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Asphodelus cirerae, a forgotten species of *Asphodelus* sect. *Verinea* (*Liliaceae*). Morphological, palynological, karyological and ecogeographical characterization

Abstract

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The detailed study of morphological, palynological and karyological characters of *Asphodelus* sect. *Verinea* (Pomel) Maire, has resulted in the recognition within this section of the following species: *A. fistulosus* L., *A. tenuifolius* Cav. and *A. cirerae* Sennen, the latter hitherto included in *A. fistulosus*.

Introduction

Within *Asphodelus* L. (*Liliaceae*), sect. *Verinea* (Pomel) Maire can be distinguished by the presence of fibrous roots, by its fistulose cylindric or semicylindric leaves, by its flowers that are slightly zygomorphic and stellate-patent at anthesis, and by its triquetrous seeds with flat and alveolate lateral faces.

Cavanilles (1801) separated *A. tenuifolius* Cav. from *A. fistulosus* L. on account of its smaller leaves, flowers and fruits, and the section has since been regarded as to comprise these two species. However, the taxonomic value of *A. tenuifolius* Cav. has been considered differently by several authors.

A. tenuifolius has often been sunk in the synonymy of *A. fistulosus*, but some authors, such as Kunth (1843), Willkomm (1862), Boissier (1882), Halácsy (1904), Durand & Barratte (1910), Hayek (1932-1933), Post (1933), Zangheri (1976), El-Gadi (1978) and Pignatti (1982), have separated both taxa at specific level, a separation which was supported by Ruíz Rejón & al. (1990) using electrophoretic characters; others still (Baker 1876, Bonnet & Barratte 1896, Pampanini 1930, Quézel & Santa 1962, Fiori 1923-1925, Täckholm & Drar 1954) have subordinated *A. tenuifolius* to *A. fistulosus* as a subspecies or variety.

Some authors such as Ball (1878), Eig (in Feinbrun-Dothan 1986) and Smythies (1986) have reported intermediate forms between both taxa. These seem apparently responsible for the difficulty to key out both species by following some floras (i.e., Fiori 1923-1925, Maire 1958, Quézel & Santa 1962, Zangheri 1976).

The taxonomic complexity of this section was increased by the description of *A. cirerae* and *A. mauritii* by Sennen (1936) and by the segregation of *A. fistulosus* var. *atlanticus* Jahandiez & al. (Jahandiez & Maire 1931) on account of its wider leaves and almost "bulbous" base of the leaf rosette.

The aim of this paper is to improve the taxonomic knowledge of *A.* sect. *Verinea* by the study of the variability of a large number of populations from the Mediterranean Region, especially from the west where the highest diversity is found, including morphological, palynological and karyological characters.

A. fistulosus and *A. tenuifolius* have been previously studied karyologically by several authors, especially by Ruíz Rejón (1978) and Ruíz Rejón & al. (1990), which have carefully investigated the chromosome morphology and meiotic behaviour of both species. All authors agree to consider *A. tenuifolius* as a diploid species with $2n = 28$ and to recognize two ploidy levels within *A. fistulosus*, with $2n = 28$ and $2n = 56$.

Van Campo (1960), Nair & Sharma (1965), Rao & Shukla (1975), Díez & al. (1985) and Díaz Lifante & al. (1991) have studied the pollen characters of *A. tenuifolius* and *A. fistulosus*, and Panelatti (1960) those of *A. fistulosus* var. *atlanticus*. Ruíz Rejón & al. (1990) pointed out the usefulness of these characters to strengthen the separation of *A. tenuifolius* from *A. fistulosus*, and indicated within the latter differences in size between the two ploidy levels so far recognized.

The present study has resulted in the recognition of three species: *A. fistulosus* L., *A. tenuifolius* Cav. and *A. cirerae* Sennen, the latter included to date within the range of *A. fistulosus* from which it can be distinguished not only by its morphological, palynological and karyological characters, but also by its ecological preferences.

Material and methods

Morphological characters have been assessed by the study of over one hundred and fifty natural populations from the Iberiàn Peninsula and Morocco, supplemented by the study of Mediterranean herbarium material from the following herbaria: BC, BCF, CAT, COI, FI, FCO, G, GDA, GDAC, GE, JACA, L, LEB, LISE, LISU, LOU, LY, MA, MGC, PI, PO, SANT, SEV, STR, TFC (for abbreviations see Holmgrem & al. 1990). Detailed floral studies were made from living plants and from flowers fixed in the field in FAA (alcoholic acetic formalin).

Pollen studies were made on plants from the following 15 populations (5 each of *A. fistulosus*, *A. tenuifolius* and *A. cirerae*). The vouchers are kept in the herbarium of the Department of Plant Biology and Ecology, Faculty of Biology, Sevilla (SEV):

A. tenuifolius. Morocco. Nador, 13.4.1988, *Díaz Lifante & al.* (SEV 127500) (AT-1). Spain. Almería: Entre Almuñécar y Nerja, 8.3.1989, *Díaz Lifante* (SEV 127491) (AT-4); entre Venta de los Yesos y Tabernas, 7.3.1989, *Díaz Lifante* (SEV 127492) (AT-3). Málaga: Cala del Moral, 8.3.1989, *Díaz Lifante* (SEV 127490) (AT-2). Murcia: Totana, 29.1.1988, *Díaz Lifante* (SEV 127487) (AT-5).

A. fistulosus. Morocco. Alhoceima, 12.4.1988, *Díaz Lifante & al.* (SEV 127378) (AF-5). Portugal. Algarve: Vila Real do Santo Antonio, 10.1.1988, Cubero, *Díaz Lifante & Delgado* (SEV 127344) (AF-4). Spain. Huelva, 21.1.1988, *Díaz Lifante* (SEV 127351)

Figs. 1-6. Representative specimens, flowers and fruits of *A. tenuifolius* (1; 4, 5 and 6 left), *A. fistolosus* (2; 4, 5 and 6 centre) and *A. cirerae* (3; 4, 5 and 6 right). Scale bar in Figs. 4, 5 and 6: 1 cm.

