

## CORRELATIONS BETWEEN MORPHOLOGICAL-ANATOMICAL LEAF CHARACTERISTICS AND ENVIRONMENTAL TRAITS IN SOUTHWEST AFRICAN SPECIES OF *ANDROCYMBIUM* (COLCHICACEAE)

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**Key words:** *Androcymbium*, Colchicaceae, South Africa, morphology, anatomy, environmental traits, correlations.

### SUMMARY

We studied 32 populations belonging to 17 Southwestern African taxa of the genus *Androcymbium* in order to explore the relationships between leaf morphological and anatomical variation and environmental characteristics as measured by distribution in two different type velds (Fynbos and Karoo-Karoid types) and the values of 16 edaphic parameters from 22 soil samples. Our results show that only hydric disponibility (measured as the amount and distribution of annual rainfall, and the water retention capacity) correlates significantly with morphological leaf characteristics in *Androcymbium*. We detected no significant correlations between pairwise combinations of anatomical traits and climatic or edaphic parameters. These results conform to the hypothesis that the diversification of Southwestern African species of *Androcymbium*, has been mainly influenced by the arid gradient that already existed when these species began to diversify in the Late Miocene. Thus, they seem to agree with the hypothesis of Stebbins that predicts relatively rapid plant evolution in arid to semiarid regions. Because solely some combinations between characteristics related to aridity and morphological traits are significantly correlated, our results reflect only partially Axelrod and Raven's suggestion that the specific diversity in South Africa is a consequence of climatic and edaphic fragmentation.

### RESUMEN

Se estudiaron 32 poblaciones pertenecientes a 17 taxones del género *Androcymbium* distribuidas en Sudáfrica Occidental con el objetivo de explorar las relaciones entre características morfológicas y anatómicas foliares y características ambientales medidas según la distribución en dos tipos de vege-

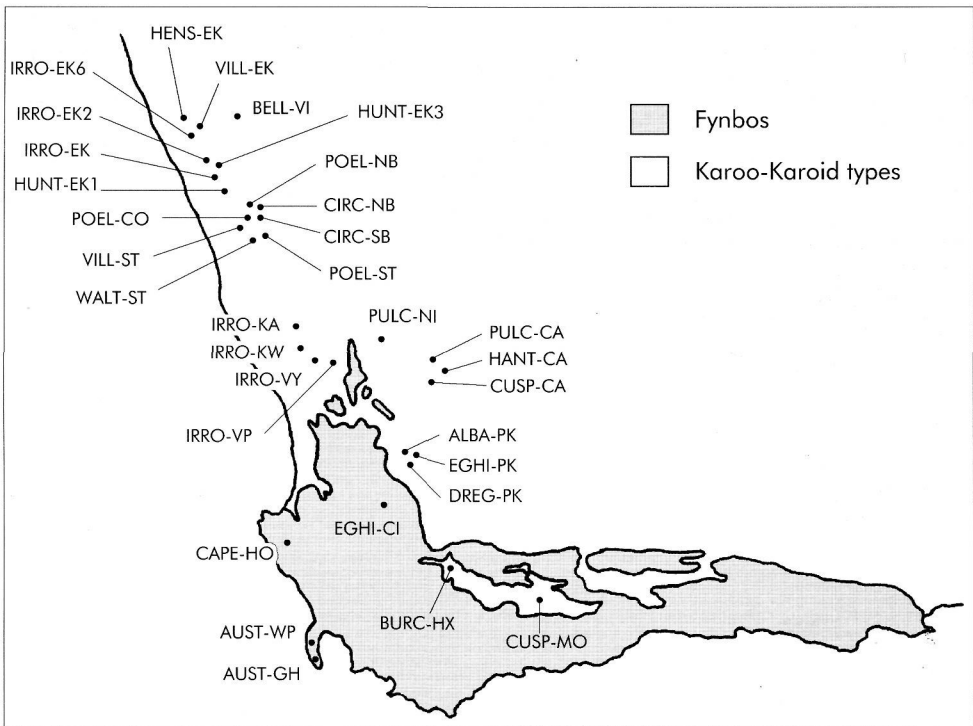
tación diferentes (Fynbos y Karoo-tipos karoides) y los valores de 16 parámetros edáficos procedentes de 22 muestras de suelos. Los resultados obtenidos mostraron que solamente la disponibilidad hídrica (medida a partir de la cantidad y distribución de las lluvias anuales, y de la capacidad de retención de agua) se correlaciona significativamente con las características morfológicas de las hojas en *Androcymbium*. Respecto a los caracteres anatómicos, no se observaron correlaciones significativas con parámetros climáticos o edáficos. Estos resultados sugieren que la diversificación de las especies de *Androcymbium* en Sudáfrica Occidental ha estado condicionada principalmente por el gradiente de aridez desde el inicio de su especiación a finales del Mioceno. Estos resultados están de acuerdo con la hipótesis de Stebbins que sostiene una rápida evolución de las especies vegetales en regiones áridas y semiáridas. Nuestros resultados reflejan sólo parcialmente la hipótesis de Axelrod y Raven que sugiere que la diversidad específica en Sudáfrica es una consecuencia de la fragmentación climática y edáfica, debido a que únicamente algunas combinaciones entre características relacionadas con la aridez y aspectos morfológicos están significativamente correlacionadas.

