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Reproductive biology of the genus *Androcymbium* (Colchicaceae) in western southern Africa

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Abstract

We characterized reproductive biology traits in 32 populations belonging to 17 western southern African taxa of the genus *Androcymbium* (Colchicaceae) using artificial pollination experiments conducted under homogeneous environmental conditions in a greenhouse. The species surveyed displayed differences in phenological periods between emergence, flowering and senescence. We observed three types of vegetative reproduction that give rise to (1) globose corms, (2) compressed corms, and (3) a dichotomous underground networking of corms that, unlike (1) and (2), entails the elongation of the stem. Seed germination was low in most of the populations. The artificial pollination experiments allowed us to recognize three reproductive systems: self-incompatible, preferentially self-incompatible and self-compatible. In most cases, the reproductive system inferred from the artificial pollination experiments disagreed with the classification according to the P/O ratio. The variability observed in nectar characteristics (odour, amount and moment of the day of nectar production) suggests different pollinators for the taxa surveyed. Based on these data, we inferred three reproductive strategies in *Androcymbium* that assure both species' survival and the maintenance of levels of genetic variability: (1) preferential self-incompatibility associated with morphological traits that favour the attraction of pollinators; (2) preferential self-incompatibility with high levels of vegetative reproduction; and (3) self-compatibility with high levels of seed production.

Key words: Reproductive biology, genetic variability, *Androcymbium*, Colchicaceae.

Resumen. *Biología reproductiva del género* Androcymbium *(Colchicaceae) en Suráfrica Occidental*

Se estudiaron diversos aspectos de la biología reproductiva en 32 poblaciones pertenecientes a 17 taxones del género *Androcymbium* (Colchicaceae) de la región Occidental de Suráfrica usando experimentos de polinización artificial realizados en invernaderos bajo condiciones ambientales homogéneas. Las especies estudiadas mostraron diferencias en los períodos fenológicos entre la emergencia, la floración y la senescencia. Se observaron tres tipos de reproducción vegetativa que dan lugar a (1) cormos globosos, (2) cormos comprimidos, y (3) una red dicótoma subterránea de cormos que, a diferencia de (1) y (2), provoca el alargamiento del tallo. La tasa de germinación fue baja en la mayoría de las poblaciones. Los experimentos de polinización artificial permitieron reconocer tres sistemas reproductivos: auto-incompatible, preferentemente autoincompatible y autocompatible. En la mayoría de los casos, el sistema de reproducción derivado de los experimentos de polinización artificial no se ajustó a la clasificación según el cociente P/O. La variabilidad observada en las características del néctar (olor, cantidad y momento del día de producción de néctar) sugieren polinizadores diferentes para los taxones estudiados. En base a estos datos, se deducen tres estrategias reproductivas en *Androcymbium* que aseguran a la vez la supervivencia de las especies y el mantenimiento de los niveles de variabilidad genética: (1) preferentemente autoincompatible con características morfológicas que favorecen la atracción de polinizadores; (2) preferentemente autoincompatible con una tasa alta de reproducción vegetativa; y (3) autocompatible con altos niveles de producción de semillas.

Palabras clave: Biología reproductiva, variabilidad genética, *Androcymbium*, Colchicaceae.

Introduction

The reproductive system of a species consists of the mechanisms that contribute to the reproduction of a sufficient number of individuals to ensure the survival of future generations. Thus, knowledge on the reproductive system is crucial to understand the flow of genetic information in time and, by extension, to interpret the organization of the population genetic variability in space.

Species of genus *Androcymbium* Willd. (Colchicaceae) are geophytes with an annual vegetative cycle, and pass the unfavourable period buried like a tunicated corm. The genus includes about 40 species (Arnold & Wet, 1993; Müller-Doblies & Müller-Doblies, 1984, 1990, 1998; Pedrola-Monfort et al., 1999a, 1999b, in press.) whose distribution (Fig. 1A) embraces arid areas in western southern Africa (with about 35 species), eastern southern Africa (with six species), northern southern Africa and eastern Africa (with two species), the Mediterranean area (with four species) and the Canary Islands (with two species).

Previous reproductive biology studies for the northern African taxa of *Androcymbium* (Pedrola-Monfort, 1993; Ardanuy, 1997) described a mixed-animal reproductive system and a pollination conducted by insects, mainly bees. These species feature mechanisms to attract the pollinators, like many flowers per inflorescence, white tepals and high nectar production. In contrast, there is a paucity of information about the reproductive biology of southern African *Androcymbium* species. The only published reference known by us (Scott Elliot, 1891) refers to the pollinators of *A. capense* (at that time *A. leucanthum*): «the flowers are completely enclosed by the dome-shaped floral leaves, and within the cavity so formed many insects appear to take refuge... The insects most common in the cavity are *Forficaria*, always very abundant, a species of *Anthicus*, two other ants and *Heteroodeus pulchilus*. These probably usually creep into the flowers by the base and may leave by the upper opening after crawling over stigma and anthers”.

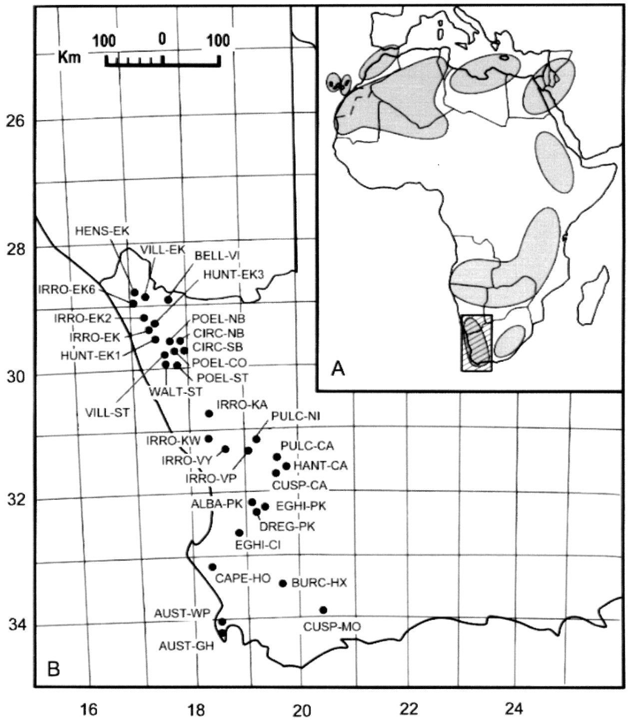

Figure. 1. A. Geographical distribution of the genus *Androcymbium*. B. Location of the 32 South African populations of *Androcymbium* sampled for the reproductive analysis. Population codes are described in the Appendix.

The objective of this work is double. First, to describe the phenology and reproductive traits of a broad representation of western southern African species of *Androcymbium* and compare the arising results with the available information for their northern African congeners. And second, to describe and discuss the mechanisms that probably influence in the maintenance of genetic variability in these populations.