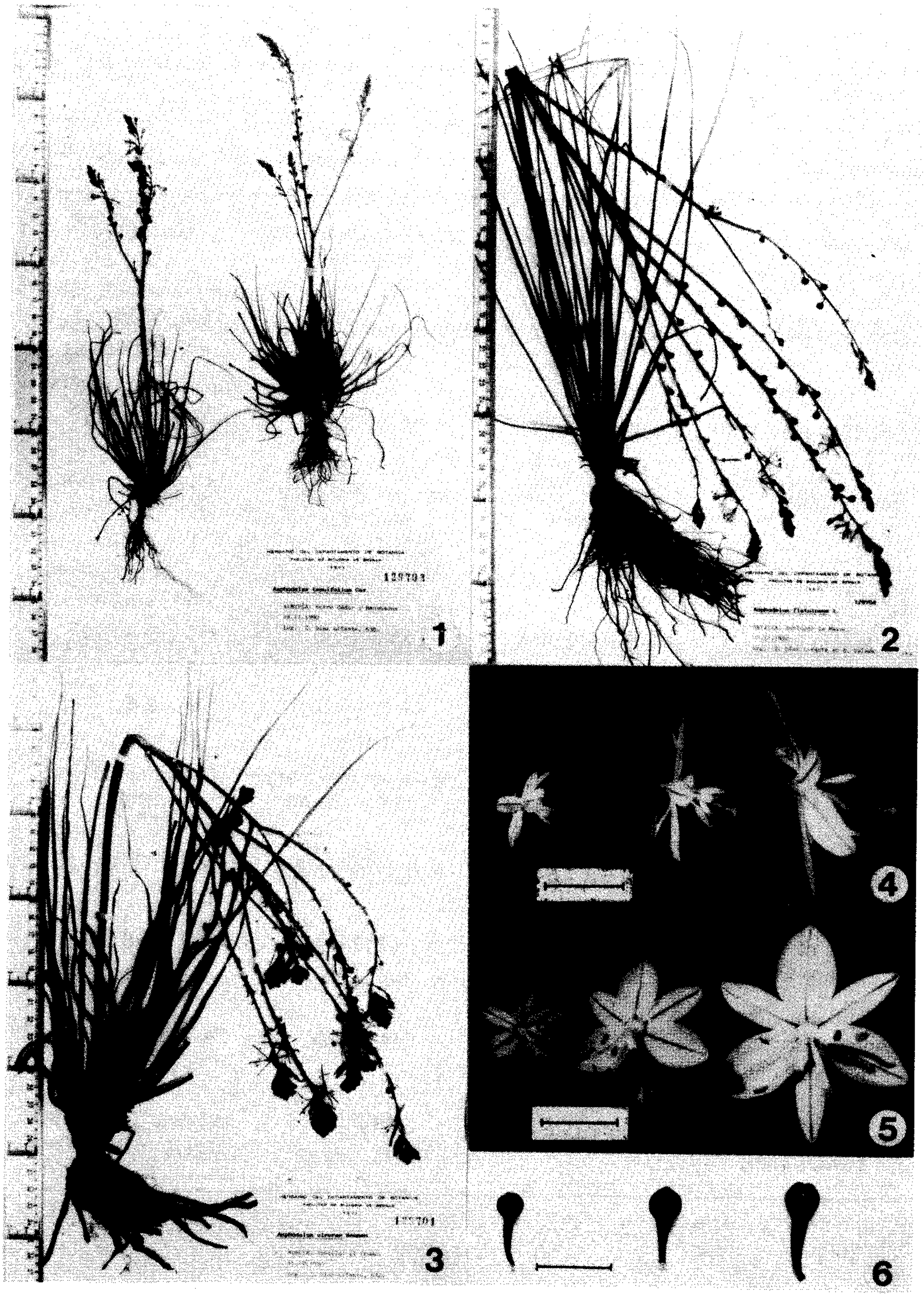

1
2
3
4
5
6

Table 1. Differential morphological characters of *A. tenuifolius*, *A. fistulosus* and *A. cirerae*.

Characters	*A. tenuifolius*	*A. fistulosus*	*A. cirerae*
Life cycle	annual	annual or short-lived perennial	perennial
Root system	thin fibrous roots	fibrous roots on a thin rhizome	thick cylindric roots on a thick rhizome
Length of stem (cm)	up to 40(-70)	up to 70(-90)	up to 70(-90)
Base of stem	scabrous, rarely smooth	smooth to slightly scabrous	smooth
Leaves			
length (cm)	(5-)7-20(-35)	15-45(-50)	(12-)20-40(-45)
width (mm)	1-3(-4.5)	1-3.5(-4.5)	2-5
scabrosity	on nerves and margin, rarely absent	on nerves and margin, rarely absent	absent or only in margin
Size of bracts (mm)	1.5-6 x 1.5-2.5	3-7(-11) x 2.5-5.5	4-12(-15) x 3-4
Length of flowering pedicels (mm)	(1.5-)2-4.5	(3-)3.5-6	3.5-6.5
Length of fruiting pedicels (mm)	3.5-7(-10)	(4.5-)5-8	(4.5-)5-9
Distance between flowers (mm)	(3.5-)4-5.5	7-9	7-10.5

Characters	*A. tenuifolius*	*A. fistulosus*	*A. cirerae*
Flowers			
length of perianth segments (mm)	(3-)5-7.5(-8)	(7.5-)8-12.5(-13)	(12-)13-16.5(-18)
width of outer perianth segments (mm)	2-3	3-4.5	4-6
width of inner perianth segments (mm)	(2.5-)3-4.5	4.5-6	6-8
length of outer filaments (mm)	3-4.5(-5.5)	(4.5-)5.5-6	(6-)6.5-7.5
length of inner filaments (mm)	(3.5-)4-5.5	(6.5-)7-8.5(-9)	(7.5-)8-9(-10.5)
Base of filaments	geniculate in the middle	geniculate in the middle	geniculate in the upper part
length of anthers (mm)	1-1.6	(1.5-)1.7-2.5	2-3
length of style + ovary (mm)	3.5-5.5	7-8.5	9.5-12
Fruits			
size (mm)	3-4(-4.5) x 3-4	4.5-6 x 3.5-6	4-6 x 3.5-5.5
shape	globose	obovoid-globose to obovoid	obovoid
Length of seeds (mm)	2.2-2.8(-3)	3-3.5	3-3.5

(AF-1). Málaga: Marbella, 4.3.1988, *Díaz Lifante* (SEV 127343) (AF-3). Murcia: Cieza, Venta del Olivo, 29.1.1988, *Díaz Lifante* (SEV 128242) (AF-2).

A. cirerae. Morocco: Mont-Arroui, 14.4.1988, *Díaz Lifante & al.* (SEV 127520) (AC-5). Spain. Almería: Huércal-Overa, 10.3.1988, *Diosdado & Valdés* (SEV 127515) (AC-2). Málaga: Cala del Moral, 8.3.1989, *Díaz Lifante* (SEV 127508) (AC-5). Murcia: Jumilla, 7.5.1986, *Díaz Lifante* (SEV 127524) (AC-1). Toledo: Mora de Toledo, 23.5.1988, *Díaz Lifante, Diosdado & Pérez* (SEV 127512) (AC-3).

Pollen was obtained from flowers fixed in the field in FAA or glacial acetic acid, and acetolysed according to the Erdtman (1960) method as modified by Reitsma (1969), but by using a proportion of acetic anhydrite and sulphuric acid of 18 : 1 (Díez & al. 1985). Size has been measured for the polar (P), longitudinal equatorial (E1) and transverse equatorial (E2) axis, and calculated for the proportion P/E1. For each sample, 20-30 pollen grains have been measured for P, E1 and E2, and 10 for exine thickness. The terminology of Erdtman (1945, 1952, 1969) has been followed.

Root tips of plants dug up in the field and grown in the experimental garden or of seedlings grown in Petri dishes from seeds collected in nature have been used for the study of chromosomes in mitosis. Root tips were treated with 8-hydroxiquinoline 0.002M (Tjio & Levan 1950) for 3-3,5 hours and fixed in ethanol-acetic acid (3 : 1) for at least 24 hours. Meiotic studies have been carried out on microsporogenesis of flower buds fixed in the field in Carnoy's fluid. All samples were stained with alcoholic hydrochloric acid-carmine (Snow 1963) and mounted in 45 % acetic acid.

