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Dysploidy and polyploidy in the *Euphorbia flavicoma* aggregate *(E.* subsect. *Galarrhaei; Euphorbiaceae)*

Abstract

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Euphorbia subsect. *Galarrhaei* includes about 200 species found in Eurasia. Previous karyological studies in the subsection report three basic numbers, $x = 5$, 6, 7 (most common), 8, and 10. There is a great diversity of chromosome numbers, since both dysploidy and polyploidy have played an important role in the evolution of the subsection. Neopolyploidy ($2n = 14 \rightarrow 28$) and dysploidy ($2n = 14 \rightarrow 12$) are here reported for populations of the *E. flavicoma* aggregate at the northern limit of its distribution area. Chromosomal changes show little concomitant morphological differentiation within the aggregate and are interpreted as being of recent date.

Introduction

Euphorbia subsect. *Galarrhaei* (Boiss.) Pax is widespread in the Euro-Asiatic circumboreal and Mediterranean regions and includes many species groups of remarkable taxonomic, karyological and phylogenetic complexity.

A great diversity of chromosome numbers, including different basic numbers, has been reported in the literature for the subsection (Table 1) and is confirmed by our own results (Table 2). More than 50 % of the taxa have the basic number $x = 7$, from which $x = 5$, $x = 6$, $x = 8$ and $x = 10$ should be considered as secondarily derived.

In addition to dysploidy, polyploidy is frequent within *Euphorbia* subsect. *Galarrhaei*. For nearly one third of the taxa of which the chromosomes have been counted more than one ploidy level is known to exist (18% show diploid and tetraploid cytotypes, 20% are either triploid or tetraploid). Dysploidy is difficult to recognize in a groups for which different basic numbers have been proposed. About 20% of the taxa may be affected by both phenomena.

Table 1. Chromosome counts published for *Euphorbia* subsect. *Galarrhaei*

Euphorbia	*n*	2*n*	*Reference*
acanthothamnos Heldr. & Sart. ex Boiss.		14	Cesca (1966)
		14	Cesca (1969b)
altissima Boiss.	16		Perry (1943)
angulata Jacq.	5	10	Cesca & Mussi (1972)
		10	Cesca (1976)
		10	Májovský & al (1987)
		12	Bauer (1971)
		18	Harrison ex Tischler (1931)
		20	Wiebecke (1989)
apios L.	12		Kožuharov & Kuzmanov (1964)
		14	Damboldt & Phitos (1971)
		14	Phitos & Kamari (1974)
		28	Cesca (1967b)
		30	Papanicolaou (1984)
bivonaê Steud.		14	D'Amato (1947)
		14	Cesca (1969b)
		24	Shimoyama (1958)
		24	Hurusawa & Shimoyama (1976)
brittingeri Opiz ex Samp.		14	Shimoyama (1958)
		14	Wiebecke (1989)
		18	Harrison in Tischler (1931)
capitulata Rchb.		12	Strid & Franzén (1981)
carniolica Jacq.		16	Polatschek (1971)
carpatica Woł.		20	Skalińska & al. (1976)
ceratocarpa Ten.		26	Cesca (1967b)
corallioides L.		26	Cesca & Bitonti (1981)
dimorphocaulon P. H. Davis		18	Phitos & Kamari (1974)
dulcis L.		12	Perry (1943)
		12	Shimoyama (1958)
		12	Cesca (1961)
		12	Cesca & Mussi (1972)
		12	Queirós (1975)
		12	Cesca (1976)
		12	Hurusawa & Shimoyama (1976)
		18	Cesca (1961)
		18	Cesca & Mussi (1972)
		18	Cesca (1976)
		24	Cesca (1961)
		24	Bauer (1971)
		24	Cesca & Mussi (1972)
		24	Queirós (1975)
		24	Cesca (1976)
		24	Micieta (1981)
		28	Carano (1926)

Table 1 (continued).