## INTRODUCTION

The species of *Androcymbium* Willd. (Colchicaceae) are geophytes with an annual vegetative cycle that spend the unfavourable period buried like tunicated corms. The genus includes about 50 species (ARNOLD & WET, 1993; MÜLLER-DOBLIES & MÜLLER-DOBLIES, 1984, 1998; PEDROLA-MONFORT *et al.*, 1999a, 1999b, 2000) with a disjunct distribution in arid regions of South Europe and Africa.

The six species in Northern Africa distribute all along the Mediterranean Basin and in the Canary Islands. The rest of species in the genus (approximately 45) are distributed in South Africa, mainly in the Western region. Southwestern African species display much higher variability levels at the morphological (BAKER, 1974; KRAUSE, 1920; MEMBRIVES, 2000), seminal (MEMBRIVES *et al.*, 2000a), palynological (MARTÍN *et al.*, 1993; MEMBRIVES, 2000), anatomical (MATEU-ANDRÉS *et al.*, 1996; MEMBRIVES *et al.*, 2000b), karyological (MARGELI *et al.*, 1998; MONTSERRAT *et al.*, in prep.), allozymatic (MEMBRIVES, 2000), and cpDNA levels (CAUJAPÉ-CASTELLS *et al.*, 1999), than their Northern African congeners (PEDROLA-MONFORT, 1993; PEDROLA-MONFORT & CAUJAPÉ-CASTELLS, 1996).

STEBBINS (1952 in AXELROD, 1972) suggested that there are several reasons why plant evolution would be relatively rapid in arid and semiarid regions. First, local diversity of soils (and other factors) in areas where the moisture is limited has a greater effect on the flora and vegetation than in regions where moisture is adequate. Second, the regional diversity of semi-arid climates promotes the fragmentation of medium to large-sized populations into smaller units which are isolated from each other but can exchange genes by occasional migration and establish populations that may give rise to new species. And third, in dry regions, many different specialized vegetative structures (e.g., reduced leaf size, specialized leaf covering, deciduous habit, deep root system, swollen trunks or bulbs) can evolve which may enable plants to withstand periods of severe drought. More recent works argued that the climatic and edaphic fragmentation that characterizes Southwest Africa (RICHERSON & LUM, 1980; SHMIDA & WILSON, 1985; BROWN, 1988; DIAMOND, 1988; WILLIAMSON, 1983; CORNELL, 1993; COWLING *et al.*, 1997) is the main cause of the specific diversity of its flora and fauna (AXELROD & RAVEN, 1978). Thus, climatic and edaphic heterogeneity could be one relevant factor to explain the observed morphological and anatomical differentiation among the species of



**Figure 1.-** Geographical distribution of genus *Androcymbium* according to the veld types (Fynbos and Karoo-Karoid types). Abbreviations of populations are described in Table 1.

*Androcymbium* distributed in this area, and between them and their Northern African congeners. The main objective of this work is to explore the possible relationships between the morphological and anatomical variation and environmental (climatic and edaphic) parameters in this geographical circumscription of *Androcymbium*.

## MATERIAL AND METHODS

The material studied comes from 32 populations belonging to 17 Southwestern African taxa of the genus *Androcymbium* (Table 1, Fig. 1). These samples are currently in cultivation at the greenhouses of the "Estació Internacional de Biologia Mediterrània-Jardí Botànic Marimurtra". Morphological and anatomical characteristics were taken from MEMBRIVES *et al.* (2000b) and are summarized in Table 2.

**Climatic and edaphic parameters-** The studied populations are distributed in two veld types –Fynbos, and Karoo-Karoid- (Table 1, Fig. 1) according to the classification in ACOCKS (1988). Twenty-two soil samples from these populations of *Androcymbium* (Table 3) were analyzed following the analytic methods described in HERRERO-BORGOÑON (1992). The measures of pH were taken from a pH-meter Beckman H-2 with glass electrodes and calomelans. Water retention capacity

**Table 1.-** Populations of *Androcymbium* analyzed, according to the type veld where inhabit (Fynbos and Karoo-Karoid types).