For each species, six metaphasic plates have been studied in detail, with measurement and morphological characterization of chromosomes. The mean apparent size of chromosomes and the ratio between the largest and the smallest (L/S) chromosomes have been evaluated for each species.

The percentage of chromosomes with an arm ratio (r) higher than or equal to 2 (Stebbins 1971) has also been evaluated, as well as the TF% value, i.e., the percent ratio between the sum of the lengths of the short arms and the total length of the chromosome complement (Kapoor & Löve 1970). Finally, the overall asymmetry of the karyotype in relation to shape and size of chromosomes (parameters A1 and A2 of Romero Zarco 1986) has also been evaluated.

For chromosome morphology and chromosome size, the classification of Levan & al. (1965) and Stebbins (1938) has been followed.

Results

Morphology. — Morphological differences of the three recognized species are summarized in Table 1. *A. tenuifolius* behaves as an annual species and *A. cirerae* as a perennial, while *A. fistulosus* can be either an annual or a short lived perennial (biennial or triennial). Vegetative and flower characters allow a clear separation of the three species (Figs. 1-5).

The base of the stem is very scabrous (rarely smooth) in *A. tenuifolius* and totally smooth in *A. cirerae*; in *A. fistulosus* it is usually smooth but can sometimes be scabrous on some of the nerves. The leaves are shorter and narrower in *A. tenuifolius* than in the other species, and they are cylindrical or semicylindrical in cross section; in *A. fistulosus* and *A. cirerae* leaves are more or less equal in length. In the former they are cylindrical to subcylindrical in cross section but semicylindrical in the latter, in which the outer leaves develop a well marked scarious margin. In *A. tenuifolius* and *A. fistulosus* the leaves are generally very scabrous, whereas *A. cirerae* has smooth leaves except for the scarious margin and, rarely, some of the nerves.

The stem is shorter in *A. tenuifolius* than in the other two species; *A. fistulosus* and *A. cirerae* are more or less equal in size, but *A. cirerae* is more openly branched than *A. fistulosus*, which has erect to erecto-patent branches. The inflorescence is clearly denser and the pedicels are shorter in *A. tenuifolius* than in the other two species which do not significantly differ in that respect.

Table 2. Quantitative pollen characters of *A. tenuifolius*, *A. fistulosus* and *A. cirerae*. Mean value, standard deviation and average variation of the populations studied are indicated.

Taxa	P (μm)	E1 (μm)	E2 (μm)	P/E1	exine thickness (μm)
A. tenuifolius	46.07±7.31 (38.66-55.86)	66.91±3.32 (62.56-71.70)	70.70±2.81 (67.45-73.77)	0.65±0.10 (0.54-0.79)	3-4(-4.5)
A. fistulosus	57.23±8.87 (44.78-68.05)	86.55±4.23 (82.35-91.6)	87.94±2.98 (84.36-91.53)	0.64±0.09 (0.47-0.96)	4-4.5
A. cirerae	43.01±0.22 (42.85-43.16)	74.70±4.42 (74.38-78.8)	76.76±2.67 (71.74-80.03)	0.56±0.01 (0.45-0.64)	4(-4.5)

Floral characters differentiate the three species even more clearly (Figs. 4 and 5). Shorter and narrower perianth segments, shorter filaments, anthers and style are found in *A. tenuifolius*, whose stigma is placed at a level half-way between the two whorls of anthers. On the contrary, longer and wider perianth segments, longer filaments, anthers and style are characteristic of *A. cirerae*, whose stigma is placed well above the anthers. *A. fistulosus* is more or less intermediate between the two other species.

The widened base of the filaments also shows clear differences. Its outer surface is covered by long papillae in all three species, and has a marked inflexion at about the middle in *A. tenuifolius* and *A. fistulosus* but in the upper part in *A. cirerae*. This gives a rather distinct appearance to the basal part of the staminal apparatus of *A. cirerae*.

The flowers are pinkish-white in all three species, with a more markedly pinkish shade in *A. tenuifolius* and *A. fistulosus*, especially along the main nerve of the perianth segments, than in *A. cirerae*, whose flowers are almost white. The anthers are orange-brown in *A. tenuifolius* and *A. fistulosus* and yellowish-orange in *A. cirerae*. Fruits and seeds are smaller in *A. tenuifolius* than in the other two species, which differ only in the somewhat more globular fruits of *A. fistulosus* (Fig. 6).

To summarize, *A. fistulosus* and *A. cirerae* agree in several vegetative features but

Table 3. Voucher specimens, chromosome numbers and idiogrammatic formulas for the populations studied.

Taxa	Vouchers	2*n*	*n*	idiogrammatic formulas
A. tenuifolius				
	Algeria: Tamanraset, In Salah (G)	28		
	Algeria: Tamanraset, Ilamane (G)	28		
	Algeria: Tamanraset, Hirafok (G)	28		
	Algeria: Tamanraset, Mertoutek (G)	28		
	Morocco: Alhoceima (SEV 127497)	28		
	Morocco: Nador (SEV 127500)	28	14	
	Spain: Alicante, Cabo de las Huertas (SEV 127496)	28		$4M+12m+2m^{sat}+8sm+2sm^{sat}$
	Spain: Almería, Urcal (SEV 127503)	28		
	Spain: Almería, Tabernas (SEV 127495)	28		$4M+12m+2m^{sat}+8sm+2sm^{sat}$
	Spain: Almería, Huércal Overa (SEV 129709)	28		$4M+12m+2m^{sat}+8sm+2sm^{sat}$
	Spain: Almería, Venta de los Yesos (SEV 127492)	28		
	Spain: Granada, Almuñécar (SEV 127494)	28		
	Spain: Málaga, Nerja (SEV 127494)	28	14	
	Spain: Málaga, Cala del Moral (SEV 127490)	28		
	Spain: Murcia, Totana (SEV 127499)	28		$2M+12m+2m^{sat}+10sm+2sm^{sat}$
	Spain: Murcia, Totana (SEV 127487)		14	
	Spain: Murcia, Entre Puerto Lumbreras y Lorca (SEV 127489)	28		$4M+12m+2m^{sat}+8sm+2sm^{sat}$

Taxa	Vouchers	2*n*	*n*	idiogrammatic formulas
	Spain: Murcia, Puerto Lumbreras (SEV 129708)		28	$4M+10m+2m^{sat}+10sm+2sm^{sat}$
A. fistulosus				
	Morocco: Alhoceima (SEV 127378)	56		
	Morocco: Tres Fourches (SEV 127383)	56		
	Portugal: Algarve, Tavira (SEV 127356)	56	28	
	Portugal: Algarve, Gralheira (SEV 129710)	56		$6M+24m+24sm+2sm^{sat}$
	Portugal: Alto Alenteixo, Elvas (SEV 127377)	56		
	Spain: Albacete, Elche de la Sierra (SEV 127384)	56	28	
	Spain: Alicante, El Maigmó (SEV 127376)	56		
	Spain: Almería, Cabo de Gata (SEV 127361)	56		
	Spain: Almería, Vélez Rubio (SEV 127349)	56		
	Spain: Cádiz, Grazalema (SEV 127369)	56		
	Spain: Cádiz, Medina Sidonia (SEV 127362)	56		
	Spain: Huelva, El Rocío (SEV 127368)	56		
	Spain: Huelva, Gibraleón (SEV 129712)	56		
	Spain: Huelva, Huelva (SEV 127790)		28	
	Spain: Lérida, Caspe (SEV 127358)	56		
	Spain: Lérida, Lérida (SEV 127357)	56		
	Spain: Málaga, Marbella (SEV 127343)	56		
	Spain: Mallorca, Alcudia (SEV 127360)	56		

