

# Pollen morphology and biometry of the genus *Androcymbium* (Colchicaceae) in southern Africa: taxonomic and biogeographic considerations

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## ABSTRACT

Pollen characters in 16 southern African type specimens of *Androcymbium* Willd. that represent the three sections into which the genus is presently divided (*Androcymbium*, *Dregeocymbium* and *Erythrostickus*), were examined to assess the possibility of sectional characterization based on pollen traits and to explore the relationship between pollen traits and geographic species distribution. Differences in pollen grain size, shape, number of apertures and exine pattern, were observed. Principal Component Analysis, using both qualitative and biometric pollen characters, distinguished four groups of species with four different pollen types. Most of the species have a microreticulate exine pattern with either diaperturate or triaperturate grains. The remaining species have either a rugulate exine pattern with diaperturate grains, or a rugulate-reticulate exine pattern with thickened (hypertrophied) muri with diaperturate grains. While section *Dregeocymbium* can be well delimited by the unique thickened muri, and by a significantly larger grain size, no diagnostic pollen traits were found for sections *Androcymbium* and *Erythrostickus*. Similarly, although the six northern African species exhibit a microreticulate exine pattern, the high variability observed for this trait in their southern African counterparts, does not follow a geographic pattern.

## INTRODUCTION

The genus *Androcymbium* Willd. (Colchicaceae) comprises ± 50 species (Müller-Doblies & Müller-Doblies 1984, 1990, 1998; Arnold & De Wet 1993; Pedrola-Monfort *et al.* 1999a, b, in press) whose distribution (Figure 1) 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). *Androcymbium* is the only member of the tribe Colchiceae together with *Colchicum* L. *sensu lato* (i.e. including *Bulbocodium* L., *Merendera* Ram. and *Synsiphon* Regel). At present, the genus is divided into three sections based on tepal blade morphology (Krause 1921): section *Androcymbium*, characterized by green, curved, winged tepal blades, with representatives throughout southern Africa; section *Dregeocymbium*, possessing flat, unwinged tepals and very short stamens and styles, with representatives in western southern Africa; and section *Erythrostickus*, featuring white, unwinged tepal blades, with representatives in southern Africa, the Mediterranean area and the Canary Islands. However, these differential morphological traits are currently considered irrelevant (Müller-Doblies & Müller-

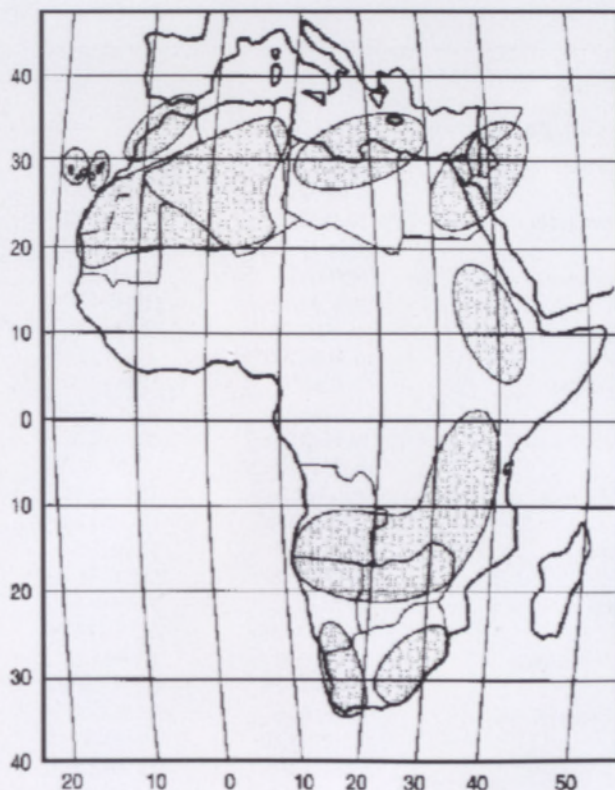


FIGURE 1.—Distribution of the genus *Androcymbium*.