Species	Code	Locality
<b>Taxa inhabiting the Fynbos</b>		
<i>A. austrocapense</i> Müll.-Doblies	U.Müll.-Doblies & D. AUST-GH	3418AC (SIMONSTOWN) Good Hope Cape
	AUST-WP	3418AD (SIMONSTOWN) Whales Point. Cape Point Reserve
<i>A. capense</i> (L.) K.Krause	CAPE-HO	3318AB (CAPE TOWN) Malmesbury to Hopefield Road, Km 49
<i>A. eghimocymbion</i> Müll.-Doblies	U.Müll.-Doblies & D. EGHI-CI	3218DB (CLANWILLIAM) Piketberg to Citrustal Pass
<b>Taxa inhabiting Karoo-Karoid vegetation types</b>		
<i>A. albanense</i> Schönland subsp. <i>clanwilliamense</i> Pedrola, Membrives & J. M.Monts	ALBA-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road. Km 10
<i>A. bellum</i> Schltr. & K. Krause	BELL-VI	2817DC (VIOOLSDRIFT) Steinkopf to Vioolsdrift Road, Km 40
<i>A. burchellii</i> Baker subsp. <i>burchellii</i>	BURC-HX	3319BC (WORCESTER) Worcester to Towsrivier Road.
<i>A. burchellii</i> Baker subsp. <i>pulchrum</i> Pedrola, Membrives, J. M. Monts & Caujapé	PE-PULC-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km turnoff to Kreitzberg
	PULC-NI	3118AA (CALVINIA) Wild flower reserve of Nieuwoudtville
<i>A. circinatum</i> Baker	CIRC-NB	2917DB (SPRINGBOK) Springbok to Naba-beep Road, 100 m
	CIRC-SB	2917DB (SPRINGBOK) 3 km W of Springbok
<i>A. cuspidatum</i> Baker	CUSP-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km turnoff to Kreitzberg
	CUSP-MO	3320CD (MONTAGU) Near Montagu-Badskloof. W of the Gorgo
<i>A. dregei</i> C.Presl	DREG-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road, Km 28
<i>A. eghimocymbion</i> Müll.-Doblies	U. Müll.-Doblies & D. EGHI-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road, Km 28
<i>A. hantamense</i> Schinz	HANT-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km turnoff to Kreitzberg
<i>A. henssenianum</i> Müll.-Doblies	U. Müll.-Doblies & D. HENS-EK	2817CC (VIOOLSDRIFT) Eksteenfontein to Modderfontein Road
<i>A. huntleyi</i> Monts & Caujapé-Castells	Pedrola, Membrives, J. M. HUNT-EK1	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 14 km to Eksteenfontein
	HUNT-EK3	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 20 km to Eksteenfontein
<i>A. irroratum</i> Schltr. & K. Krause	IRRO-EK	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 6 km to Eksteenfontein
	IRRO-EK2	2917AD (SPRINGBOK) Springbok to Port Nolloth, 15 km to Eksteenfontein
	IRRO-EK6	2817CC (VIOOLSDRIFT) Eksteenfontein to Modderfontein Road
	IRRO-KA	3018CB (KAMIESBERG) Bitterfontein to Kliprand Road
	IRRO-KW	3118BC (VANRHYNSDORP) Vredental to Koekenaap Road, 100 m to train station
	IRRO-VP	3119AC (CALVINIA) Vanrhynspass
	IRRO-VY	3118AD (VANRHYNSDORP) Vredental to

<i>A. poeltianum</i> U. Müll.-Doblies & D. Müll.-Doblies	POEL-CO	Vanrhynsdorp Road 2917DB (SPRINGBOK) Springbok to Concordia Road
	POEL-NB	2917DB (SPRINGBOK) Springbok to Nababoop Road, 100 m
	POEL-ST	2917DC (SPRINGBOK) Steinkopf to Springbok Road, 5 km
<i>A. villosum</i> U. Müll.-Doblies & D. Müll.-Doblies	VILL-EK	2817CC (VIOOLSDRIFT) 1 km S of Eksteenfontein
	VILL-ST	2917BC (SPRINGBOK) 3 km S of Steinkopf
<i>A. walteri</i> Pedrola, Membrives & M.Monts	J. WALT-ST	2917DC (SPRINGBOK) Steinkopf to Springbok Road, 5 km