Taxa	Vouchers	2*n*	*n*	idiogrammatic formulas
	Spain: Murcia, Jumilla (SEV 127350)	56	28	
	Spain: Murcia, Totana (SEV 127390)	56		
	Spain: Murcia, Totana (SEV 127348)		28	
	Spain: Murcia, Santomera (SEV 127355)	56		
	Spain: Murcia, Venta del Olivo (SEV 129711)	56		
	Spain: Murcia, Estación de Blanca (SEV 127346)		28	
	Spain: Murcia, Estación de Blanca (SEV 127386)	56		8M+22m+24sm+2sms^{sat}
	Spain: Oviedo, Soto del Barco (SEV 127387)	56		8M+20m+26sm+2sm^{sat}
	Spain: Sevilla, Alcalá de Guadaira (SEV 127373)	56		
	Spain: Sevilla, Alcalá de Guadaira (SEV 128134)		28	
	Spain: Sevilla, Sanlúcar la Mayor (SEV 129704)	56		8M+22m+26sm 8M+20m+28sm+2sm^{sat}
	Spain: Toledo, Los Yébenes (127375)	56		
	Spain: Toledo, Urda (SEV 127379)	56		
	From botanic garden seed samples:			
	France: Marseille (Chatellerault)	56		
	Italy: (Pisa)	56		
	Italy: (Padua)	56		
	Italy: Marche: Porto Recanati (Pesaro)	56		6M+22m+26sm+2sm^{sat}
	Portugal: (Lisboa)	56		
	Spain: Valencia: Burjassot (Valencia)	56		
	Spain: Tarragona: Torredembarra (Barcelona)	56		

Taxa	Vouchers	2*n*	*n*	idiogrammatic formulas
	Turkey: (Bornova-Izmir)	56		
A. cirerae				
	Morocco: Saka (SEV 127514)	28		4M+10m+12sm+2sm^{sat}
	Morocco: Guercif (SEV 127519)	28		
	Morocco: Mont Arroui (SEV 127520)	28		
	Morocco: Alhoceima (SEV 127513)	28		
	Spain: Albacete, Elche de la Sierra (127538)	28		
	Spain: Albacete, Caudete (SEV 129713)	28		4M+10m+12sm+2sm^{sat}
	Spain: Alicante, Maigmó (SEV 129714)	28		
	Spain: Alicante, Cabo de las Huertas (SEV 129715)	28		4M+10m+12sm+2sm^{sat}
	Spain: Almería, Vera (SEV 129707)	28		4M+10m+14sm
	Spain: Almería, Vélez Rubio (SEV 127518)	28	14	
	Spain: Málaga, Cala del Moral (SEV 127508)		14	
	Spain: Murcia, Ulea (SEV 129716)	28	14	
	Spain: Murcia, Casas del Puerto (SEV 127530)	28	14	4M+10m+14sm
	Spain: Murcia, Totana (SEV 127535)	28		
	Spain: Murcia, Jumilla (SEV 127524)	28		
	Spain: Murcia, Casas de D. Gonzalo (SEV 129706)	28		
	Spain: Toledo, Urda (SEV 127534)	28		
	Spain: Toledo, Mora de Toledo (SEV 127512)	28		4M+10m+12sm+2sm^{sat}

clearly differ in floral and some vegetative characters such as roots and cross section and scabrosity of leaves. On the other hand, *A. tenuifolius* and *A. fistulosus* are similar in several qualitative characters but differ in most quantitative ones, *A. tenuifolius* being smaller in stem, leaf, flower, fruit and seed size.

Palynology. — Pollen grains of *Asphodelus* sect. *Verinea* are monoanasulcate, heteropolar, iso- to heterobisymmetric, large in size and with a reticulate exine, with lumina of 1-5 µm in diameter which are wider in the distal than in the proximal area.

In Fig. 7 the mean value, the 95% confidence interval and the range of variation of the two equatorial axes (E1, E2) is represented for each of the 15 populations studied.

In Table 2 the mean value and the average variation of pollen measurements are given for each species. The pollen grains of *A. fistulosus* are significantly larger than those of *A. tenuifolius* and *A. cirerae*, but the P/E1 ratio is similar for the three species. *A. tenuifolius* and *A. cirerae* clearly differ with respect to E1 and E2 values. In *A. fistulosus* and *A. cirerae* the exine is thicker than in *A. tenuifolius.*

Table 4. Size of chromosome (Sc) and of the total haploid chromosome complement (Sch) as well as different karyological parameters of the karyotypes of *A. tenuifolius*, *A. fistulosus* and *A. cirerae*. Mean, standard deviation and average variation of the populations studied is given for each character. (For abbreviations, see "Material and methods").

Taxa	Sc (µm)	Sch (µm)	L/S	TF%	A1	A2
A. tenuifolius	1.65±0.12	23.23±1.63	2.14±0.24	39.95±1.70	0.30±0.05	0.22±0.02
	1.44-1.27	20.22-24.84	1.88-2.54	38.02-41.71	0.25-0.36	0.20-0.27
A. fistulosus	1.85±0.07	25.98±0.89	2.74±0.33	38.02±0.74	0.35±0.01	0.25±0.02
	1.80-1.98	25.27-27.62	2.52-3.39	25.00-39.28	0.34-0.39	0.22-0.30
A. cirerae	1.91±0.01	27.23±2.12	2.49±0.25	37.74±0.80	0.34±0.02	0.25±0.01
	1.75-2.03	24.57-29.90	2.22-2.81	36.41-38.75	0.31-0.36	0.24-0.26

Karyology. — Chromosome counts in somatic mitosis have been made for 75 populations, whose origin and chromosome numbers are given in Table 3. All populations morphologically belonging to *A. tenuifolius* (18) and *A. cirerae* (18) are diploid, with $2n = 28$ chromosomes. In the 39 populations karyologically studied whose morphology is indicative of *A. fistulosus* the chromosome number $2n = 56$ has been found, which corresponds to a tetraploid level of chromosomes.

In Table 4 the mean, standard deviation and variation range of the mean values of the various karyological parameters studied are indicated for the three species.