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Doblies 1990, 1998; Pedrola-Monfort 1993) and, consequently, of little taxonomic value. A previous taxonomic study based on pollen morphological characters of 11 *Androcymbium* species representing the sections *Erythrostickus* and *Androcymbium* (Martín *et al.* 1993),



TABLE 1.—Herbarium specimens of *Androcymbium* studied in South Africa. Abbreviations of the herbariums follow Holmgren *et al.* (1990)

Species	Province	Collector and herbarium
Section <i>Androcymbium</i>		
<i>albomarginatum</i> Schinz (holo. <i>A. schlechteri</i> K.Krause)	NC	<i>Schlechter 11081</i> (B)
<i>burchellii</i> Baker subsp. <i>pulchrum</i> (Baker) Pedrola, Membrives, J.M.Monts. & Caujapé (holo. <i>A. pulchrum</i> Schltr. & K.Krause)	NC	<i>Schlechter 10953</i> (B)
<i>ciliolatum</i> Schltr. & K.Krause	WC	<i>Schlechter 8409</i> (B)
<i>circinatum</i> Baker (iso. <i>A. guttatum</i> Schltr. & K.Krause)	NC	<i>Schlechter 11280</i> (B)
<i>crispum</i> Schinz (holo. <i>A. pritzelianum</i> Diels)	NC	<i>Diels 701</i> (MO)
<i>decipiens</i> N.E.Br.	KZN	<i>Rich 5764</i> (NH)
<i>hantamense</i> Engl.	NC	<i>Meyer 1869</i> (B)
<i>henssenianum</i> U.Müll.-Doblies & D.Müll.-Doblies	NC	<i>U. &amp; D. Müller-Doblies 79177a</i> (B)
<i>irroratum</i> Schltr. & K.Krause	WC	<i>Schlechter 8016</i> (B)
<i>natalense</i> Baker	KZN	<i>Movd 200</i> (NH)
<i>scabromarginatum</i> Schltr. & K.Krause	NC	<i>Schlechter 11188</i> (B)
<i>villosum</i> U.Müll.-Doblies & D.Müll.-Doblies	NC	<i>U. &amp; D. Müller-Doblies 80081j</i> (B)
<i>volutare</i> Burch.	NC	<i>Hanekon 2413</i> (K)
Section <i>Dregeocymbium</i>		
<i>dregei</i> C.Presl	NC	<i>Baker 2705</i> (B)
<i>exiguum</i> Roessler subsp. <i>vogelii</i> U.Müll.-Doblies & D.Müll.-Doblies	NC	<i>U. &amp; D. Müller-Doblies 79173a</i> (B)
Section <i>Erythrostickus</i>		
<i>cruciatum</i> U.Müll.-Doblies & D.Müll.-Doblies	NC	<i>U. &amp; D. Müller-Doblies 80099n</i> (B)

KZN, KwaZulu-Natal; NC, Northern Cape; WC, Western Cape.

TABLE 2.—Morphological and biometrical pollen characters of *Androcymbium* species. Values correspond to the mean  $\pm$  standard deviations. Numbers in parenthesis are the minimum and maximum values of each parameter