Materials and methods

We used a total of 1153 individuals collected from 32 populations belonging to 17 taxa of the genus *Androcymbium* distributed in western southern Africa (Fig. 1B and Appendix). This collection is currently in cultivation in the greenhouse of the «Estació Internacional de Biologia Mediterrània-Jardí Botànic Marimurtra» in Blanes (Spain). The controlled environmental parameters in the greenhouse allowed us to establish homogeneous conditions, so that we assume that the differences observed among species or populations have a genetic basis. The study was mainly focused on the analysis of the morphological characteristics (shape and color of the tepal and the bract), phenology and reproductive traits.

Phenology was analyzed for two consecutive years (1996-97 and 1997-98) during which we scored emergence, flowering and senescence data for all adult individuals (i. e., those that flowered).

Although the greenhouse conditions were favorable for emergence, some individuals showed dormancy. Generally, this involves a period of rest of one or two years and subsequent emergence. Such cycle is controlled genetically (Pedrola-Monfort, 1993; Ardanuy, 1997) and was called "fluctuant corm dormancy" by Membrives (2000) to differentiate it from the normal summer rest. The percentage of fluctuant corm dormancy was calculated for three consecutive years (1996-97, 1997-98 and 1998-99).

The seed dormancy was inferred from the percentage of germination of two batches of seeds: one of them made up of seeds collected in the field, and the other one consisting of seeds from the *Androcymbium* specimens cultivated at the Jardí Botànic Marimurtra.

The corm of *Androcymbium* renews itself every biological cycle and shows two active buds: the renewal bud and the apical or vegetative reproduction bud (Fig. 2). The emergence of an individual always initiates from the renewal bud, and a new corm replaces the progenitor corm at the end of the cycle. In many of the studied species, a second corm is formed through the vegetative division of the apical bud. The apical bud and the renewal bud are opposed in the corm (Fig. 2A). The incidence of vegetative reproduction was studied after two years of cultivation by removing the corms from the plant pot and scoring the number and type of vegetative divisions.

Three artificial pollination experiments were carried out. In the first one, individuals were bagged without any manipulation, with the aim to detect spontaneous self-pollination. In the second experiment, individuals were bagged and pollinated with their own pollen, without previous emasculation (this is an autogamous/geitonogamous cross –following the terminology of Richards (1986)- that we called forced self-pollination for the sake of simplicity). In the third experiment, individuals were emasculated before the anthesis and were pollinated with pollen of a different individual (a xenogamy cross that we refer to as cross-pollination). The remaining individuals were left unbagged (and thus liable to be visited by pollinators) as a control. It is worth outlining that the fourth experiment might not be representative of the conditions in the wild, because these species are cultivated «ex situ» in a milieu that lacks their specific pollinators. For every experiment, three individuals were bagged before the anthesis. All experiments were repeated on the same flowers every 1-2 days during the flowering time. The number of developed seeds were counted when capsules were mature (about three months later).

To measure the number of pollen grains, we dissolved the content of an anther in 1 or 2 ml (depending on the size of the anther) of distilled water mixed with detergent. Measurements were made for a minimum of three individuals per population using a Fusch-Rosenthal (Braubrand) counter chamber, scoring the po-

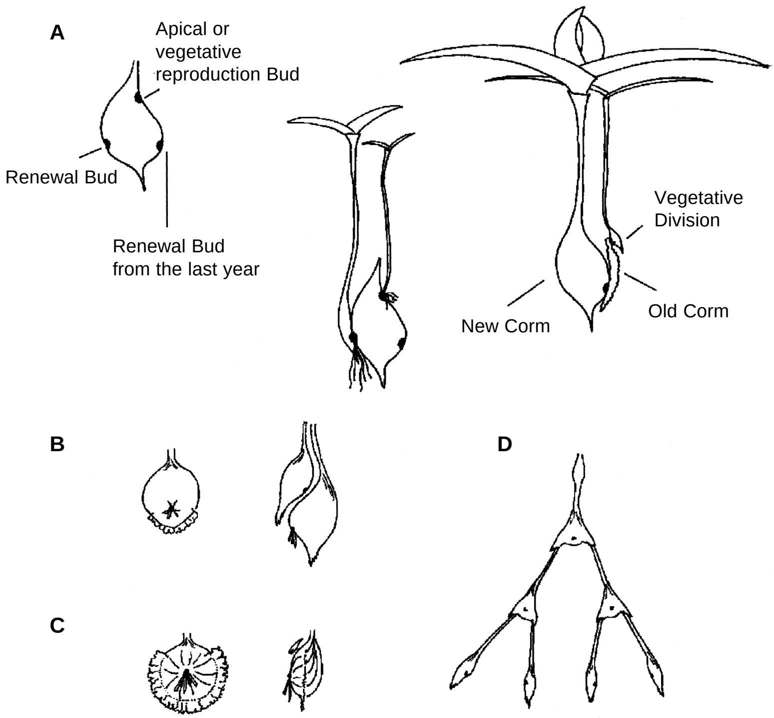

Figure 2. Vegetative reproduction in genus *Androcymbium* (A), and details of the different types observed in the species included in this survey: globose corm (B), small compressed corm (C), and dichotomical net (D).

llen grains in the two squares with a volume of 3.2 mm^3 (0.0625 mm^2 x 0.200 mm). The number of ovules were counted under a Olympus VMZ binocular magnifying glass using immature capsules.

The nectar production was measured in three individuals (one flower per individual) per population twice a day (at 9.00 am and at 18.00 pm) during all the flowering period using capillar micropipettes of 1, 5 and 10 µl to figure out if nectar was produced mainly in light hours or in dark hours.

Results

Phenology

The average observed duration for the biological cycle of the western southern African *Androcymbium* taxa examined ranged between 132 ± 33 days in *A. bellum* to 205 ± 7 days in *A. burchellii* subsp. *burchellii*. The differences observed in terms of the time elapsed between emergence and flowering (Table 1, Fig. 3) allowed us to separate these taxa in two groups. One contains the taxa with a period between emergence and flowering lower than 60 days (*A. albanense* subsp. *clanwilliamense, A. bellum, A. capense, A. circinatum, A. dregei, A. hensseninanum, A. huntleyi, A. irroratum, A. poeltianum* and *A. villosum*). The other group consists of the taxa with a period between emergency and flowering higher than 70 days (*A. austrocapense, A. burchellii* subsp. *burchellii, A. burchellii* subsp. *pulchrum, A. cuspidatum, A. eghimocymbion, A. hantamense* and *A. walteri*).

Fluctuant corm dormancy

The species with fluctuant corm dormancy were *A. bellum, A. huntleyi* and only three (IRRO-KW, IRRO-EK and IRRO-EK2) out of the seven populations of *A. irroratum* studied. The percentages of corm dormancy calculated for three consecutive years are summarized in Table 1.

