanché, Molero & Simon, Collect. Bot. (Barcelona) 18:70, 1990.
TYPUS: *D. balansae* Boiss. & Reuter
Sp. Incl.:

8. *D. balansae* Boiss. & Reuter in Boiss., Diagn. Pl. Orient. ser. 2,5:12, 1856 (Algeria, Morocco, Tunisia)

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Ser. *Halterata* B. Pawl., Fragm. Flor. Geobot. 9:438, 1963
TYPUS: *D. halteratum* Sm.
Sp. Incl.:

9. *D. halteratum* Sm., Fl. Graec. Prodr. 1:371, 1809 (France, Italy, Sicily, Malta, Sardinia, Algeria)

10. *D. balcanicum* B. Pawl., Fragm. Flor. Geobot. 9:439, 1963. (Greece, Jugoslavia, Bulgaria, Albania, European Turkey, Sporades Islands)

11. *D. cinereum* Boiss., Diagn. Pl. Orient. 1:67, 1843 (Turkey)

12. *D. cossonianum* Batt., Bull. Soc. Hist. Nat. Afrique N. 8:215, 1917. (Morocco)

13. *D. davisii* Munz, J. Arnold. Arbor. 48:256, 1967 (Turkey)

14. *D. gracile* DC., Syst. Nat. 1:347, 1817 (Spain, Portugal, Eivissa Island, Morocco, Algeria, Tunisia)

15. *D. hellenicum* B. Pawl., Fragm. Flor. Geobot. 9:442, 1963 (Greece, Pori and Strophades Islands).

16. *D. verdunense* Balbis, Cat. Stirp. Hort. Bot. Taur. 1813:31, 1813. (France, Spain, Portugal, Andorra).

17. *D. viciosoi* Pau, Trab. Mus. Nac. Ci. Nat., Ser. Bot. 14:12, 1918 (Iran)

18. *D. venulosum* Boiss., Fl. Orient. 1:86, 1867 (Turkey, Syria)

Ser. *Macropetala* Blanché, Molero & Simon, Collect. Bot. (Barcelona) 18:70, 1990
TYPUS: *D. macropetalum* DC.
Sp. Incl.:

19. *D. macropetalum* DC., Syst. Nat. 1:350, 1817 (Morocco)

20. *D. nanum* DC., Syst. Nat. 1:349, 1817 (Spain, Portugal, Morocco, Algeria, Tunisia, Lybia, Egypt)

Species inexplorata:

21. *D. syncarpum* Freyn. ex Stapf, Denkschr. Akad. Wien Math. Naturw. 51:26, 1886. (Iran)

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