Species	P	E1	E2	P/E1 ratio	Ap	Exine pattern
<i>albomarginatum</i>	9.97 $\pm$ 1.38 (7.00-13.44)	14.98 $\pm$ 1.88 (11.59-18.23)	11.08 $\pm$ 1.44 (8.51-13.56)	0.67	3	MR
<i>burchellii</i> subsp. <i>pulchrum</i>	10.19 $\pm$ 1.37 (8.20-13.35)	17.88 $\pm$ 1.80 (12.82-20.30)	12.53 $\pm$ 2.02 (7.58-15.72)	0.57	2	MR
<i>ciliolatum</i>	9.69 $\pm$ 3.24 (5.02-14.10)	16.14 $\pm$ 3.51 (10.43-22.76)	11.52 $\pm$ 0.70 (10.78-13.39)	0.59	3	MR
<i>circinatum</i>	10.97 $\pm$ 1.28 (8.34-12.82)	16.95 $\pm$ 1.86 (14.88-21.15)	10.39 $\pm$ 1.07 (8.84-12.11)	0.65	3	MR
<i>crispum</i>	10.42 $\pm$ 1.31 (7.98-12.35)	17.00 $\pm$ 2.20 (13.82-21.12)	12.73 $\pm$ 1.78 (9.51-15.15)	0.62	2	MR
<i>cruciatum</i>	10.16 $\pm$ 2.50 (6.89-14.25)	20.13 $\pm$ 2.38 (14.91-24.77)	11.69 $\pm$ 0.80 (9.99-12.93)	0.50	2	MR
<i>decipiens</i>	19.13 $\pm$ 2.76 (15.92-23.23)	26.06 $\pm$ 3.44 (18.90-32.07)	18.90 $\pm$ 2.21 (16.07-22.28)	0.74	2	R
<i>dregei</i>	22.58 $\pm$ 2.17 (18.63-26.67)	31.20 $\pm$ 3.28 (23.37-35.36)	23.03 $\pm$ 0.0 (23.03)	0.73	2	RA
<i>exiguum</i> subsp. <i>vogelii</i>	29.61 $\pm$ 2.01 (25.84-36.86)	37.14 $\pm$ 0.85 (35.54-39.78)	35.23 $\pm$ 3.14 (24.34-42.97)	0.79	2	RA
<i>hantamense</i>	13.51 $\pm$ 0.79 (11.56-15.88)	18.99 $\pm$ 1.02 (15.93-22.67)	17.62 $\pm$ 1.42 (11.27-20.01)	0.71	3	MR
<i>henssenianum</i>	19.16 $\pm$ 5.00 (12.75-27.49)	25.66 $\pm$ 3.97 (19.30-30.71)	18.02 $\pm$ 3.39 (12.85-23.56)	0.74	2	R
<i>irroratum</i>	10.62 $\pm$ 1.87 (7.37-13.34)	18.80 $\pm$ 2.58 (13.83-24.68)	12.59 $\pm$ 3.17 (7.63-18.38)	0.57	3	MR
<i>natalense</i>	17.83 $\pm$ 2.18 (15.37-22.80)	24.96 $\pm$ 4.30 (15.67-34.28)	18.84 $\pm$ 2.87 (13.76-23.83)	0.73	2	R
<i>scabromarginatum</i>	10.04 $\pm$ 3.13 (5.76-16.57)	14.65 $\pm$ 2.82 (9.34-20.91)	9.70 $\pm$ 1.80 (7.94-15.37)	0.69	3	MR
<i>villosum</i>	9.12 $\pm$ 1.64 (4.12-11.63)	14.87 $\pm$ 1.73 (12.66-20.55)	9.85 $\pm$ 1.12 (7.59-11.43)	0.62	3	MR
<i>volutare</i>	8.60 $\pm$ 1.31 (6.01-11.16)	14.43 $\pm$ 1.93 (11.66-19.51)	8.93 $\pm$ 0.80 (7.21-10.10)	0.60	2	MR

Ap, no. apertures; E1, equatorial long axis; E2, equatorial short axis; MR, microreticulate; P, polar axis; R, rugulate; RA, rugulate-reticulate with thickened (hypertrophied) muri.



offered four important insights. Firstly, there is no single pollen character that separates the two sections. Secondly, a microreticulate exine pattern was observed in all but the Canary Island species, *A. psammophilum* Svent., which has a rugulate exine pattern. Thirdly, whereas the pollen in section *Erythrodictus* is always diaperturate, both di- and triaperturate forms co-exist within section *Androcymbium*. And lastly, the pollen size of the western southern African *A. bellum*, that was historically ascribed to section *Erythrodictus*, fits the range of values observed for the species in section *Androcymbium*.

Given the variability in pollen traits noted in that survey, we undertook the analysis of all the measurable pollen characters, the number of apertures and the exine patterning in a broader geographic representation of the genus. The aims of this study are to assess whether there might be traits of diagnostic value for the three sections of the genus currently recognized and to examine the relationship between pollen morphology and geographic distribution.

#### MATERIAL AND METHODS

Sixteen type specimens of *Androcymbium* were examined (Table 1), representing southern African species housed in the Museum Botanicum Berlinense (B), Royal Botanic Gardens, Kew (K), and Natal Herbarium (NH).

Pollen was extracted from the anthers with a drop of alcohol (96%) and then acetolysed according to the Avetissian micromethod (Avetissian 1950). For the biometric study, pollen grains were mounted in glycerol jelly and measured with the image analyser IMAT at the facilities of the Serveis Científico-Tècnics of Barcelona University.

The four biometric characters used (Table 2), follow Erdtman (1969) and Reitsma (1970). The arithmetical mean, standard deviation, and maximum and minimum values were calculated after 15 measurements for each parameter (Table 2) using the SPSS/PC+ program (SPSS 1984). Exine patterning and the number of apertures were determined with the aid of a scanning electron microscope (SEM). The pollen was first mounted onto SEM stubs and then coated with gold in a diode sputter-coater. The stubs were observed using a Hitachi 52300 electron microscope at 15 kv at the facilities of the Serveis Científico-Tècnics of Barcelona University.