Table 1. Phenology and percentage of fluctuant corm dormancy for western southern African species of *Androcymbium*. EM-SE: Days elapsed between emergency and senescence. EM-FL: Days elapsed between emergency and flowering. n: number of individuals studied. 0 year: percentage of individuals without fluctuant dormancy; 1 year: percentage of individuals with only 1 year of dormancy; 2 years: percentage of individuals with two years of dormancy; 3 years: percentage of individuals with three years of dormancy.

	Phenology			Fluctuant corm dormancy (%)				
Taxa	**n**	**EM-SE**	**EM-FL**	**n**	**0 year**	**1 year**	**2 years**	**3 years**
A. albanense subsp. *clanwilliamense*	184	173±15	56±5	99	97.0	3.0	0.0	0.0
A. austrocapense	113	193±10	107±10	65	89.2	10.8	0.0	0.0
A. bellum	6	132±33	31±6	109	4.6	28.4	56.0	11.0
A. burchellii subsp. *burchellii*	47	205±7	95±9	27	74.1	25.9	0.0	0.0
A. burchellii subsp. *pulchrum*	120	185±20	88±12	67	94.0	6.3	0.0	0.0
A. capense	108	191±9	36±6	54	100.0	0.0	0.0	0.0
A. circinatum	42	176±22	43±6	61	77.0	13.1	8.2	1.6
A. cuspidatum	82	176±15	74±10	54	92.6	3.7	3.7	0.0
A. dregei	40	136±16	58±11	31	87.1	9.7	0.0	3.2
A. eghimocymbion	42	163±12	75±8	29	69.0	20.7	10.3	0.0
A. hantamense	53	191±13	84±9	39	92.3	5.1	0.0	2.6
A. hensseniamum	93	168±18	22±4	56	89.3	10.7	0.0	0.0
A. huntleyi	11	163±16	32±8	31	3.2	25.8	48.4	22.6
A. irroratum	163	162±19	51±7	120	55.0	22.5	21.7	0.8
A. poeltianum	40	167±17	52±7	25	88.0	12.0	0.0	0.0
A. villosum	33	172±26	40±8	63	73.0	19.0	6.3	1.6
A. walteri	58	179±13	74±11	40	82.5	15.0	2.5	0.0

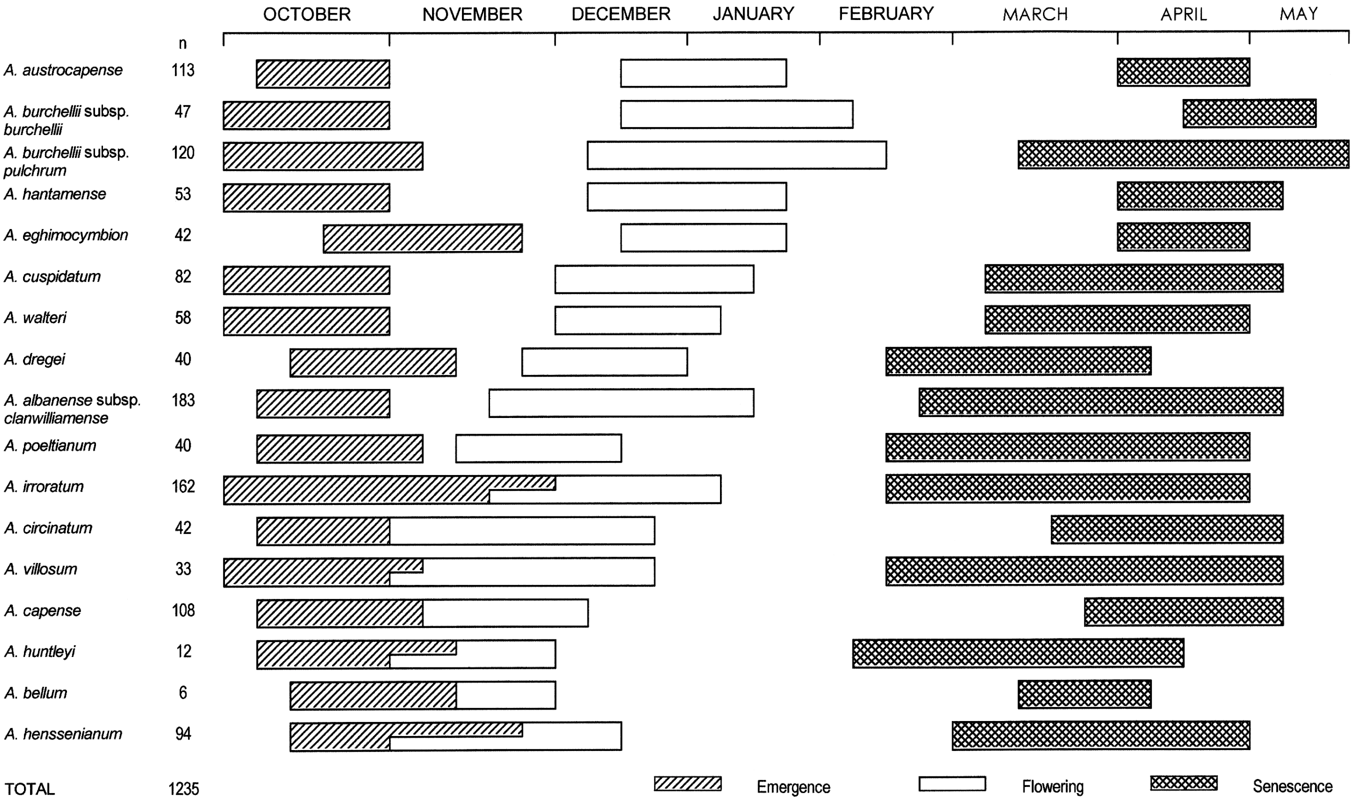

Figure 3. Periods of emergence, flowering and senescence in western southern African species of *Androcymbium* during the periods 1996-97 and 1997-98. n = number of individuals studied.

Seed germination

For seeds collected from the field, the percentages of germination were low and the percentages of mortality were high during the first and second year of experimentation (1994-95 and 95-96 in Table 2). Conversely, germination in the third year (1996-97 in Table 2) was higher than 50 % in most populations.

For seeds from cultivation, we obtained no seed germination in the first year of experimentation (1996-97 in Table 3). Conversely, the percentage of germination for the second year (1997-98 in Table 3) was higher than 40 % in *A. bellum*, *A. cuspidatum* (CUSP-CA and CUSP-MO), *A. huntleyi* (HUNT-EK3) and *A. irroratum* (IRRO-EK6 and IRRO-KW), and higher than 40 % in the third year (1998-99 in Table 3) in *A. burchellii* subsp. *burchellii*, *A. cuspidatum* (CUSP-MO), *A. hantamense*, *A. irroratum* (IRRO- KW and IRRO-VP), *A. poeltianum* (POEL-CO) and *A. walteri*. In general, the percentage of seed mortality observed in these two years was lower than that of seeds collected in the field. This trait could suggest that a substantial percentage of seeds collected in the field could be damaged or immature.