Euphorbia	*n*	2*n*	*Reference*
duvalii Lecoq & Lamotte		12	Wiebecke (1989)
epithymoides L.	7		Cesca (1966)
	7	14	Cesca (1969a)
		16	Pólya (1950)
flavicoma DC. subsp. *occidentalis* Laínz	7		Delay & Vivant (1978)
		14	Valdés-Berm. & Castrov. (1979)
		14	García & Valdés (1981)
fragifera Jan		26	Cesca (1976)
		26	Kieft & Loon (1978)
glabriflora Vis.		14	Sušnik & Lovka (1973)
		14	Strid & Andersson (1985)
		16	Aldén (1976)
guyoniana Boiss. & Reut.		16	Reese (1957)
hirsuta L.	7	14	Garcia & Valdés (1981)
		14	Björkqvist & al. (1969)
		14	D'Amato (1939)
		14	D'Amato (1945)
		14	D'Amato (1947)
		14	Shimoyama (1958)
		14	Queirós (1975)
		14	Hurusawa & Shimoyama (1976)
		14	Queirós (1979)
		16	Perry (1943)
		18	Perry (1943)
		36	Perry (1943)
hyberna L.		36	Contandriopoulos (1962)
		36	Cesca (1963)
isatidifolia Lam.	9		Molero & Montserrat (1986)
		18	Benedí & Blanché (1992)
lingulata Heuff.		14	Strid & Andersson (1985)
melitensis Parl.		14	Cesca (1967 a)
		14	Cesca (1967 b)
		14	Raffaelli & Ricceri (1988)
nereidum Jahand. & Maire		30	Perry (1943)
palustris L.	10		Laane (1971)
		16	Hurusawa & Shimoyama (1976)
		20	Perry (1943)
		20	Pólya (1950)
		20	Shimoyama (1959)
		20	Gadella & Kliphuis (1968)
		20	Bauer (1971)
		20	Cesca (1972)
papillaris (Jan) Raffaelli & Ricceri		14	Cesca (1969b)
		14	Raffaelli & Ricceri (1988)

Table 1 (continued).

Euphorbia	*n*	*2n*	*Reference*
pekinensis Rupr.		24	Perry (1943)
polychroma A. Kern.		14	Shimoyama (1958)
		16	Perry (1943)
		16	Pólya (1950)
		16	Shimoyama (1958)
		16	Hurusawa & Shimoyama (1976)
spinosa L.		14	Cesca (1963)
		14	Cesca (1966)
		14	Cesca (1969b)
		14	Wiebecke (1989)
sultan-hassei Strid & al.		14	Strid & al. (1989)
uliginosa Welw. ex Boiss.		14	Queirós (1975)
		14	Queirós (1980)
villosa Waldst. & Kit. ex Willd.	16		Choda & Mehra (1972)
	16		Mehra & Choda (1978)
		16	Modilewski (1910)
		16	Perry (1943)
		18	Perry (1943)
		18	Shimoyama (1958)
		18	Hurusawa & Shimoyama (1976)
		18	Rostovceva (1977)
		20	Murin (1976)
		20	Skalińska & al. (1976)
		32	Benedí & Blanché (1992)
welwitschii Boiss. & Reut.		12	Harrison in Tischler (1931)
		18	Perry (1943)
		36	Perry (1943)

Material and methods

The method used for the karyological investigation has been described in Blanché & al. (1987).

Voucher specimens of the material examined have been deposited at the Herbarium of the Facultat de Farmàcia of the Universitat de Barcelona (BCF).

Results

The species belonging to the *Euphorbia flavicoma* aggregate *(E. flavicoma, E. spinosa, E. brittingeri, E. duvalii, E. polygalifolia,* and *E. uliginosa)* have a basic chromosome number of $x = 7$ and are mainly diploid with $2n = 14$, in spite of a high phenotypic variability observed, both within and among species.

Very strong chromosomal similarities between the taxa can be observed (Table 2). Of the six species, only two show numerical alterations: there are polyploid counts for some

Table 2. Chromosome numbers and chromosome formula of the populations studied of the *Euphorbia flavicoma* aggregate.