(WRC) was measured as the percentage of water retained in the soil after the centrifugation of 1000 g of moist sample by capillar ascension. The total percentage of carbonate was analyzed with a Bernard calcimeter. The percentage of organic material was measured following the Jackson method, which is based on the oxidation in cold of the organic matter with Potassium bichromate in acid solution. The surplus of dicromate was calculated with ferric sulphate. The quantity of mineral nitrogen (the only kind assimilable by plants) was determined by distillation of a soil extract in KCl 2N and collected with a flask containing a mixture of indicators. This solution was titrated with sulphuric acid 0.001 N. The amount of assimilable phosphor was evaluated by the Olsen method, and the colorimetric measures were made with a Zeiss spectrophotometer using a wavelength of 660 mu. The amount of assimilable potassium was estimated by atomic absorption spectrophotometry. Cathionic interchange capacity (CIC) was evaluated by the Bower method, with little modifications. The mechanic analysis consisted of evaluating the soil texture and the amounts of sand, mud and clay contained in samples with the method of the Bouyoucos densimeter.

*Data analysis.*- The differences among pairwise combinations of morphological and anatomical characteristics and veld types were evaluated using a student-t test. Associations among morphological and anatomical characteristics and edaphic parameters were calculated with Pearson's correlation. Qualitative characteristics were coded with numerical values (leaf color: 0=green, 1=glaucous; leaf margin indument: 0=smooth or with papillae, 1=hairy; epidermic cells shape: 1=rectangular, 2=romboidal, 3=polygonal; mesophyll cells: 0=undifferentiated, 1=differentiated; section: 1=flat, 2=semi-flat, 3=V-shaped; idyoblasts at leaves: 0=unfrequent, 1=frequent; central lamina cells: 0=different in size from the other cells; 1=similar in size to the other cells). Data analyses were made using the statistic package SPSS/PC+ version 6.1.2 (1995).

## RESULTS

a) Correlations between morphological-anatomical characteristics and veld types

Leaf length, leaf section and the central epidermic cells sizes were the only three characters that differed significantly between the two veld types where the examined populations occur (Table 4). The four populations from the Fynbos

Taxa	Leaves			Bracts			Leaf							
	Shape	Length	C	Shape	Length	C	SECT	Margin	ECSad	STad	STab	M	Id	CCS
<i>A. albanense</i> subsp. <i>clanwilliamense</i>	L-LA	13.3	GR	DE	2.7	GR	V	Papillae	RE	35.7	38.6	UD	F	D
<i>A. austrocapense</i>	L-LA	23.8	GR	DE	3.8	GR	V	Papillae	RO	34.1	34.0	D(2-3)	F	S
<i>A. bellum</i>	L	13.0	GL	E	3.3	GL	V	Smooth	RE	25.4	18.2	UD	FF	S
<i>A. burchellii</i> subsp. <i>burchellii</i>	OV-LA	15.9	GR	OR	3.9	WH	F	Hairy(4-6)	PO	25.7	24.5	D(4)	F	D
<i>A. burchellii</i> subsp. <i>pulchrum</i>	OV-LA	13.0	GR	OV-OR	7.4	RD	F	Hairy(5-9)	PO	32.7	30.0	D(2-4)	F	D
<i>A. capense</i>	LA	15.3	GR	E	4.7	WH	F	Hairy(8-10)	RE	32.9	32.7	D(1)	F	D
<i>A. circinatum</i>	L-LA	19.3	GL	E-DE	4.5	GL	F-V	Smooth	RE	29.7	18.6	UD	F	D
<i>A. cuspidatum</i>	OV-LA	4.1	GR	DE	4.1	GR	F	Smooth	RE	27.6	20.7	UD	FF	S
<i>A. dregei</i>	A	7.9	GL	A	4.3	GR	V	Papillae	RE	25.9	28.9	D(1)	FF	S
<i>A. eghimocymbion</i>	L-LA	21.6	GR	DE	4.1	GR	V	Papillae	RE	39.6	40.0	UD	F	S
<i>A. hantamense</i>	LA	15.2	GL	E-LA	7.7	WH	F	Hairy(3-5)	RO	36.7	27.7	D(5-7)	F	D
<i>A. henssenianum</i>	A	15.0	GL	LA	5.7	GL	F-V	Smooth	RE	-	-	UD	FF	D
<i>A. huntleyi</i>	L-LA	8.1	GL	E-DE	3.1	GL	F-V	Smooth	-	-	-	UD	F	D
<i>A. irroratum</i>	OV-LA	11.4	GR	E-DE	3.8	GR	F	Papillae	RO	36.1	31.6	D(2-3)	F	D
<i>A. poeltianum</i>	L-LA	12.4	GL	LA	4.6	GL	F	Papillae	RE	25.5	18.8	UD	FF	D
<i>A. villosum</i>	L-LA	13.4	GL	E-DE	5.5	GL	F-V	Hairs(1)	RE	20.0	20.0	UD	F	D
<i>A. walteri</i>	L-LA	16.9	GL	E-DE	4.3	GL	F	Papillae	RE	31.1	28.4	UD	FF	D