On the whole, western southern African species of *Androcymbium* exhibited low seed germination percentages, with the highest levels of seed germination during the second and third year of cultivation.

Table 2. Seed germination and mortality for seeds collected in the field. G (%): Percentage of germination. M (%): Percentage of mortality. ni: seed number at the beginning of the experiment. n1, n2 and n3: Number of dormant seeds for the first, second and third year respectively. Populations codes are described in the appendix.

		1994-95			1995-96			1996-97			1997-98	
Population	**ni**	**G (%)**	**M (%)**	**n1**	**G (%)**	**M (%)**	**n2**	**G (%)**	**M (%)**	**n3**	**G (%)**	**M (%)**
ALBA-PK	65	2	58	26	0	23	20	80	20	0	–	–
AUST-GH	114	9	11	91	0	5	86	1	16	71	0	10
BELL-VI	12	0	92	1	0	100	0	–	–	–	–	–
CAPE-HO	994	2	60	376	6	65	110	86	11	3	0	100
CIRC-SB	6	0	100	0	–	–	–	–	–	–	–	–
DREG-PK	34	0	21	27	0	22	21	57	14	6	0	33
EGHI-CI	80	0	5	76	0	1	75	0	13	65	0	49
EGHI-PK	287	1	9	258	0	29	182	32	45	42	0	24
HENS-EK	547	3	69	150	0	23	116	36	21	50	0	12
HUNT-EK3	91	3	54	39	0	21	31	97	3	0	–	–
IRRO–EK2	54	0	35	35	3	80	6	83	17	0	–	–
IRRO–KA	7	0	100	0	–	–	–	–	–	–	–	–
IRRO–KW	987	5	77	181	33	47	37	14	49	14	0	64
IRRO-EK	313	0	100	0	–	–	–	–	–	–	–	–

Table 3. Seed germination and mortality for seeds from cultivation. G (%): Percentage of germination. M (%): Percentage of mortality. ni: seed number at the beginning of the experiment. n1: Dormant seeds from first year. The percentage of mortality in the second year (97-98) was calculated from the initial number of seeds. Populations codes are described in the appendix.

		96-97	97-98	96-98		98-99	
Population	**ni**	**G (%)**	**G (%)**	**M(%)**	**n1**	**G (%)**	**M (%)**
ALBA-PK	274	0	0	11	244	4	14
AUST-GH	95	0	0	92	8	1	9
AUST-WP	100	0	1	12	87	0	20
BELL-VI	255	0	53	38	23	30	52
BURC-HX	123	0	13	30	70	84	13
CAPE-HO	200	0	0	23	155	5	0
CUSP-CA	100	0	92	8	0	–	–
CUSP-MO	193	0	45	8	92	85	13
DREG-PK	121	0	2	24	89	1	6
EGHI-CI	101	0	5	0	96	1	5
EGHI-PK	100	0	11	2	87	0	78
HANT-CA	37	0	8	30	23	74	13
HENS-EK	153	0	0	2	150	0	3
HUNT-EK1	161	0	7	46	75	0	23
HUNT-EK3	100	0	42	16	44	7	5
IRRO-EK	100	0	0	10	90	0	1
IRRO-EK6	100	0	42	33	25	20	0
IRRO-KW	380	0	44	5	193	81	10
IRRO-VP	198	0	25	11	126	68	27
IRRO-VY	126	0	13	17	87	21	26
POEL-CO	100	0	0	30	70	44	54
POEL-NB	100	0	0	5	95	0	4
PULC-CA	138	0	6	18	105	10	1
PULC-NI	47	0	2	13	40	5	0
WALT-ST	231	0	4	11	196	50	5

Floral morphology

The leaves and bracts in *Androcymbium* can be different in shape and color. The flowers show six tepals differenciated in lamina and claw, and every tepal support an stamen inserted in the base of the lamina. The nectary is situated in the base of the filament. Three main morphological traits associated with different taxa could be related to the attraction of pollinators in *Androcymbium* (Table 4): (1) the flat and white tepal in *A. bellum*; (2) the high number of flowers observed in *A. austrocapense*, *A. burchellii* subsp. *burchellii*, *A. burchellii* subsp. *pulchrum*, *A. capense*, *A. cuspidatum*, *A. eghimocymbion*, *A. hantamense* and *A. irroratum*; and (3) the wide and coloured bracts (white in *A. burchellii* subsp. *burchellii*, *A. capense* and *A. hantamense*, and reddish in *A. burchellii* subsp. *pulchrum*).

Vegetative reproduction

Different types and frequencies of vegetative reproduction were observed in western southern African species of *Androcymbium* (Fig. 2; Table 4). The three types of vegetative reproduction give rise to (1) globose corms, (2) compressed corms, and (3) a dichotomous underground networking of corms. In types (1) and (2), vegetative reproduction does not involve stem elongation. Type (1) results in a globose corm which is smaller than the progenitor corm and remains attached to it under the old tunic (Fig. 2B). Type (2) results in a tiny and compressed corm that remains attached to the progenitor corm under the coriaceous tunics for many years (only in *A. bellum*, *A. poeltianum* and *A. walteri*, Fig. 2C). In these species, the corm and the offspring emerge by the same point. We observed a third type of vegetative reproduction, where two corms of the same size elongate their stem

Table 4. Morphological traits, mean and maximum number of flowers and vegetative reproduction (frequency and type) in western southern African Androcymbium. G = globose corm; C = tiny, compressed corm; VD = vegetative dichotomical division.

Taxa	Morphological traits	Number of flowers		Vegetative reproduction	
		Mean	Maximum	%	Type
A. albanense subsp. *clanwilliamense*	–	1.85	4	37.5	VD
A. austrocapense	–	6.72	16	19.2	G
A. bellum	Flat and white tepal lamina	1.07	2	72.2	C
A. burchellii subsp. *burchellii*	White bracts	2.77	6	1.6	G
A. burchellii subsp. pulchrum	Reddish bracts	2.46	5	2.2	G
A. capense	White bracts	2.68	5	21.3	VD
A. circinatum	Red spots in leaves and bracts	1.20	2	31.8	VD
A. cuspidatum	–	2.94	7	0	G
A. dregei	–	1.55	3	0	–
A. eghimocymbion	–	2.00	5	0	G
A. hantamense	White bracts	2.77	5	49.1	VD
A. henssenianum	–	1.17	2	0	–
A. huntleyi	–	1.31	2	31.3	G
A. irroratum	–	1.61	4	2.3	G
A. poeltianum	–	1.08	2	45.7	C
A. villosum	Unicellular hairs in the abaxial leaf face	1.07	2	16.2	VD
A. walteri	–	1.30	2	64.3	C