Euphorbia	Locality	ploidy	*n*	2*n*	formula
brittingeri	Hs: Huesca, Bonanza	2*x*		14	3m + 4sm
	Hs: Huesca, Barbaruens	2*x*		14	4m + 3sm
	Hs: Girona, Sallent de Santa Pau	2*x*		14	1m + 6sm
	Ga: Alpes-Maritimes, Caussols	2*x*		14	–
	Ga: Alpes-Maritimes, Lopin du Pin	2*x*		14	4m + 1m^{sat} + 2sm
duvalii	Ga: Hérault, Le Caylar	2*x*		14	7m
	Ga: Lozère, Saint Enimie	2*x*		12	2m + 4sm
	Ga: Aveyron, Le Rozier	2*x*		12	3m + 3sm
flavicoma subsp. *costeana*	Ga: Aveyron, Firmy	2*x*		14	5m + 2sm
flavicoma subsp. *flavicoma*	Hs: Málaga, Sierra Bermeja	2*x*		14	2m + 5sm
	Hs: Almería, Mesa Roldán	2*x*		14	5m + 2sm
	Hs: Murcia, Sierra de Espuña	2*x*	7	14	5m + 2sm
	Hs: Alacant, Carrascal d'Alcoi	2*x*		14	6m + 1sm
	Hs: Cuenca, Aras de Alpuente	2*x*		14	5m + 2sm
	Hs: Tarragona, Ports de Beseit	2*x*		14	3m + 4sm
	Hs: Barcelona, Montserrat	4*x*		28	6m + 8sm
	Hs: Girona, L'Estartit	2*x*		14	6m + 1sm
	Ga: Aude, La Clape	4*x*		28	6m + 8sm
	Ga: Aude, La Tauch	4*x*		28	6m + 8sm
flavicoma subsp. *occidentalis*	Hs: Asturias, Puerto de la Tarna	2*x*		14	4m + 3sm
	Hs: León, Puebla de Lillo	2*x*		14	5m + 2sm
	Hs: La Coruña, Brandomil	2*x*		14	–
polygalifolia subsp. *polygalifolia*	Hs: Burgos, Corconte	2*x*	7	14	–
	Hs: Burgos, Alto Campo	2*x*		14	2m + 3sm + 2st
polygalifolia subsp. *hirta*	Hs: Asturias, Vegadeo	2*x*		14	6m + 1sm
	Hs: La Coruña, Brandoñas de Arriba	2*x*		14	7m
spinosa	Ga: Alpes-Maritimes, Villars-sur-Var	2*x*		14	5m + 1m^{sat} + 1sm
	It: Liguria, Airole	2*x*		14	–
uliginosa	Hs: La Coruña, Lamas-Zas	2*x*		14	7m

populations of *Euphorbia flavicoma* subsp. *flavicoma* and dysploid counts for two *E. duvalii* populations (Fig. 1).

Euphorbia flavicoma subsp. *flavicoma*. – This taxon consists of diploid ($2n = 14$) and tetraploid ($2n = 28$) populations, seemingly of parapatric distribution. The two cytotypes cannot be differentiated macro-morphologically, but can be separated by the larger stomata of the tetraploid.

The similarity between the haploid idiograms of the diploid and tetraploid races (see Fig. 2), together with their phenotypic likeness, suggests a possible autopolyploid origin for the tetraploid race. The more northerly (parapatric) distribution of the tetraploids and their scant morphological differentiation with respect to the diploids is suggestive of neopolyploidy.