**Table 2.** Morphological and anatomical characteristics of genus *Androcymbium* in Southwest Africa (from MEMBRIVES *et al.*, 2000b). Shape: A=Acicular; DE=Deltoidous; E=Elliptic; L=Linear; LA=Lanceolate; OR=Orbicular; OV=Ovate. Color (C): WH=White; GL=Glaucous; RD=Reddish; GR=Green. Section (SECT): F=flat; V=V-shaped. Leaf margin: n° of cells of the hairs in brackets. Epidermic cells shape in adaxial side (ECS): RE=Rectangular, RO=Romboidal, PO=Polygonal. STab and STad=Stomata indexes in adaxial and abaxial side (in %). Mesophyll (M): D=diferenciated (n° of layers of palysade parenchyma in brackets); ND=Undiferenciated. Idyoblasts (Id): F=frequent; FF=few frequent. Central cells size (CCS): D=diferent size; S=similar size. Long measures are expressed in cm.

Taxa	pH	WRC	Salinity (mmhos)	C	o.m.	N	P	K	CIC	Sand	Mud	Clay	Texture	Sand		
														Thick	Middle	Thin
ALBA-PK	7.06	4.76	0.36	0.78	1.24	0.03	1.99	1.51	5.14	90.73	4.23	5.04	AR	41.75	36.89	12.09
AUST-GH	7.85	9.65	0.18	6.25	1.76	0.46	3.25	0.09	4.59	92.65	5.21	2.14	AR	53.57	30.37	8.71
AUST-WP	7.06	3.59	0.09	3.51	9.50	2.07	3.08	0.74	19.20	92.65	6.95	0.40	AR	42.90	36.04	13.71
AUST-WP	7.09	6.08	0.93	0.98	5.04	0.49	2.60	0.55	10.99	83.80	14.38	1.82	AR-F	30.34	47.06	6.40
BURC-HX	6.99	17.40	0.24	3.32	1.09	0.13	1.71	0.13	15.07	58.96	15.26	25.78	F-AC-AR	7.43	38.13	13.40
CAPE-HO	7.08	25.34	0.95	0.87	0.59	0.06	2.84	0.41	12.34	54.64	23.03	22.33	F-AC-AR	4.93	32.58	17.13
CIRC-SB	5.05	6.89	0.31	0.46	1.94	0.11	1.90	0.25	9.55	71.53	17.12	11.35	F-AR	18.73	43.18	9.62
CIRC-SB	6.68	5.12	0.27	0.68	1.21	0.08	1.82	1.37	5.33	84.61	9.56	5.83	AR-F	21.87	54.42	8.32
CUSP-CA	6.57	40.65	0.51	1.09	1.64	2.24	2.73	0.68	21.22	44.02	20.10	35.88	F-AC	5.55	26.50	11.97
DREG-PK	6.32	5.37	0.42	0.60	1.77	0.12	2.18	0.61	6.42	82.96	11.27	5.77	AR-F	16.95	49.26	16.75
EGHI-CI	7.84	7.73	0.31	1.86	1.23	0.31	2.71	0.31	6.55	87.57	4.25	8.18	AR-F	34.63	24.66	28.28
EGHI-PK	6.54	5.14	0.44	0.71	2.40	0.16	2.81	0.42	6.97	82.62	13.04	4.34	AR-F	52.61	17.63	12.38
HANT-CA	7.19	62.12	0.99	1.61	0.72	0.21	2.77	0.76	18.82	54.79	10.44	34.77	F-AC-AR	11.94	33.29	9.56
HENS-EK	8.49	5.96	1.27	1.80	0.40	0.28	1.96	0.75	3.69	77.94	16.28	5.78	AR-F	20.19	33.90	23.85
IRRO-EK	7.88	5.17	0.33	0.42	0.26	0.48	3.97	0.82	1.93	83.70	13.47	2.73	AR-F	24.29	40.79	18.62
IRRO-KA	7.69	6.98	0.64	2.07	0.40	0.25	2.23	0.80	4.42	80.48	12.28	7.24	AR-F	39.74	23.13	17.61
IRRO-KW	8.25	6.59	1.51	1.71	0.26	0.23	2.10	1.03	3.37	76.97	17.32	5.71	AR-F	22.25	33.18	21.54
PULC-CA	7.17	24.23	0.78	1.23	2.11	1.62	3.12	0.39	18.24	54.99	16.97	28.04	F-AC-AR	10.35	15.17	29.47
PULC-NI	6.57	36.71	0.32	1.04	1.08	1.89	2.86	0.40	18.03	40.98	27.27	31.75	F-AC	4.26	15.39	21.33
VILL-EK	8.23	14.10	0.89	6.64	0.53	0.49	4.08	0.11	4.97	61.88	30.25	7.87	F-AR	17.00	19.86	25.02
VILL-ST	6.54	9.08	0.48	1.15	1.08	0.10	2.07	0.19	10.21	69.81	14.11	16.08	F-AR	34.87	27.02	7.92
WALT-ST(1)	7.28	6.86	0.57	1.20	0.24	0.07	3.16	0.68	3.36	78.82	15.42	5.76	AR-F	45.31	21.37	12.14