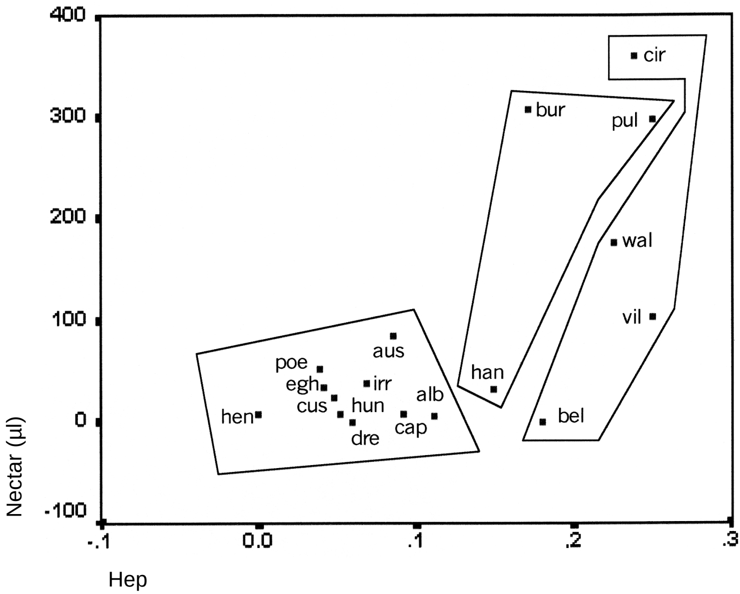

Figure 4. Two axis graphic showing the groups of species in *Androcymbium* inferred from reproductive data. The nectar production was measured in µl. The Hep values were taken from Membrives et al. (2001).

underground forming new corms interconnected by the empty tunics of the previous year (Fig. 2D). This results in a dichotomical underground net of corms, that we called vegetative dichotomical division. The frequency of each type of vegetative reproduction per species is summarized in Table 4.

Artificial pollination experiments

No seeds were produced by spontaneous self-pollination experiments in *A. burchellii* subsp. *burchellii, A. circinatum, A. hantamense, A. villosum* and *A. walteri* (Table 5), and only a few seeds were produced in *A. bellum* and *A. burchellii* subsp. *pulchrum* (up to a maximum of four). The rest of species produced a high number of seeds per flower. The forced self-pollination experiments allowed us to infer whether the individuals were genetically self-incompatible or the low seed production was a consequence of the lack of contact between stigma and anthers. Only *A. circinatum* produced no seeds in both spontaneous and obligated forced self-pollination; therefore, this species was considered strictly self-incompatible. *Androcymbium bellum, A. burchellii* subsp. *burchellii, A. burchellii* subsp. *pulchrum, A. hantamense, A. villosum* and *A. walteri* produced a small number of seeds (usually between 0 and 35, although one flower of *A. burchellii* subsp. *pulchrum* produced 132 seeds), and were considered preferentially self-incompatible. Unfortunately, possible con-

Table 5. Seed production per capsule in the artificial pollination experiments. In the first line: mean ± standard desviation, and number of flowers studied in brackets. In the second line: minimum and maximum in brackets. t: results of the t-test to infer self-compatibility vs. self-incompatibility (forced self-pollination vs. cross-pollination). RS=Reproductive system inferred (SC=self-compatibility, SI=self-incompatibility, PSI=preferential self-incompatibility). *P < 0.05; ** P < 0.01."

Taxa	**Control**	**Spontaneous self-pollination**	**Forced self-pollination**	**Cross-pollination**	**t**	**RS**
A. albanense subsp. *clanwilliamense*	52±35(83)	64±40(10)	74±40(7)	86±46(5)	-0.45	SC
	(1-138)	(4-137)	(18-128)	(25-139)		
A. *austrocapense*	71±37(90)	58±38(38)	101±39(52)	81±18(10)	1.16	SC
	(1-157)	(2-146)	(24-172)	(50-113)		
A. bellum	11±10(9)	3(1)	4±4(5)	109±60(4)	-3.87**	PSI
	(0-29)	-3	(0-8)	(7-166)		
A. burchellii subsp. *burchellii*	0(7)	0(2)	3±6(5)	74±63(8)	-2.46*	PSI
	0	0	(0-13)	(1-169)		
A. burchellii subsp. *pulchrum*	1±3(4)	1±2(4)	26±39(16)	98±56(8)	-3.61*	PSI
	(0-5)	(0-4)	(0-132)	(22-172)		
A. capense	153±83(55)	166±50(5)	139±73(2)	148±91(11)	-0.13	SC
	(6-340)	(95-206)	(87-190)	(42-299)		
A. circinatum	0(5)	0(1)	0(2)	6±8(8)	-0.94	SI
	0	0	0	(0-26)		
A. cuspidatum	58±34(48)	66±28(9)	73±34(14)	90±21(3)	-0.78	SC
	(0-139)	(31-114)	(10-116)	(67-108)		

(continuation)

Taxa	Control	Spontaneous self-pollination	Forced self-pollination	Cross-pollination	t	RS
A. dregei	29±17(45) (5-72)	22±17(4) (7-36)	22±12(7) (8-44)	57±0(2) -57	-4.07**	SC
A. eghimocymbion	145±60(8) (32-211)	73±65(3) (12-142)	130±65(6) (79-180)	–	–	SC
A. hantamense	6±11(7) (0-29)	0(4) 0	3±4(18) (0-13)	2±3(5) (0-8)	0.46	PSI
A. henssenianum	27±11(16) (9-49)	9±9(6) (0-26)	25±11(7) (14-45)	51±21(8) (19-77)	-2.94*	SC
A. huntleyi	114±34(4) (79-158)	73±47(2) (40-106)	112±57(3) (69-176)	100(1) -100	0.18	SC
A. irroratum	117±79(60) (0-364)	199±142(10) (4-370)	166±102(18) (13-347)	207±107(18) (35-387)	-1.16	SC
A. poeltianum	71±58(9) (0-145)	145±70(5) (36-220)	121±41(3) (84-165)	101±64(8) (6-199)	0.49	SC
A. villosum	0(5) 0	0(1) 0	8±7(3) (0-13)	73±69(5) (0-173)	-1.57	PSI
A. walteri	0(4) 0	0(1) 0	16±4(3) (12-19)	157±105(14) (14-337)	2.27*	PSI

taminations produced by the free entry of insects must be considered as a factor of bias in these experiments (e. g., ants do creep upwards by the sides of the pots and then into the bagged flowers). The rest of species produced a high number of seeds by spontaneous and obligated forced self-pollination experiments and were considered self-compatible.