A test of comparison of means was conducted using the program SPSS/PC+ (SPSS 1984) to assess the possible relationship between the pollen parameters considered. Principal component analysis (PCA) was conducted using the program NTSYS-PC (Rohlf 1992) to visualize the relationships among the studied species based on pollen data. For this multivariate analysis, four continuous quantitative characters (P, E1, E2 and P/E1 ratio), one discrete quantitative character (aperture number) and one qualitative character (exine patterning) were included. The latter was coded as: 1 = microreticulate, 2 = rugulate, or 3 = rugulate-reticulate with thickened

(hypertrophied) muri. We used the arithmetical mean values of quantitative characters across species to build a  $6 \times 16$  data matrix that was standardized and used to calculate the correlation matrix after which the principal components were derived.

#### RESULTS

*General morphology:* the pollen of *Androcymbium* is heteropolar, planoconvex in equatorial view and elliptic in polar view, with bilateral symmetry. This pollen morphology is typical of the Colchicaceae (Erdtman 1952, 1969; Díez 1987; Díez *et al.* 1985; Martín *et al.* 1993). The values of P, E1, E2 and P/E1 ratio are summarized in Table 2. The smallest pollen is produced by *A. volutare*,  $8.60 \times 14.43 \times 8.93 \mu\text{m}$ , and the largest by *A. exiguum* subsp. *vogelii*,  $29.61 \times 37.14 \times 35.23 \mu\text{m}$ . The pollen grains of the *Androcymbium* species examined are considerably smaller than those of the closely related genera *Colchicum* L. and *Merendera* Ram. (Erdtman 1952, 1969; Faegri & Iversen 1975; Díez 1987; Díez *et al.* 1985).

Among the species studied, the most frequent pollen shape is oblate ( $0.5 < P/E1 < 0.69$ ) and found in *A. albomarginatum*, *A. burchellii* subsp. *pulchrum*, *A. ciliolatum*, *A. circinatum*, *A. crispum*, *A. irroratum*, *A. scabromarginatum*, *A. villosum*, and *A. volutare*. However, the grains of *A. cruciatum* tended to be peroblate ( $P/E1 = 0.5$ ), and those of *A. dregei*, *A. decipiens*, *A. hantamense*, *A. henssenianum*, *A. natalense*, and *A. exiguum* subsp. *vogelii* are suboblate ( $0.70 < P/E1 < 0.79$ ).

*Apertural system:* *Androcymbium*'s pollen apertures are circular or elliptic pores. Seven of the species examined (Table 2) are two-zonoporate, anaporate with two pores either in zonal or in presumed equatorial position and the third in distal position (Figure 2A). The remaining nine species are two-zonoporate (two pores in zonal position, Figure 2C, E, G). We have not studied the tetrad of pollen grains in *Androcymbium*, but the position of the pollen grains in the tetrad was well studied in the closely related genus *Colchicum* (Béguin & Huynh 1978).

*Exine patterning:* three different exine patterns were observed among the species of *Androcymbium* analysed: 1, microreticulate (Figure 2A–D; Table 2), with the lumina less than  $1 \mu\text{m}$  diameter, observed in *A. albomarginatum*, *A. burchellii* subsp. *pulchrum*, *A. ciliolatum*, *A. circinatum*, *A. crispum*, *A. cruciatum*, *A. hantamense*, *A. irroratum*, *A. scabromarginatum*, *A. villosum*, and *A. volutare*; 2, rugulate (Figure 2E, F), observed in *A. decipiens*, *A. henssenianum*, and *A. natalense*; and 3, rugulate-reticulate with thickened (hypertrophied) muri (Figure 2G, H) and lumina's diameter higher than  $1 \mu\text{m}$ , observed in *A. dregei* and *A. exiguum* subsp. *vogelii*. Pollen terminology follows Blackmore *et al.* (1992).

*Comparison of means:* the ANOVA test revealed significant differences among species only in terms of the number of pores and pollen grain size, with diaperturate pollen tending to be larger than triaperturate pollen. Furthermore, there are significant differences in the values of P, E1, E2 and P/E1 ratio for the exine patterning.