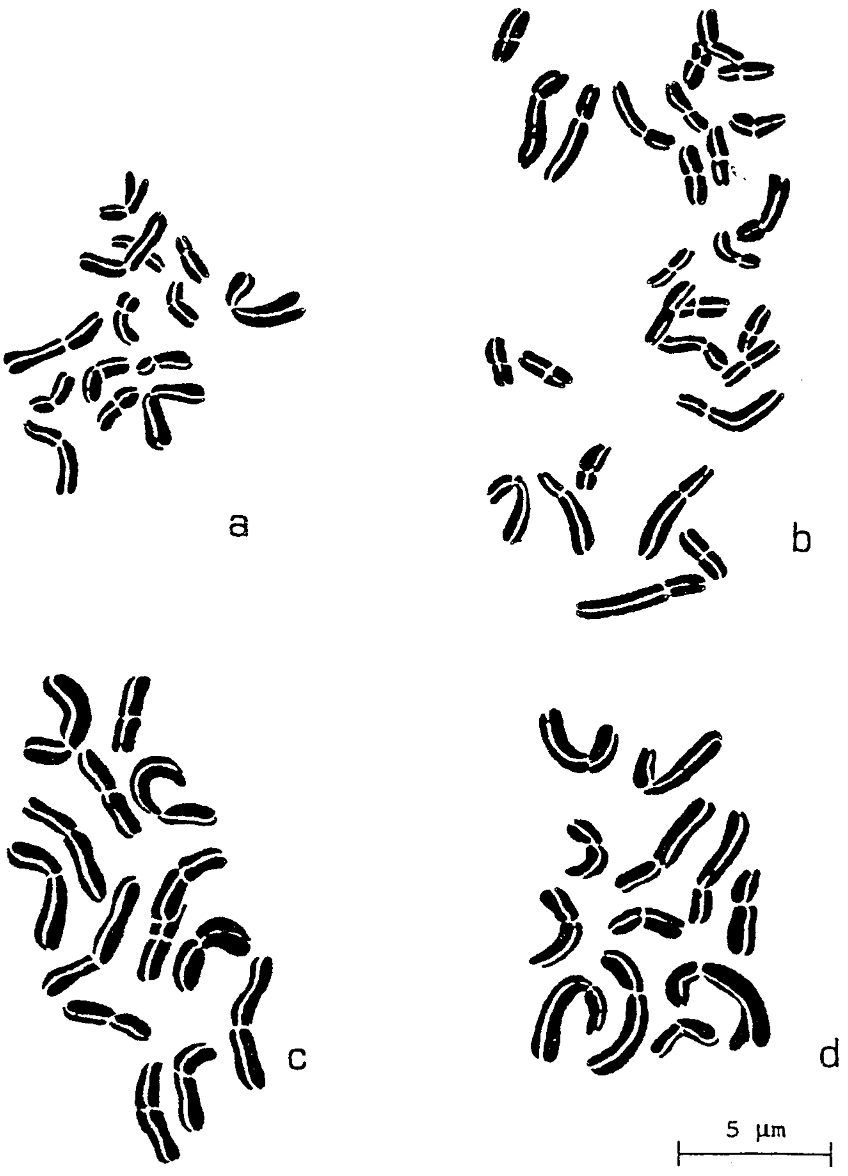

Fig. 1. Mitotic metaphase plates. – **a,** *Euphorbia flavicoma* subsp. *flavicoma*, 2*n* = 14 (Hs: Girona, L'Estartit); **b,** id., 2*n* = 28 (Hs: Barcelona, Montserrat); **c,** *E. duvalii*, 2*n* = 14 (Ga: HÈrault, Le Caylar); **d,** id., 2*n* = 12 (Ga: Aveyron, Le Rozier).

Euphorbia duvalii. – As can be seen from our data, this species also comprises two chromosome races, one of $2n = 12$ ($x = 6$), the other of $2n = 14$ ($x = 7$). Contrary to *E. flavicoma* they show a sympatric distribution.

The haploid idiograms (Fig. 3) do not show significant differences. Neither morphological nor ecological characteristics separate the two cytotypes. The lack of one chromosome pair in the $x = 6$ cytotype does not seem to be in any way advantageous.

Euphorbia duvalii is not yet karyologically stabilized, and in some of its populations both cytotypes co-exist. We can thus assume a recent origin of dysploidy in this case, which may serve as a model of how a lower level of descending dysploidy can become stabilized, as has already occurred in other complexes in this subsection.

Discussion

Both new examples of chromosome number variation presented here are simple and straightforward genomic changes, but even as such they can open pathways toward a wide