Although the size of the karyotype is often of little diagnostic value (Bentzer & al. 1971), it proved to be of importance for the separation of the three species studied. In *A.*

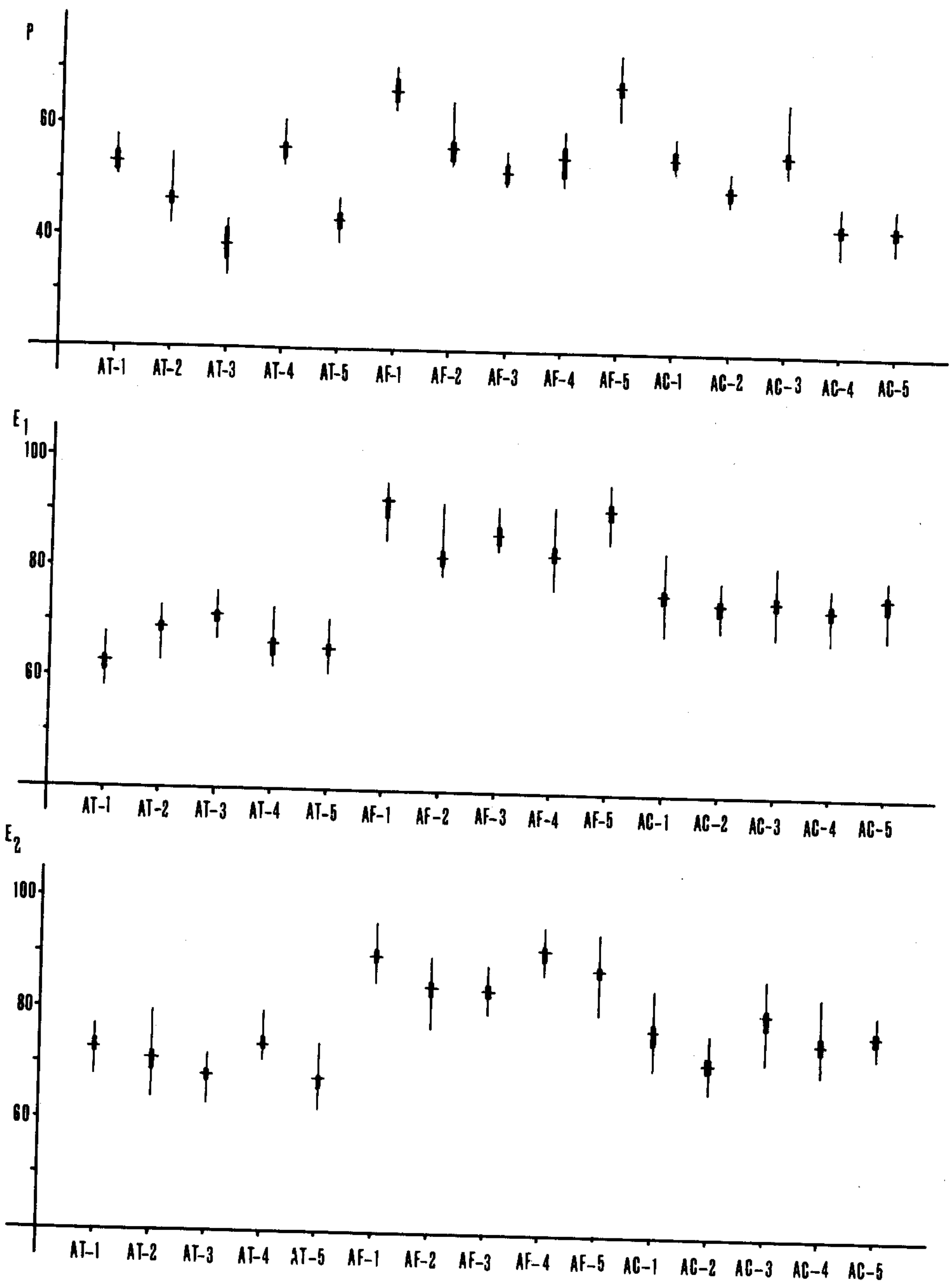


Fig. 7. Size of P, E1 and E2 axis (in µm) of pollen of 5 populations each of *A. tenuifolius* (AT-1-5), *A. fistulosus* (AF-1-5) and *A. cirerae* (AC-1-5). Mean (cross-bar), 95 % confidence interval (thick line) and range of values (thin line) are shown. (For origin of sample, see under "Material and methods).

tenuifolius the mean chromosome size, and consequently the total length of the haploid complement, is significantly lower (p>0.01, for a 95% confidence level) than in *A. fistulosus* and *A. cirerae*, while the two latter do not show significant differences. *A. tenuifolius* has an average of 6 medium-sized to small chromosomes, while *A. cirerae* has 9 and *A. fistulosus* 16. There are also differences in the ratio between the largest and the smallest chromosomes of the karyotype (in %), although these are not significant (p>0.10, for a 95% confidence level).

The karyotypical asymmetry of the three species is of type 2B, according to the nomenclature of Stebbins (1971). The values of A1 and A2 for six populations of each species are plotted in Fig. 8, which gives an idea of the global karyotypical asymmetry with respect to the variability in size and shape of the chromosomes of a same karyotype. Although the differences are statistically of little importance, Fig. 8 shows that the karyotypes of *A. fistulosus* and *A. cirerae* are slightly more asymmetrical than those of *A. tenuifolius*, which besides shows a higher dispersion of values than the other two species. As to the TF%, the highest value is found in *A. tenuifolius*.

The idiogrammatic formulas for the six populations of each species that were studied in