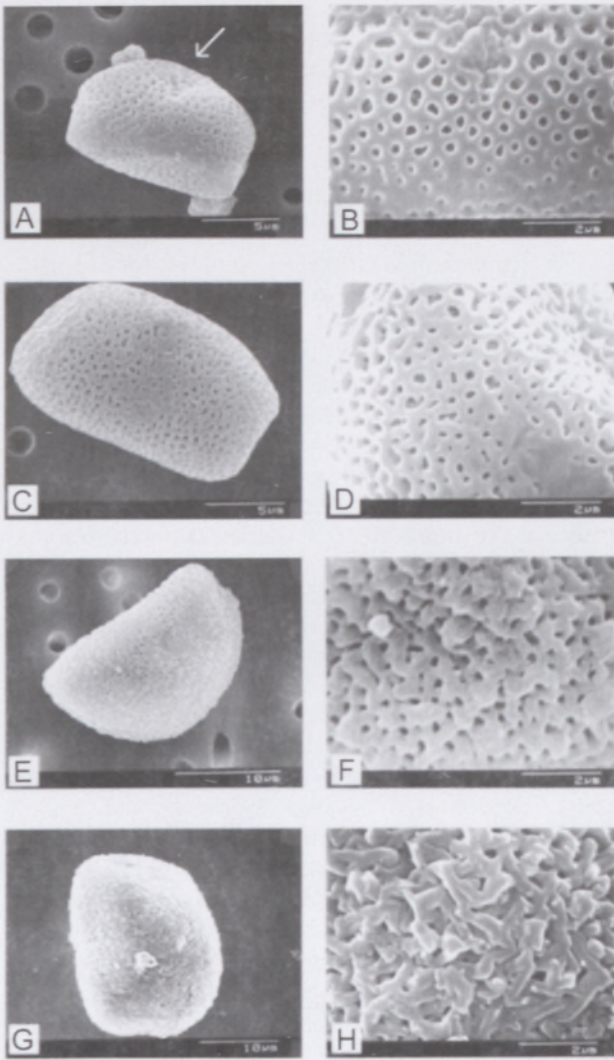


FIGURE 2.—Scanning electron micrographs showing the four pollen types of *Androcymbium* observed. A, B, *A. scabromarginatum*, Type 1: triaperturate microreticulate, arrow points to third aperture. C, D, *A. cruciatum*, Type 2: diaperturate microreticulate. E, F, *A. henssenianum*, Type 3: diaperturate rugulate. G, H, *A. exiguum* subsp. *vogelii*, Type 4: diaperturate rugulate-reticulate with thickened (hypertrophied) muri.

TABLE 3.—Values of first and second principal components from multivariate analysis of pollen characters studied

Character	Principal component	
	First	Second
P	0.994	0.076
E1	0.978	-0.067
E2	0.958	0.080
Exine pattern	0.971	-0.011
P/E1 ratio	0.785	0.476
No. apertures	-0.571	0.787

E1, equatorial long axis; E2, equatorial short axis; P, polar axis

with rugulate and rugulate-reticulate grains with thickened (hypertrophied) muri, larger than microreticulate pollen grains.

*Principal component analysis:* the first and second principal components (Table 3) explain 93.5% of the variance of the sample, 79.1% for the first component—Factor 1; and 14.4% for the second—Factor 2. Whereas the former is mainly determined by the biometric characters and the exine pattern (P, E1, exine patterning, E2 and P/E ratio, in order of importance), the latter is most influenced by the number of apertures. The relationships among species according to this analysis are represented in a two-dimensional graph (Figure 3).

The results of the PCA indicate four groups of species with different pollen types:

Type 1: triaperturate (two-zonoporate anaportate), microreticulate (Figure 2A, B), found in *A. albomarginatum*, *A. ciliolatum*, *A. circinatum*, *A. hantamense*, *A. irroratum*, *A. scabromarginatum*, and *A. villosum* (section *Androcymbium*);

Type 2: diaperturate (two-zonoporate), microreticulate (Figure 2C, D), observed in *A. crispum*, *A. burchellii* subsp. *pulchrum* and *A. volutare* (section *Androcymbium*) and in *A. cruciatum* (section *Erythrostickus*);