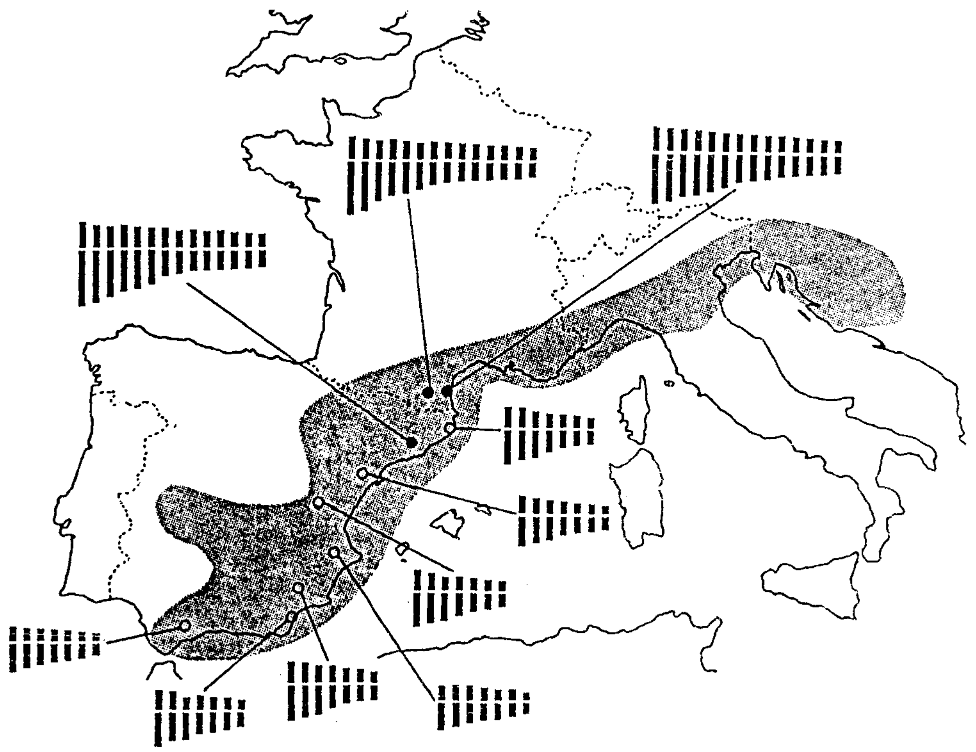

Fig. 2. Geographical distribution of diploid (circles) and tetraploid (dots) cytotypes of *Euphorbia flavicoma* subsp. *flavicoma* ($2n = 14, 28$), within the total range of the taxon (shaded).

chromosomal diversity by successive dysploidy/polyploidy events. Reproductive isolation barriers may result, enhancing the probability of new speciation events.

The cytogenetic trends (see Table 1) in the groups that have the closest phylogenetic and morphological links with the *Euphorbia flavicoma* aggregate (*E. dulcis-angulata* and *E. squamigera-bivonae* aggregates) support such a scenario. They show a repetitive pattern of decreasing dysploidy ($x = 7 \rightarrow 6$). Simultaneously, polyploidy-dysploidy or dysploidy-polyploidy phenomena seem to occur.

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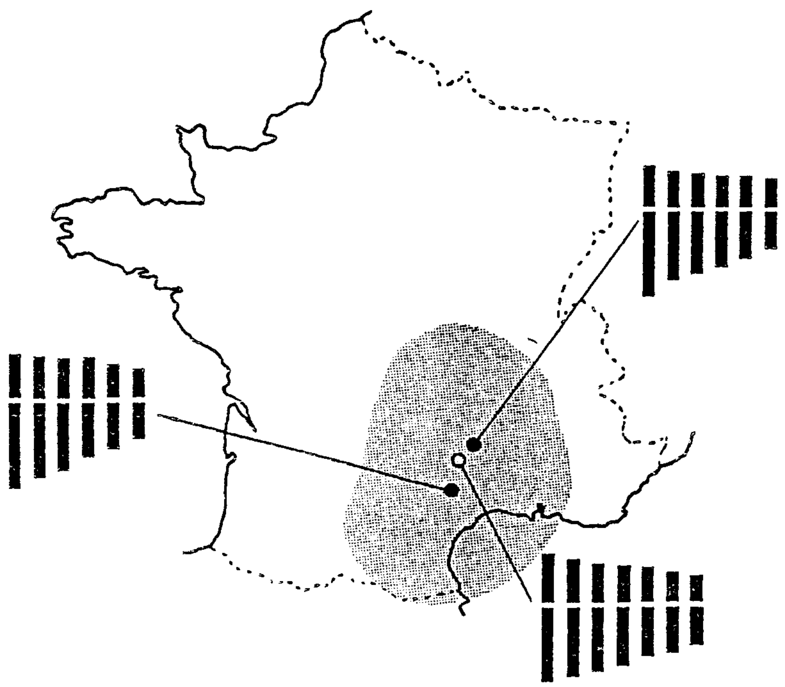

Fig. 3. Geographical distribution of $2n = 14$ (circles) and $2n = 12$ (dots) cytotypes of *Euphorbia duvalii*, within the total range of the species (shaded).

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