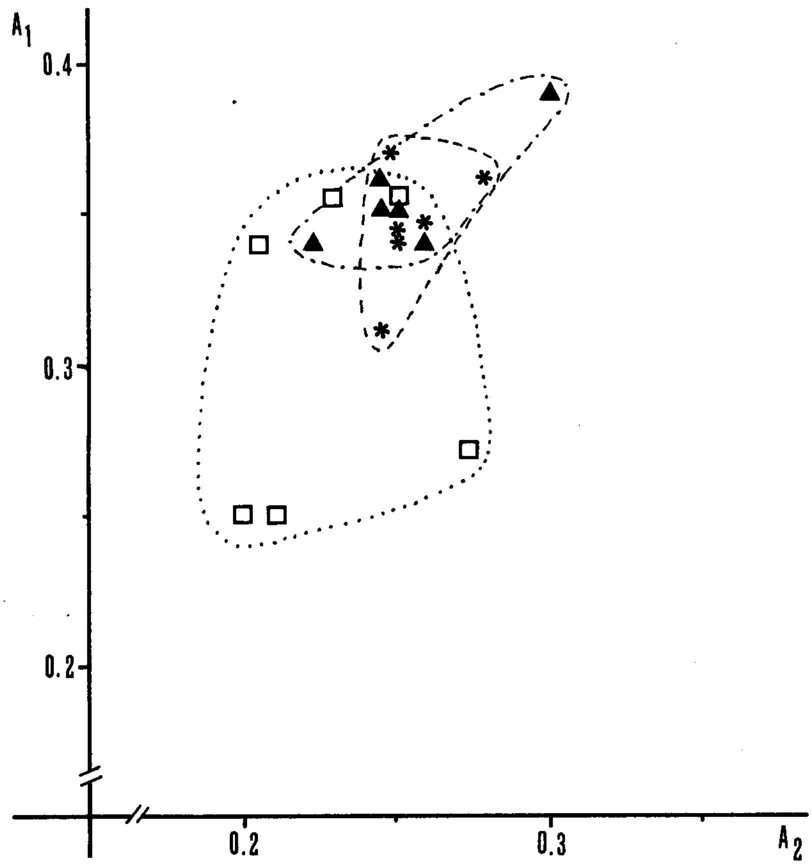
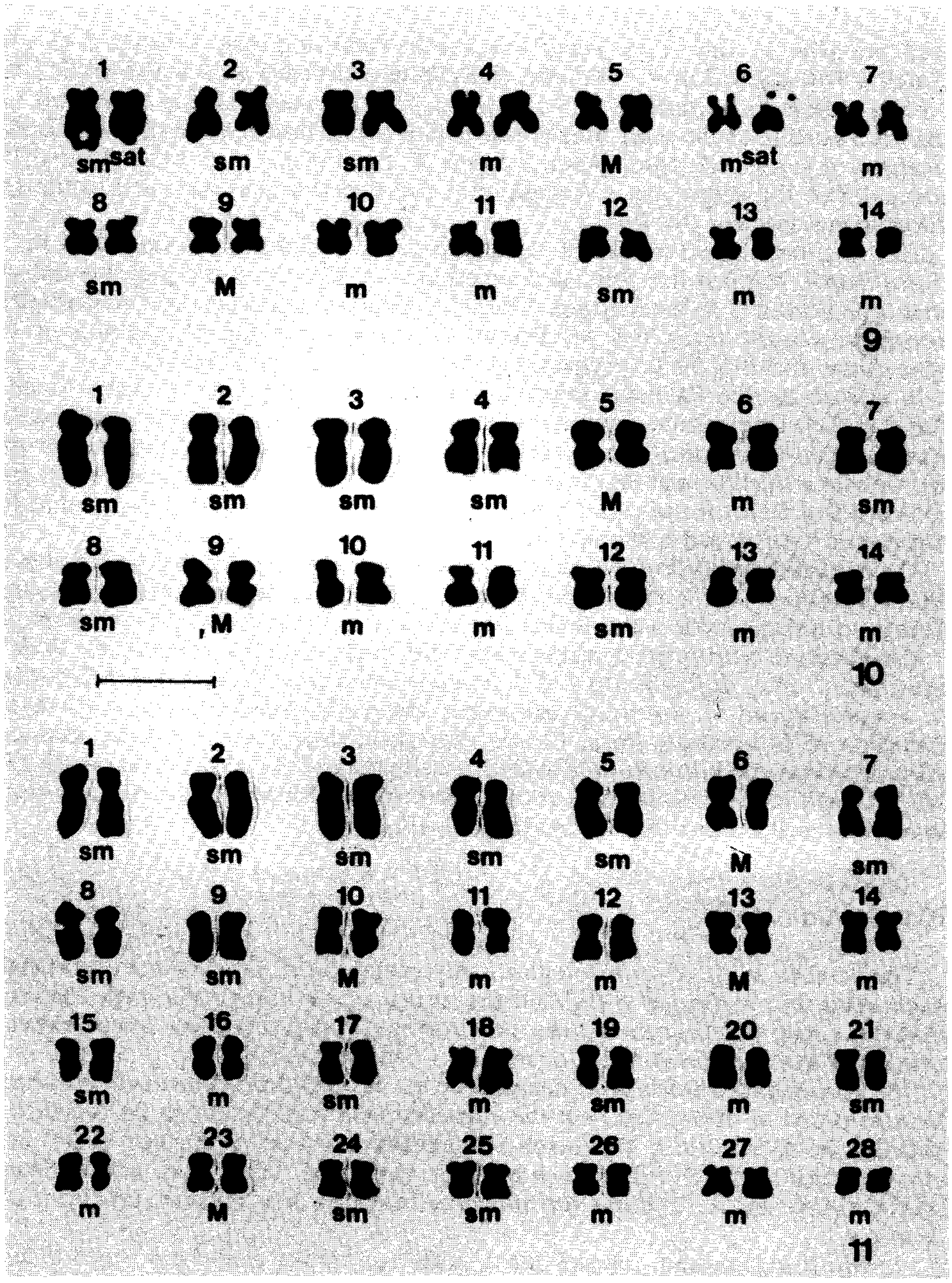


Fig. 8. Scatter diagram of karyotype asymmetry for the A1 and A2 parameters (Romero 1986) for *A. tenuifolius* (squares), *A. fistulosus* (triangles) and *A. cirerae* (asterisks).



Figs. 9-11. Karyograms. **9:** *A. tenuifolius*, $2n = 28$, Tabernas (Almería, Spain, SEV 127495); **10:** *A. cirerae*, $2n = 28$, Vera (Almería, Spain, SEV 129707); **11:** *A. fistulosus*, $2n = 56$, Sanlúcar la Mayor (Sevilla, Spain, SEV 129704). Scale bar: 5 µm.

detail are given in Table 3. *A. tenuifolius* has the following basic formula: 2-4M+10-12m+2m^{sat}+8-10sm+2sm^{sat}. The three first chromosome pairs are submetacentric (sm), the first of them with a satellite on the long arm. The sixth pair is always metacentric (m) and has a satellite on the short arm. The seventh is metacentric (type m or M). There are two pairs of metacentric chromosomes of type M: the fifth and ninth or tenth pairs. The remainder of the karyotype is formed by submetacentric (sm) and metacentric (m) chromosomes (see Fig. 9).

The idiogrammatic formula of *A. fistulosus* is as follows: 4-8M+20-24m+24-28sm+2sm^{sat}. The first five pairs of chromosomes are submetacentric (sm), the first one often with a satellite on the long arm. The sixth, tenth and thirteenth pairs are formed by metacentric chromosomes (type M). Pair no. 23 can be metacentric of type M or m. The other chromosomes of the karyotype are of the types m or sm (see Fig. 11).

A. cirerae has the following idiogrammatic formula: 4M+10m+12-14sm+0-2sm^{sat}. The four first chromosome pairs are submetacentric (sm), with an often well marked secundary constriction on the long arm of the first pair. The sixth pair is metacentric (type m), without a satellite, and the seventh submetacentric (sm). As in *A. tenuifolius*, pairs no. 5 and 9 or 10 are metacentric (type M). The remainder of the karyotype is formed by metacentric (type m) and submetacentric (sm) chromosomes (see Fig. 10).

The chromosome types of the tetraploid *A. fistulosus* are the same that are found in the diploid *A. cirerae*, but it has not been possible to group the chromosomes by four, since there is not a single group with chromosomes of equal length and identical arm ratios.

Chromosome behaviour at meiosis has been studied for 14 populations: 3 of *A. tenuifolius*, 7 of *A. fistulosus* and 4 of *A. cirerae*, whose origin is indicated in Table 3. In *A. tenuifolius* and *A. cirerae* chromosomes always behave normally, with regular formation of 14 bivalents (Figs. 12 and 15, respectively), though with an occasional association between bivalents. *A. fistulosus* usually forms 28 bivalents at diakynesis (Fig. 14), although in some plates uni-, tri- and quadrivalents have been observed, as well as some occasional associations between bivalents (Fig. 13).