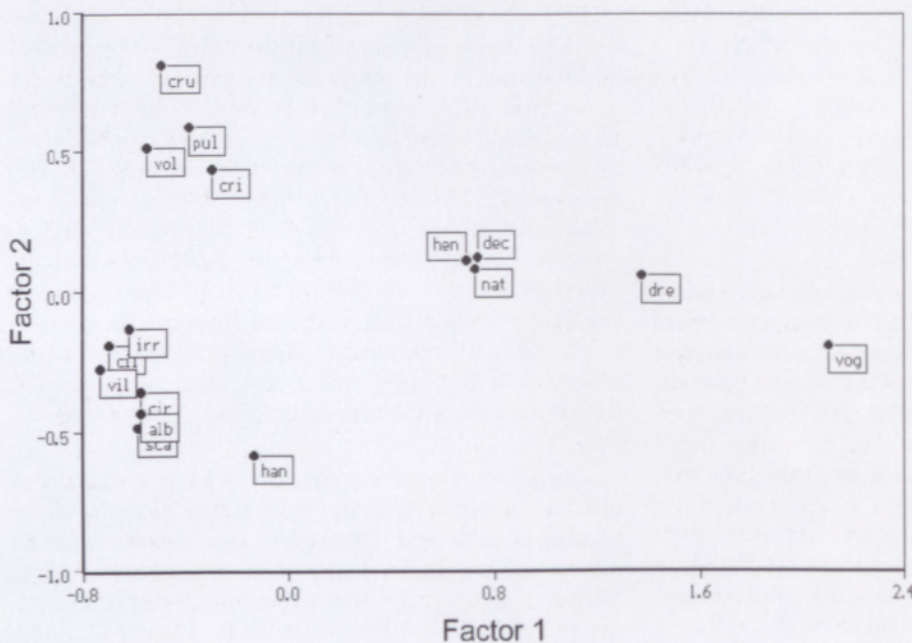


FIGURE 3.—Two-dimensional graph representing species in the PCA. Variance of sample is 93.5 % (79.1 % for factor 1, and 14.4 % for factor 2). Names of spp. abbreviated with first three letters of epithet. Distribution of spp. indicates four pollen types. Type 1: in left lower part, *A. albomarginatum*, *A. ciliolatum*, *A. circinatum*, *A. hantamense*, *A. irroratum*, *A. scabromarginatum*, *A. villosum*. Type 2: in left upper part: *A. crispum*, *A. burchellii* subsp. *pulchrum*, *A. volutare*, *A. cruciatum*. Type 3: central: *A. decipiens*, *A. henssenianum*, *A. natalense*. Type 4: on right, *A. dregei*, *A. exiguum* subsp. *vogelii*.



Type 3: diaperturate (two-zonoporate) rugulate (Figure 2E, F), observed in *A. decipiens*, *A. henssenianum*, and *A. natalense* (section *Androcymbium*);

Type 4: diaperturate (two-zonoporate), rugulate-reticulate with thickened (hypertrophied) muri (Figure 2G, H), found in *A. dregei* and *A. exiguum* subsp. *vogelii* (section *Dregeocymbium*).

## DISCUSSION

### Taxonomic implications

According to our results, the southern African species of *Androcymbium* contain most of the diversity of pollen types described for the entire genus (Figure 2). The most common exine patterning observed in this geographical region is microreticulate (Figure 2A–D) and was found both in species from section *Androcymbium* and in section *Erythrodictus* (*A. cruciatum* in Müller-Doblies & Müller-Doblies 1984). Although all the species with triaperturate pollen (Type 1) are in section *Androcymbium*, this fact is of very limited taxonomic value, since roughly half of the species within this section exhibit diaperturate pollen (Types 2 and 3) and pollen Type 2 was also observed in most of the North African *Androcymbium* species (section *Erythrodictus*) by Martín *et al.* (1993).

The diversity of pollen shape notwithstanding, two additional facts hinder an unambiguous sectional characterization in the genus *Androcymbium*. Firstly, the pollen of the taxa within section *Androcymbium* (*A. burchellii* subsp. *pulchrum*, *A. crispum* and *A. volutare*) is indistinguishable from that of *A. cruciatum*, which belongs to section *Erythrodictus*. Secondly, the rugulate exine patterning (Type 3; Figure 2E, F) observed in *A. decipiens*, *A. henssenianum* and *A. natalense* (section *Androcymbium*) was also found in the Canary Island *A. psammophilum*, which belongs to section *Erythrodictus* (Martín *et al.* 1993). However, the relevance of the latter observation is only minor because, unlike *A. decipiens*, *A. henssenianum*, and *A. natalense*, the structural elements of *A. psammophilum* are always less than 1 µm in diameter and might be considered as a different pollen pattern.