**Table 3.-** Results from the edaphic analyses. WRC= water retention capacity (%). C= total carbonates (%). o.m.= organic material (%). N= mineral nitrogen (mg N/100g). P= assimilable phosphor (mg P<sub>2</sub> O<sub>5</sub>/100g). K= assimilable potassium (meq K/100g). CIC= cationic interchange capacity (meq/100g). The amounts of sand, mud and clay are expressed in %. Texture: F=Franco, AC=Clayey, AR=Sandy. <sup>(1)</sup> same data for population POEL-ST. Abbreviations of populations are described in Table 1.

studied showed leaves significantly longer than those of populations from the Karoo, a V-shaped section and central cells similar in size to the rest. *Androcymbium capense*, that exhibited a flat leaf section and whose central epidermic cells were larger than the rest was the only exception to this pattern (MEMBRIVES *et al.*, 2000b). Conversely, species distributed in the Karoo-Karoid types showed flat or semi-flat section (except for *A. bellum*, *A. dregei* and *A. eghimocymbion*), and central cells larger than the rest (except for *A. cuspidatum* and *A. dregei*).

b) Correlations between morphological-anatomical characteristics and edaphic parameters

Table 5 shows that only the edaphic characteristics related to soil texture showed significant correlations with most morphological variables studied. Leaf length and shape (length/width) were significantly correlated with the percentage of clay. Soils with a low percentage of clay were associated with long and lanceolate leaves, while soils with a high percentage of clay were associated with predominantly short and rounded leaves. Bract length was positively correlated with CIC, WRC and percentage of mud and clay, and negatively correlated with the percentage of sand. Leaf section was significantly correlated with WRC and percentage of clay and sand. Flat leaf sections were associated with soils with high WRC, while V-shaped sections were observed predominantly in low WRC soils. Leaf color (green or glaucous) and bract shape did not correlate significantly with any of the edaphic parameters analyzed.

The morphology of the epidermic cells on the adaxial face of the lamina was positively correlated with CIC, WRC, and with the percentage of clay. Romboidal and polygonal cell shapes were associated to soils with high CIC, WRC and percentage of clay, whereas rectangular cells were associated with more arid conditions. Adaxial side stomatic indices were significantly correlated only with the percentage of mud and in abaxial side were significantly correlated with percentage of sand, mud and clay. Presence of hairs in the leaf margin was positively correlated with CIC, WRC and the percentage of clay, and negatively correlated with the percentage of sand. Mesophyll cell types and the amount of idyoblasts on the leaves were not significantly correlated with any of the edaphic traits considered.

On the whole, the variability of some morphological and anatomical structures in genus *Androcymbium* was only associated with water disponibility (i.e., with the edaphic characteristics related to the percentage of clay and WRC). Species that grow in soils with low WRC and low percentage of clay were characterized by long and linear or linear-lanceolate leaves, rectangular epidermic cells, smooth or with papillae at margin, V-shaped leaf section, and short bracts. By contrast, species that occur in soils with high WRC and high percentage of clays were characterized by short and ovate leaves, romboidal or polygonal epidermic cells, pluricellular hairs at the leaf margin, flat leaf section and long bracts.

## DISCUSSION

Large amounts of variability in morphological and anatomical characteristics were described for Southwest African species of *Androcymbium*, reflecting the large variation detected in other variables (palynological, flower morphology,



allozymes or cpDNA RFLPs). By contrast, Northern African species of *Androcymbium* showed large variation in some anatomical leaf characteristics, despite the narrow morphological similarity (MATEU-ANDRÉS *et al.*, 1996).