Discussion

The detailed study of morphological, palynological and karyological characters of *Asphodelus* sect. *Verinea* (Pomel) Maire proves that the recognition of a single species, *A. fistulosus*, can not be upheld. The group shows a wide diversity whose extremes correspond to *A. tenuifolius* and *A. cirerae*.

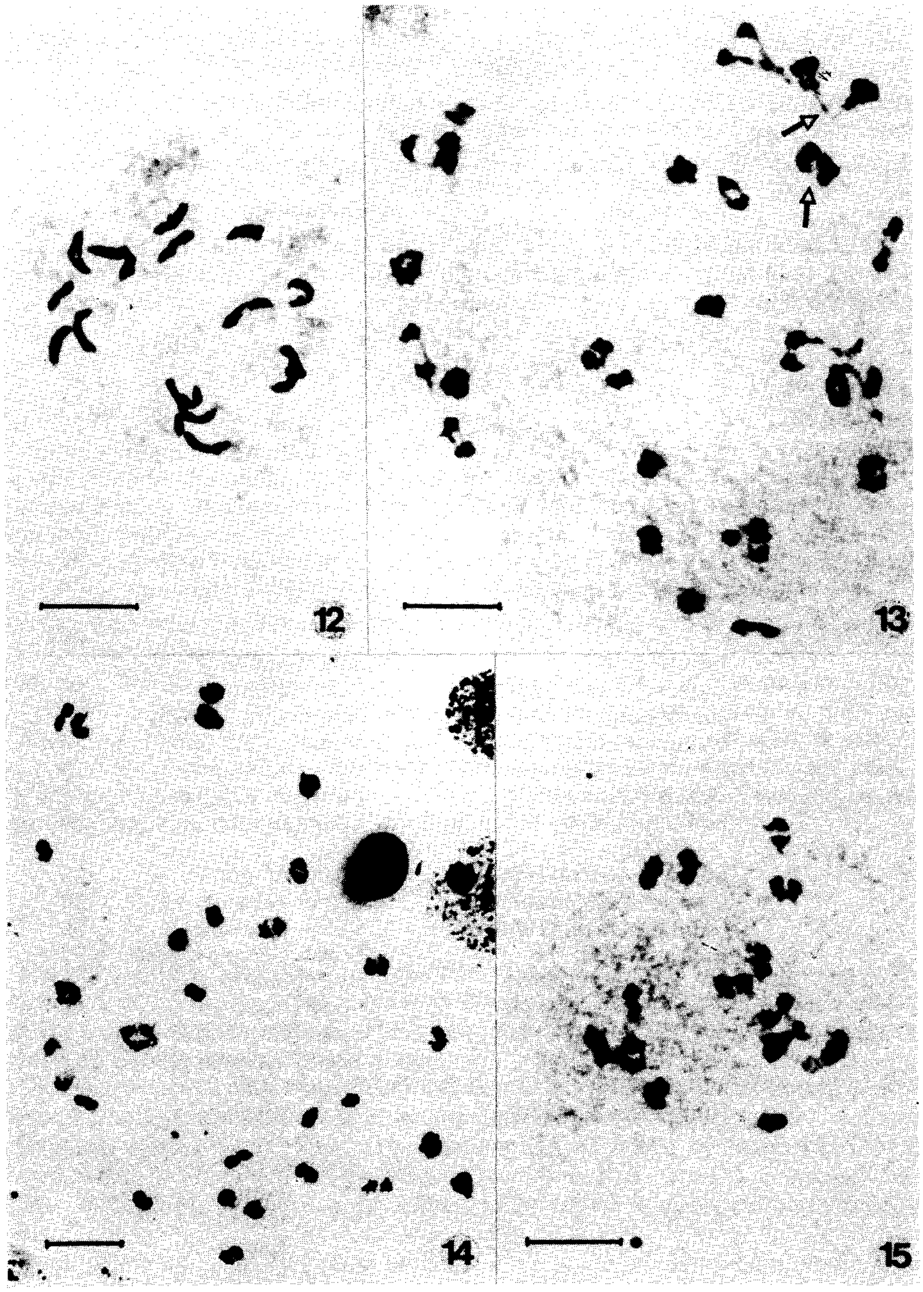
The data presented in this paper demonstrate not only the clear discontinuity between *A. fistulosus* and *A. tenuifolius*, but the existence of a third taxon, so far included by botanists in *A. fistulosus*. This taxon was already described by Sennen (1936) as *A. cirerae*, which has been verified by checking the type of that name (*). *A. mauritii* Sennen, nomen nudum, and *A. fistulosus* var. *atlanticus* Jahandiez & al. are mere synonyms of *A. cirerae*.

A. tenuifolius is a small annual plant, with a scabrous stem base, cylindrical or subcylindrical, generally scabrous leaves and small flowers, fruits and seeds. *A. fistulosus* is an annual or short-lived perennial, with an almost smooth stem base, subcylindrical or semicylindrical, scabrous leaves and medium-sized flowers, fruits and seeds. *A. cirerae* is a long-lived perennial, with a smooth stem base, semicylindrical leaves that are totally

(*)Type: "Leride: Sites arides autour de Gardeny", *Sennen* (BCF 4313, MA 20255, isotypi).

Table 5. Previous chromosome counts on *A. tenuifolius* and *A. fistulosus* s.l. When known, the origin of populations studied is indicated.

Taxa	Authors	Localities	2*n*	*n*
A. tenuifolius				
	Reese (1957)	Algerie: N Sahara		
	Amin (1972)	Egypt: Burg El Arab		14
	Sharma & Bhattacharyya (1957)	India: Bengalia	30	15
	Arora (1960)	India	28	
	Sharma & Chaurasia (1974)	India	28	
	Gupta & Srivastava (1971)	India: Meerut		14
	Ruíz Rejón (1976)	Spain: Granada		14
	Ruíz Rejón (1978)	Spain: Granada		14
		Almería		14
	Ruíz Rejón (1990)	Spain: Almería (4 loc.)	28	
		Granada (2 loc.)	28	
A. fistulosus s.l.			28	
	Larsen (1956)	Italy: Salerno		
	Capineri & al. (1978)	Italy: Cosenza	56	
	Diana-Corrias & Villa (1980)	Italy: Sardinia (4 loc.)	56	
	Humphries & al. (1978)	Morocco: SW Safi	28	
	Fernandes & Queirós (1971)	Portugal: Algarve	28	
	Barros Neves (1973)	Portugal: Algarve	56	
	Lorenzo-Andreu & García-Sanz (1950)	Spain: Aragón	28	
	Lorenzo-Andreu (1951)	Spain: Aragón	28	
	Gadella & al. (1966)	Spain: Alicante	28	
	Björkqvist & al. (1969)	Spain: Granada	56	
	Borgen (1969)	Spain: Canary Islands	28	
	Dahlgren & al.(1971)	Spain: Mallorca	56	
	Nilsson & Lassen (1971)	Spain: Mallorca	56	
	Ruíz Rejón (1976)	Spain: Granada (2 loc.)		14,28
	Ruíz Rejón (1978)	Spain: Granada (2 loc.)	28,56	14,28
	Ubera (1979)	Spain: Cádiz		28
	Ruíz Rejón & al. (1981)	Spain: Albacete		14
		Almería (2 loc.)		14,28
		Granada		28
		Jaén		14
		Murcia		28
		Toledo		14
		Valencia		28
	Ruíz Rejón & al (1990)	Spain: Almería (10 loc.)	28,56	
		Granada (1 loc.)	56	
		Toledo (1 loc.)	28	