Cross-pollination experiments produced seeds in all species, except for some cases in *A. circinatum*, *A. hantamense* and *A. villosum*. The most probable explanation for these failures could be a high inbreeding among individuals due to the high levels of vegetative reproduction detected. Inferences of the breeding system (self-compatibility or self-incompatibility) were based on a Student-t test that compared the average number of seeds per capsule in the reproductive experiments of forced self-pollination with the average number of seeds obtained in the cross-pollination experiments. If the number of seeds from the cross-pollination experiments was significantly higher than that from obligate self-pollination experiments, then the breeding system was inferred to be preferentially self-incompatible. When the differences in seed number between the two kinds of experiments were not significant, then we assumed that the breeding system was self-compatible. According to these tests, self-incompatible species were *A. bellum, A. burchellii* subsp. *burchellii, A. burchellii* subsp. *pulchrum, A. dregei, A. hensseniaum* and *A. walteri*. *Androcymbium dregei* and *A. hensseniaum* were considered self-compatible regardless of these results, because the production of seeds was significantly lower in the autogamy experiments but still high enough as compared to the behaviour of the other species of the genus that we classified as self-incompatible. On the other side, *A. circinatum, A. hantamense* and *A. villosum* showed non-significant differences due to the failure of some cross pollination experiments. Seed production in control experiments was similar to the results in spontaneous self-pollination.

These results allow us to define three basic reproductive systems for these species (Table 5): i) strict self-incompatibility, characterized by obligate cross-pollination (*A. circinatum*); ii) preferential self-incompatibility, characterized by low seed production in the forced self-pollination experiments (*A. bellum, A. burchellii* subsp. *burchellii, A. burchellii* subsp. *pulchrum, A. hantamense, A. villosum* and *A. walteri*); and iii) self-compatibility, characterized by high seed production in the spontaneous autogamy experiments (*A. albanense* subsp. *clanwilliamense, A. austrocapense, A. capense, A. cuspidatum, A. dregei, A. eghimocymbion, A. henssenianum, A. huntleyi, A. irroratum* and *A. poeltianum*).

P/O ratio

The number of pollen grains ranked between more than 17 million per flower in *A. walteri* to about 14000 in *A. dregei* (Table 6). The number of ovules per flower ranked between 591 in *A. walteri* and 60 in *A. henssenianum*. According to the P/O ratios (Cruden, 1977), the species of *Androcymbium* were xenogamous, except for *A. albanense* subsp. *clanwilliamense, A. henssenianum* and *A. huntleyi* (that showed facultative xenogamy), and *A. dregei* (with facultative autogamy).

Table 6. Number of pollen grains and ovules per flower and P/O ratios for western southern African Androcymbium species. In the first line: mean ± standard desviation, and number of anthers studied in brackets. In the second line: minimum and maximum in brackets. RS: Reproductive system according to Cruden (1977): FX, Facultative xenogamy; OX, Obligate xenogamy; FA, Facultative autogamy. Populations codes are described in the appendix.

Population	Pollen/flower (P)	Ovules/flower (O)	P/O	RS
ALBA-PK	421250±93399(3) (360000-528750)	309±62(3) (237-345)	1386	FX
AUST-GH	2155500±871877(3) (1192500-2891250)	124±12(3) (114-138)	17383	OX
AUST-WP	2281500±590208(3) (1622250-2760750)	152±17(3) (141-171)	15372	OX
BELL-VI	1340000±197627(3) (1177500-1560000)	278±101(3) (162-278)	5367	OX
BURC-HX	13905416±1758537(3) (11918416-15262500)	318±128(3) (202-456)	47138	OX
CAPE-HO	780083±245862(3) (497500-945000)	273±30(3) (240-300)	2818	OX
CIRC-NB	13595833±2892178(3) (10908000-16656246)	276±44(3) (234-321)	48980	OX
CIRC-SB	10886250±1632017(3) (9870000-12768800)	179±30(3) (150-210)	61122	OX
CUSP-CA	1295833±390683(3) (872500-1642500)	122±15(3) (105-132)	10805	OX
CUSP-MO	1079167±187589(3) (870000-1232500)	174±29(3) (153-207)	6410	OX
DREG-PK	13750±3551(3) (11250-17814)	71±2(3) (69-72)	195	FA
EGHI-CI	1167083±469961(3) (780000-1690000)	430±20(3) (408-447)	2719	OX
EGHI-PK	1610000±100093(3) (1542498-1725000)	221±41(3) (174-249)	7443	OX
HANT-CA	3782625±386795(3) (3359250-4117500)	262±37(3) (222-294)	14719	OX

(continuation)

Population	Pollen/flower (P)	Ovules/flower (O)	P/O	RS
HENS-EK	42156±23110(3) (12378-67500)	60±18(4) (39-72)	715	FX
HUNT-EK3	156252±53165(3) (96252-156252)	135±71(3) (87-216)	1245	FX
IRRO-EK	1680834±268916(3) (1466250-1982500)	220±80(3) (168-312)	7640	OX
IRRO-EK2	5496250±357832(3) (5193750-5891250)	231(1) -231	23393	OX
IRRO-EK6	3203750±979475(3) (2216250-4174998)	214±52(3) (174-273)	14848	OX
IRRO-KA	1207500±339411(3) (967500-1447500)	147±119(2) (63-231)	10812	OX
IRRO-KW	1587218±360958(3) (1308656-1995000)	200±70(3) (144-279)	8528	OX
IRRO-VP	4106664±938114(3) (3114996-4980000)	394±132(3) (291-543)	10423	OX
IRRO-VY	2435000±1267346(3) (1207500-3738750)	384±172(3) (270-582)	7308	OX
POEL-CO	891417±504643(3) (417498-1422000)	176±80(3) (84-228)	5024	OX
POEL-NB	381875±27403(2) (362496-401250)	121±57(2) (81-186)	3156	OX
PULC-CA	11541250±1549317(3) (10400000-13305000)	242±85(3) (150-318)	51746	OX
PULC-NI	13744998±6976117(3) (5880000-19185000)	296±55(3) (237-345)	49322	OX
VILL-EK	7882917±1399461(3) (6375000-9139998)	278±55(3) (234-339)	29159	OX
VILL-ST	7974583±1097855(3) (7168746-9225000)	237±52(3) (192-294)	34060	OX
WALT-ST	17249250±2556688(3) (14411250-19372500)	591±40(3) (558-636)	29104	OX

In *A. dregei*, the reproductive system inferred from the P/O ratio (facultative autogamy) agrees with the results observed in our reproductive experiments. The coincidence of both sources of data was also observed for all self-incompatible or preferentially self-incompatible species. Conversely, *A. austrocapense*, *A. capense*, *A. cuspidatum*, *A. eghimocymbion*, *A. irroratum*, and *A. poeltianum* are self-compatible according to our experiments, whereas they are obligate xenogamous according to P/O ratio.