Some morphological leaf characters of Southwestern African *Androcymbium* species seem to evolve associated only with the climatic and edaphic factors related to hydric disponibility (amounts and distribution of annual rainfall, and soil texture). The two veld types where the studied populations occur are characterized by different winter rainfall regimes. The Cape Region (dominated by a Fynbos vegetation) receives more than 250 mm/year (80 % in winter), while the Karoo area receives less than 300 mm/year (60 % in winter). *Androcymbium austrocapense*, *A. eghimocymbion*, and *A. capense* occur in the Cape Region and showed bigger leaf sizes than the rest of species that inhabit in Karoo-Karoid Regions (mean leaf length values are in Table 2). We detected a significant association between leaf length and veld types. Therefore, a possible explanation for the bigger leaf size in *Androcymbium* species from the Cape Region could be the higher winter rainfall in this area. The observation that Southeastern African species of *Androcymbium* (mainly *A. burkei*, *A. decipiens*, *A. leistneri*, *A. longipes*, and *A. natalense*) live in a regime of much higher winter rainfall and show a leaf size similar to species of the Fynbos Region agrees with our hypothesis.

Although we can rule out a direct relationship between leaf length and winter rainfall regime in *Androcymbium*, other leaf characteristics lend themselves to generalization and fit better theoretical predictions. Species of *Androcymbium* with a big leaf surface (ovato-lanceolate shape) inhabit in soils with a high percentage of clay, while species with little leaf surface (linear or linear-lanceolate shapes) inhabit in soils with low percentage of clay. Thus, there seems to be an association between leaf surface and soil's texture.

Morphological and anatomical characteristics	t	P
Leaf length	3.87**	0.001
Leaf shape (length/width)	0.38	0.707
Bract length	-0.54	0.591
Bract shape (length/width)	-0.57	0.574
Leaf section	2.33*	0.027
Indument at leaf margin	0.16	0.877
Epidermic cell shapes	-0.10	0.918
Stomatic index at adaxial face	1.51	0.142
Central cell sizes	2.66*	0.013
Mesophyll cell types	1.19	0.242
Frequency of leaf idioblasts	-1.33	0.193

**Table 4.** - Results of Student's t tests to contrast morphological and anatomical characteristics in species of *Androcymbium* from the Fynbos and the Karoo-Karoid vegetation types. \*\*, significant at the 0.01 level. \*, significant at the 0.05 level.

By contrast, bract shape is not significantly correlated with soil texture, and this might indicate that the characteristics of the bracts could be more influenced by other factors, probably related to pollination effectiveness. There is a close relation between levels of allozymic diversity and pollination effectiveness in self-incompatible species of *Androcymbium* (MEMBRIVES, 2000; MEMBRIVES *et al.*, in prep.). Previous studies suggested that bract colour and other characteristics related to the reproductive system (like nectar production and odour) were important to estimate the allozymic diversity in Southwestern African species of *Androcymbium*. For instance, *A. burchellii* subsp. *burchellii* (with white bracts) has less allozymic diversity than *A. burchellii* subsp. *pulchrum* (with red bracts), even though they have the same reproduction system. This could be an important insight to consider that bract characteristics are more conditioned to pollination effectivity than to environmental conditions.

V-shaped leaves, glaucous colour, and indument in leaf surface and margin are argued to represent an adaptive strategy to reduce the transpiration in Mediterranean plants. In close agreement, the V-shape of Southwestern African *Androcymbium* leaves was correlated with low WRC. Similarly, semi-flat shapes and leaf surfaces covered by waxes (glaucous leaf colour) in *Androcymbium* species from Namaqualand (Northern Karoo) could also represent an adaptation to the aridity in this area. Presence of pluricellular hairs in *Androcymbium* is associated with soils that exhibit a high percentage of clay and a high CIC, except for *A. cuspidatum* (that lives in high percentage of clay but shows a smooth margin). The presence of an indument in the leaf margin does not seem to be an adaptation to aridity in *Androcymbium*, because species with pluricellular hairs occur in clayey soils, which exhibit high WRC.

According to these observations, hydric disponibility is associated to some morphological and anatomical characteristics in *Androcymbium*. Recent allozymic diversity studies (MEMBRIVES *et al.*, in prep.) in these populations found that there is a significant correlation between the aridity gradation described in this region and the allozymic diversity levels. According to these analyses, the reproductive system is the variable that most influences allozymic variability in *Androcymbium*. When only self-compatible populations were considered, the genetic diversity levels in populations distributed in the Northern region of Southwestern Africa (where aridity is more severe) are lower than in Southern species. As the different levels of hydric disponibility in the diverse habitats of Southwestern Africa seem to influence the allozymic diversity levels, this edaphic trait could determine inter-specific differences in terms of evolutionary potential.