Figs. 12-15. Diakinesis. **12:** *A. tenuifolius*, 14 bivalents; Almuñécar (Granada, Spain, SEV 127494); **13:** *A. fistulosus*, 28 bivalents (some secondary associations between bivalents are indicated by arrows); Huelva (Spain, SEV 127790); **14:** *A. fistulosus*, 28 bivalents; Jumilla (Murcia, Spain, SEV 127350); **15:** *A. cirerae*, 14 bivalents; Vélez Rubio (Almería, Spain, SEV 127518). Scale bar: 10 µm.

smooth, except at the margins, big flowers, and medium-sized fruits and seeds.

The three species have distinct geographical distribution areas (Fig. 16). *A. fistulosus* covers most of the Mediterranean Area, reaches to WC Asia, and has recently been introduced into N Europe (Täckholm & Drar 1973), N America (Mexico and California, Galván 1984) and Australia, where it behaves as a weed (Britton 1973). *A. tenuifolius* occurs in the southern part of the Mediterranean Region and in the Saharo-sindian Region. *A. cirerae* is restricted to the west of the Mediterranean Region.

There are also clear ecological differences between the three species. *A. tenuifolius* shows a marked capacity to adapt to xeric habitats, such as littoral sands, wadis and semiarid steppes, and it can be found in N Africa from the littoral to the high Saharian mountains. *A. cirerae* grows on stony basic hills, in littoral sandy areas and semiarid steppes, preferably in more primary habits, from the littoral to 1800 m above sea level in the Anti-Atlas. *A. fistulosus* behaves as a typical nitrophilous species with a distribution partly linked to human activity; it is very common in secondary, disturbed habitats, such as roadsides, railway tracks, waste fields, etc. It coexists with *A. tenuifolius* and *A. cirerae* in several places in the Iberian Peninsula and N Africa, always occupying the most disturbed habitats.

Pollen and karyological characters also support the separation of the three groups as distinct species, due to the lack of continous variation. Pollen grains are larger in *A. fistulosus* than in the other two species, as it was to be expected in view of its polyploid condition (Stebbins 1950, 1971, Lewis 1980).

The chromosome counts presented in Table 3, and almost all counts by previous authors (Table 5) agree in attributing to *Asphodelus* sect. *Verinea* a derivative base number $x = 14$, as proposed by Ruíz Rejón (1978). *A. tenuifolius* and *A. cirerae* are diploid with $2n = 28$ chromosomes and *A. fistulosus* is tetraploid with $2n = 56$ chromosomes. The number $2n = 28$ reported by several authors for *A. fistulosus* has to be referred to *A. cirerae*. The only deviating record is that of Sharma & Bhattacharyya (1957) who indicated

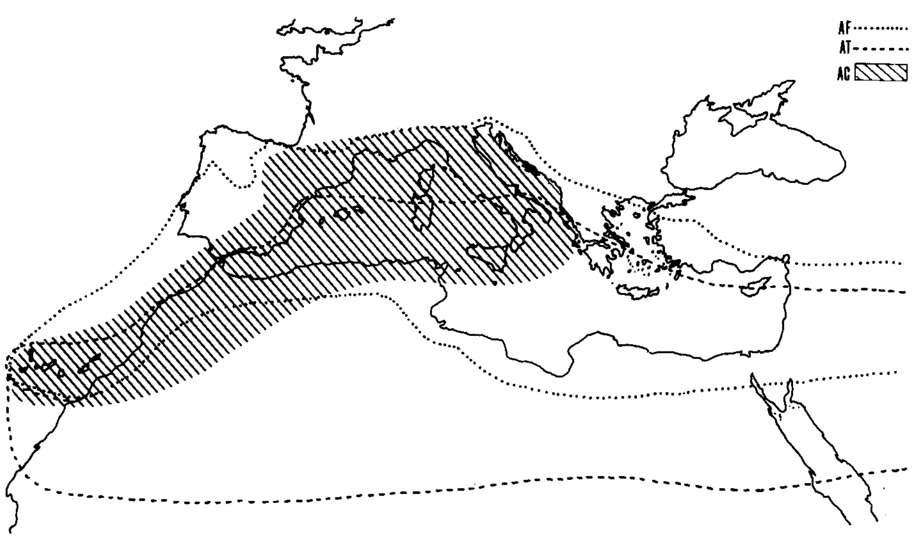


Fig. 16. Geographical distribution of *A. tenuifolius* (AT), *A. fistulosus* (AF) and *A. cirerae* (AC) in the Mediterranean Region.

$2n = 30$ for material of *A. tenuifolius* from India. Fernandes & Queirós (1971) found $2n = 28$ in plants from Cova de Gralheira (Algarve, Portugal), which were identified as *A. fistulosus*. The author has collected material of *A. fistulosus* in this same locality, and all the plants proved to be tetraploid with $2n = 56$. As *A. cirerae*, which might be misidentified as *A. fistulosus*, does not reach S Portugal, the count by Fernandes & Queirós has to be considered as anomalous.

The significantly smaller apparent chromosome size and the slightly more symmetrical karyotype, due to the presence of a large number of chromosomes of type m, differentiate *A. tenuifolius* from the other two species. Also, the pair of metacentric chromosomes (m) with a satellite on the short arm has only been found in this species.

The smaller chromosome size found in *A. tenuifolius* seems to be correlated with its apparent higher degree of morphological and physiological differentiation, which allows it to occupy more xeric habitats. Stebbins (1950) indicated that the karyotype can evolve in the sense of either an increase or decrease of size, the latter being true for *Muscari*, where the species with the highest degree of specialization have the smallest chromosomes, and for Crepis, where there is a correlation between small chromosomes, annual habit, and reduction of flower size.

To conclude, the separation of *A. tenuifolius*, *A. fistulosus* and *A. cirerae* at specific level is supported by morphological characters, ploidy level, karyotype, and pollen characters, reinforcing the differences found by Ruíz Rejón & al. (1990) in the electrophoretic pattern of esterases, alcohol dehydrogenase and glutamate oxalo-acetate transaminase in *A. tenuifolius* and *A. fistulosus*, in the latter case also between tetraploid and diploid populations of *A. fistulosus* (the diploids in fact representing *A. cirerae*).

With respect to the relationships between the three species, meiotic behaviour and karyological characters could point to an autopolyploid nature of *A. fistulosus* derived from *A. cirerae*, as proposed by Ruíz Rejón & al. (1990) for the tetraploid populations of *A. fistulosus* (i.e., *A. fistulosus* s. str.) as compared to the diploid populations (i.e., *A. cirerae*). But this hypothesis will have to be confirmed by hybridization experiments between the three species, which are being carried out by the author.

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