Nectar production

The total nectar production per flower ranked from 359.23 µl in *A. circinatum* to 0.12 µl and 0.14 µl in *A. bellum* and *A. dregei* respectively (Table 7). The number of days with nectar production ranked from 2 in *A. bellum* and *A. huntleyi* to 13 in *A. burchellii* subsp. *burchellii* and *A. burchellii* subsp. *pulchrum* (Table 7). Most of the species produced the nectar during the darker hours of the day (from 6.00 pm to 9.00 am), except for *A. bellum*, *A. dregei* and *A. hantamense*, that produced nectar preferentially during the light hours (from 9.00 h to 18.00 h). Nectar odour is variable in the species studied, with some of them giving off a disagreeable odour for humans (*A. burchellii* subsp. *burchellii*, *A. burchellii* subsp.

Table 7. Nectar production and maximum number of days with nectar production. Dark hours: production from 6.00 pm to 9.00 am; Light hours: production from 9.00 am to 6.00 pm. A mininum of three flowers per population were used.

	Nectar production (µl)			Maximum number of days
Taxa	**Dark hours**	**Light hours**	**TOTAL**	**with nectar production**
A. albanense subsp. *clanwilliamense*	3.23	1.29	4.52	5
A. austrocapense	73.52	10.13	83.66	4
A. bellum	0.03	0.09	0.12	2
A. burchellii subsp. burchellii	229.59	77.52	307.10	13
A. burchellii subsp. *pulchrum*	173.28	123.06	296.34	13
A. capense	5.02	1.72	6.74	8
A. circinatum	301.80	57.43	359.23	12
A. cuspidatum	23.19	0.81	24.00	4
A. dregei	0.03	0.10	0.14	3
A. eghimocymbion	25.09	9.26	34.35	6
A. hantamense	13.97	18.33	32.30	9
A. hensseníanum	5.73	0.66	6.39	5
A. huntleyi	7.14	0.47	7.61	2
A. irroratum	31.43	6.94	38.37	8
A. poeltianum	47.60	4.21	51.82	5
A. villosum	88.43	14.18	102.61	8
A. walteri	157.13	18.60	175.73	10

pulchrum, *A. circinatum*, *A. villosum* and *A. walteri*) and some others releasing a fresh and agreeable odour (*A. bellum* and *A. hantamense*). The rest of species are odourless for humans.

Discussion

Biological patterns to ensure the survival of species and the maintenance of genetic variability

The reproductive studies carried out with western southern African species of genus *Androcymbium* results in a much higher variation of reproductive traits related to phenology, vegetative and sexual reproduction systems, percentatge of seed germination, nectar characteristics, and morphological traits than the previously observed in the species distributed in northern Africa. The relationships between phenological and reproductive traits in the western southern African species of *Androcymbium* allowed us to infer three biological patterns:

Pattern 1.- Preferentially self-incompatible species, with mechanisms that could favour the attraction of pollinators. This pattern included *A. hantamense*, *A. burchellii* subsp. *burchellii* and *A. burchellii* subsp. *pulchrum*. Obligate cross-pollination ensures the genetic interchange among individuals within populations. The main reproductive traits of these species are their adaptations to attract pollinators (coloured bracts and strong nectar odour) and reward them (high pollen and nectar production), large seeds and a long period between emergence and flowering time. Their most remarkable morphological traits are the ovate-lanceolate or orbicular bracts, and the colored bracts (white in *A. burchellii* subsp. *burchellii* and *A. hantamense*, and reddish in *A. burchellii* subsp. *pulchrum*). The inflorescences of these species showed up to six flowers with a high nectar production, mainly in *A. burchellii* subsp. *burchellii* and *A. burchellii* subsp. *pulchrum* (Table 7). Although the nectar odour was variable, it was fresh and aromatic only in *A. hantamense*. The nectar was mainly produced during the light hours in *A. hantamense*, while it was produced during the dark hours in the other two species. These variable nectar characteristics suggested to infer that specific pollinisators exist for these species in nature.

Pattern 2.- Preferentially self-incompatible species with high levels of vegetative reproduction. The species exhibiting this pattern (*A. bellum*, *A. circinatum*, *A. villosum* and *A. walteri*) are characterized by high levels of vegetative reproduction and only 1 or 2 flowers per inflorescence. Two types of vegetative division are found within this group. *Androcymbium bellum* and *A. walteri* (Fig. 2C) divide forming a small compressed corm, a type also observed in *A. poeltianum* (a species belonging to pattern 3). On the other side, *A. circinatum* and *A. villosum* (Fig. 2D) divide forming a underground dichotomical net. In both types of vegetative reproduction, all the corms emerge by the same point, thereby making the plant more attractive. Other mechanisms that we construe as pollinator-attractive in some of these species are flat white tepals (in *A. bellum*) and a high production of nectar with either aromatic smell (*A. bellum*) or unpleasant smell (in *A. circinatum, A. villosum* and *A. walteri*).

Species within the two self-incompatible patterns described high levels of seed dormancy. This trait can be considered a strategy with two main evolutionary implications (Bonner, 1990): i) in the short term, a mode of dispersal in time that acts like an alternative to seed dispersal in space, and ii) in the long term, the formation of a permanent seed bank in the soil.

All the species of pattern 1 and 2 show high levels of polymorphic loci and heterozygosity at population level, and low differentiation between populations (Membrives et al., 2001). So, in these cases, the high genetic variability at population level could be explained by the reproductive characteristics, that force a gene flow in populations.

Pattern 3.- Self-compatible species with high levels of seed production. This pattern includes *A. albanense* subsp. *clanwilliamense*, *A. austrocapense*, *A. capense, A. cuspidatum, A. dregei, A. irroratum, A. eghimocymbion, A. hensseníanum, A. huntleyi* and *A. poeltianum*. These species feature a high seed production (by spontaneous self-pollination), flowers enclosed by bracts, short period between emergency and flowering and, in most of them, high percentages of seed germination. These species have a limited capability to attract pollinators, as they produce low amounts of pollen (Table 6) and the nectar is odourless for human. On the whole, the levels of vegetative reproduction in these taxa are low except for *A. capense* (with a dichotomical vegetative reproduction) and *A. poeltianum* (with a division generating small compressed corms).

The species of pattern 3 show low levels of polymorphic loci and heterozygosity at population level, and high differentiation between populations (Membrives et al., 2001). In these cases, the low genetic variability at population level could be explained by the lost of gene flow in populations.

These three patterns described do not agree with the clades resulting from two recent phylogenetic analyses with morphological (Membrives, 2000) and cpDNA restriction site data (Caujapé-Castells et al., 1999). Species in the same clade show different breeding system and reproductive characteristics. So, the coincidence in the reproductive characteristics do not mean closely phylogenetic relationships in *Androcymbium*.

Comparison with northern African Androcymbium species

Phenological analysis for northern African taxa showed a short period between emergence and flowering time (Pedrola-Monfort, 1993; Ardanuy, 1997). The artificial crosses in the greenhouse concluded that these taxa are self-compatible. The percentage of seed germination (for seeds from cultivation) in northern Africa was > 50 % after four years of study, with the highest percentages observed in the first and second year. *Androcymbium gramineum* and *A. rechingerii* showed the lowest levels of seed germination in the first year. These two species showed indehiscent capsules and the lowest levels of fluctuant corm dormancy among the northern African species (Pedrola-Monfort, 1993; Ardanuy, 1997).