Southern African species of *Androcymbium* show a considerable heterogeneity in mesophyll cell types, which was also shown for their Northern African congeners (MATEU-ANDRÉS *et al.*, 1996). Given the strikingly contrasting climatic and edaphic characteristics between the arid regions in Northern and Southern Africa where the species of *Androcymbium* inhabit, the mesophyll types do not seem either an adaptative response to environmental differences or a characteristic of *Androcymbium*'s lineage.

	Edaphic parameters					Anatomical and morphological characteristics											
	CIC	WRC	sand	mud	clay	M	ID	Margin	L (l)	L/A (l)	L (b)	L/A (b)	Color	ECS	STAd	STAb	
WRC	0.710***																
Sand	-0.657**	-0.801***															
Mud	NS	NS	-0.745***														
Clay	0.770***	0.893***	-0.922***	0.428*													
M	NS	NS	NS	NS	NS												
ID	NS	NS	NS	NS	NS	NS											
Margin	0.621**	0.698***	-0.713***	NS	0.769***	0.495*	NS										
L (l)	NS	NS	0.460*	NS	-0.424*	NS	0.425*	NS									
L/A (l)	NS	NS	0.436*	NS	-0.455*	NS	-0.530*	NS	NS								
L (b)	0.425*	0.663**	-0.659**	0.504*	0.599**	NS	NS	0.576**	NS	NS							
L/A (b)	NS	NS	NS	NS	NS	NS	-0.506*	NS	NS	0.594**	NS						
Color	NS	NS	NS	NS	NS	-0.449*	NS	NS	NS	0.427*	NS	NS					
ECS	0.495*	0.476*	NS	NS	0.447*	0.753***	NS	0.677**	NS	-0.441*	NS	NS	NS				
STAd	NS	NS	NS	-0.465*	NS	NS	NS	NS	NS	NS	NS	NS	-0.567**	NS			
STAb	NS	NS	0.449*	-0.456*	0.584*	NS	NS	NS	NS	NS	NS	NS	-0.658**	NS	0.796***		
Section	NS	-0.525*	0.695***	-0.547**	-0.623**	NS	NS	-0.539*	0.543**	0.544**	NS	NS	NS	NS	NS	NS	

**Table 5.** Pearson's correlations for morphological, anatomical, and edaphic characteristics. CIC=Cationic interchange capacity. WRC= Water retention capacity. M=Mesophyll types. ID=idyoblasts. Margin= Presence/absence of pluricellular hairs. L (l) and L/A (l)= length and shape of first leaf. L (b) and L/A (b)= length and shape of first bract. ECS: Epidermic cells shape at adaxial face. STAd and STAb=Stomatic indexes at adaxial and abaxial side. NS=not significant. \*, signification level at 0.05; \*\*, signification level at 0.01; \*\*\*, signification level at 0.001.

## CONCLUSION

Because only the characteristics associated with aridity showed a clear relationship to leaf variability in *Androcymbium*, our results agree only partially with the suggestion that the edaphic heterogeneity described in Southwest Africa is the main cause to explain the high specific diversity in this region (AXELROD & RAVEN, 1978). Some other morphological and anatomical characteristics are correlated with veld type or water disponibility. The four populations studied that occur in the Fynbos showed longer leaves with a V-shaped section, except for *A. capense*, which showed a flat leaf section. Conversely, species that inhabit the Karoo-Karoid types, showed shorter leaves, mainly flat or semi-flat in section, except for *A. bellum*, *A. dregei* and *A. eghimocymbion*, with a V-shaped section. Some morphological and anatomical structures were correlated with soil texture in *Androcymbium*. Species with short ovate leaves, polygonal or rounded epidermic cells, pluricellular hairs at the leaf margin, flat section, and long bracts occur in soils with high WRC. On the other side, species with long and linear or linear-lanceolate leaves, rectangular epidermic cells, smooth or papillae margin, V-shaped section, and short bracts inhabit soils with low WRC. The hydric gradient correlates to allozymic variability levels in *Androcymbium* in much the same way as it influences some morphological and anatomical characteristics. Species that occur in the Northern region of Southwestern Africa showed lower morphological and genetic variability values than species distributed in the Southern region and this could be associated with different evolutionary potentials.

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