The floral morphology was very similar in all the northern African species of *Androcymbium*. These species have undifferentiated leaves and bracts, and the flowers display white flat tepals, frequently with purple stripes. These morphological characteristics are similar to the western southern African species *A. bellum*. This fact led Krause (1920) to include *A. bellum* within the section *Erythrostictus*. At present, a morphological revision by Müller-Doblies and Müller-Doblies (1998), a phylogenetic analysis with cpDNA RFLPs (Caujapé-Castells et al., 1999), and a cladistic analysis with morphological data (Membrives, 2000) converge to include this species in the section *Androcymbium*.

The inflorescence in northern African species produces numerous flowers per individual, and the nectar production per flower --ranking between 143.06 µl for *A. hierrense* and 3.87 µl for *A. gramineum* (Pedrola-Monfort 1993, Ardanuy 1997)-- is high as compared with their western southern African congeners. If these traits have developed to attract pollinators, then a substantial part of the reproduction of the North African species might be attributable to the action of insects, mainly bees (Pedrola-Monfort, 1993).

The type of vegetative reproduction of the northern African species was the most frequent in the genus (a globose corm without elongation of the stem; Fig. 2B). The percentage of vegetative reproduction was lower than 25 % in most of populations analyzed (Pedrola-Monfort, 1993; Ardanuy, 1997), except for *A. palaestinum* (with 50 and 55.5 % in the two populations studied), and *A. psammophilum* (where no vegetative division was observed).

The average P/O ratio in northern African species ranked between 3911 in *A. gramineum* and 18852 in *A. hierrense* (Pedrola-Monfort, 1993) and was considered obligate xenogamous according to the classification of Cruden (1977). These values are low if we compare them with those observed in the southern African species. The self-compatibility and the short period of time between emergency and flowering included these species in pattern 3 described for western southern African species of *Androcymbium*, although their morphological traits could hint a closer relationship to the self-incompatible species.

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Appendix. Sampling details of the western southern African populations of genus Androcymbium studied.

Population	Code	Locality
A. albanense Schönland subsp. *clanwilliamense* Pedrola, Membrives & J.M.Monts	ALBA-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road. Km 10
A. austrocapense U.Müll.-Doblies & D.Müll.-Doblies	AUST-GH	3418AC (SIMONSTOWN) Good Hope Cape
A. austrocapense U.Müll.-Doblies & D.Müll.-Doblies	AUST-WP	3418AD (SIMONSTOWN) Wheal's Point. Cape Point Reserve
A. bellum Schltr. & K.Krause	BELL-VI	2817DC (VIOOLSDRIFT) Steinkopf to Vioolsdrift Road. Km 40
A. burchellii Baker subsp. *burchellii*	BURC-HX	3319BC (WORCESTER) Worcester to Towsrivier Road.
A. burchellii Baker subsp. *pulchrum* Pedrola, Membrives, J.M.Monts & Caujapé	PULC-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km turnoff to Kreitzberg
A. burchellii Baker subsp. *pulchrum* Pedrola, Membrives, J.M.Monts & Caujapé	PULC-NI	3118AA (CALVINIA) Wild flower reserve of Nieuwoudtville
A. capense (L.) K.Krause	CAPE-HO	3318AB (CAPE TOWN) Malmesbury to Hopefield Road. Km 49
A. circinatum Baker	CIRC-NB	2917DB (SPRINGBOK) Springbok to Nababeep Road. 100 m
A. circinatum Baker	CIRC-SB	2917DB (SPRINGBOK) 3 km W of Springbok
A. cuspidatum Baker	CUSP-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km turnoff to Kreitzberg
A. cuspidatum Baker	CUSP-MO	3320CD (MONTAGU) Near Montagu-Badskloof. W of the Gorgo
A. dregei C.Presl	DREG-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road. Km 28
A. eghimocymbion U.Müll.-Doblies & D.Müll.-Doblies	EGHI-CI	3218DB (CLANWILLIAM) Piketberg to Citrusdal Pass
A. eghimocymbion U.Müll.-Doblies & D.Müll.-Doblies	EGHI-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road. Km 28
A. hantamense Schinz	HANT-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km turnoff to Kreitzberg
A. henssenianum U.Müll.-Doblies & D.Müll.-Doblies	HENS-EK	2817CC (VIOOLSDRIFT) Eksteenfontein to Modderfontein Road
A. huntleyi Pedrola, Membrives, J.M.Monts & Caujapé	HUNT-EK1	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 14 km to Eksteenfontein

(continuation)

Population	**Code**	**Locality**
A. huntleyi Pedrola, Membrives, J.M.Monts & Caujapé	HUNT-EK3	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 20 km to Eksteenfontein
A. irroratum Schltr. & K.Krause	IRRO-EK	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 6 km to Eksteenfontein
A. irroratum Schltr. & K.Krause	IRRO-EK2	2917AD (SPRINGBOK) Springbok to Port Nolloth, 15 km to Eksteenfontein
A. irroratum Schltr. & K.Krause	IRRO-EK6	2817CC (VIOOLSDRIFT) Eksteenfontein to Modderfontein Road
A. irroratum Schltr. & K.Krause	IRRO-KA	3018CB (KAMIESBERG) Bitterfontein to Kliprand Road
A. irroratum *Schltr. & K.Krause*	IRRO-KW	3118BC (VANRHYNSDORP) Vredental to Koekenaap Road, 100 m to train station
A. irroratum Schltr. & K.Krause	IRRO-VP	3119AC (CALVINIA) Vanrhynspass
A. irroratum Schltr. & K.Krause	IRRO-VY	3118AD (VANRHYNSDORP) Vrendendal to Vanrhynsdorp Road
A. poeltianum U.Müll.-Doblies & D.Müll.-Doblies	POEL-CO	2917DB (SPRINGBOK) Springbok to Concordia Road
A. poeltianum U.Müll.-Doblies & D.Müll.-Doblies	POEL-NB	2917DB (SPRINGBOK) Springbok to Nababeep Road. 100 m
A. poeltianum U.Müll.-Doblies & D.Müll.-Doblies	POEL-ST	2917DC (SPRINGBOK) Steinkopf to Springbok Road. 5 km
A. villosum U.Müll.-Doblies & D.Müll.-Doblies	VILL-EK	2817CC (VIOOLSDRIFT) 1 km S of Eksteenfontein
A. villosum U.Müll.-Doblies & D.Müll.-Doblies	VILL-ST	2917BC (SPRINGBOK) 3 km S of Steinkopf
A. walteri Pedrola, Membrives & J.M.Monts	WALT-ST	2917DC (SPRINGBOK) Steinkopf to Springbok Road. 5 km