By contrast, the pollen of the constituents of section *Dregeocymbium*, *A. dregei* and *A. exiguum* subsp. *vogelii*, can be unambiguously characterized in terms of two traits: a significantly larger grain size and a rugulate exine pattern (Type 4, Figure 2G, H).

Section *Androcymbium* embraces a diverse array of pollen types, including either microreticulate or rugulate exine patterning, and di- or triaperturate pollen grains. Species from section *Erythrodictus* have microreticulate exine patterning and diaperturate pollen grains, and share these features with some of the species of section *Androcymbium*.

### Biogeographic and evolutionary implications

A microreticulate exine pattern is a general feature of species in the families Liliaceae and Colchicaceae

(Erdtman 1952, 1969; Valdés 1978; Díez 1987; Díez *et al.* 1985) and is considered to be the plesiomorphic condition for the Liliales (Goldblatt 1990; Goldblatt & Henrich 1991). Although the species of *Androcymbium* that have a microreticulate exine pattern (Type 1 and 2) occur in two of the three broad areas of distribution of the genus (western southern Africa and North Africa), we cannot assert that this feature is represented in all areas of distribution until the study of some species from eastern southern Africa (mainly those within the *Androcymbium melanthioides* complex) is completed.

By contrast, rugulate forms (Type 3) are considered evolutionarily recent and have been observed both in western southern African (*A. henssenianum*) and eastern southern African species (*A. decipiens* and *A. natalense*). Rugulate-reticulate exine pattern with thickened (hypertrophied) muri can also be considered evolutionarily recent and is present only in the western southern African species *A. dregei* and *A. exiguum* subsp. *vogelii* (section *Dregeocymbium*). Thus, available evidence indicates that more recent exine pattern types are exclusive to southern African species, whereas plesiomorphic forms occur both in this region and in northern Africa. However, our survey failed to detect a geographic pattern in the genus, because southern African species exhibit a high variability of exine patterning.

The pollen of the tribe Colchiceae is generally characterized by two, three or four apertures (Erdtman 1952, 1969; Díez 1987; Díez *et al.* 1985), although four apertures have been reported much less frequently (Dahlgren *et al.* 1985). Where the pollen grains are triaperturate, the two equatorially positioned apertures are pores, whereas the third one, situated at the distal pole, is an ulcus (Erdtman 1952, 1969). The dichotomy observed in terms of number of apertures in *Androcymbium* has evolutionary implications. As a rule, the monosulcate aperture is considered the most primitive in the monocotyledons (Nair 1970; Goldblatt 1990; Goldblatt *et al.* 1991). Some authors argue that the porate apertural system derives from a reduction of the aperture zone, and the triaperturate form represents a transition from monosulcate to two-zonoporate (Thanikaimoni 1986; Takhtajan 1991). Given that species of *Androcymbium* having triaperturate pollen occur only in western southern Africa, our data support the hypothesis that this area might be the ancestral area of distribution of the genus (Margelí *et al.* 1999; Caujapé-Castells *et al.* 1999, 2001). However, this conclusion must be complemented with the pollen morphological survey of the species of *Androcymbium* distributed in eastern southern Africa that could not be included in this work.

## CONCLUSIONS

Although our results suggest a general trend towards parallel evolution of pollen size and structural complexity of exine pattern in *Androcymbium*, they do not indicate a relationship between pollen morphology and geographic distribution. Species with pollen Type 2 (microreticulate exine pattern with diaperturate apertural system) are ubiquitous and occur throughout the range of the genus. The presence of the third aperture in the distal



position in triaperturate pollen, which has been considered by previous authors to be more primitive than the diaperturate condition, was observed only in western southern African species of *Androcymbium*. Pending the survey of some of the eastern southern African species that could not be included in this work, this result enforces the hypothesis that western southern Africa is the ancestral area of distribution for the genus. The pollen characteristics only reflect the currently accepted sectional subdivision of the genus in the two species of section *Dregeocymbium*. These results prompt a thorough re-examination of macromorphological characters in *Androcymbium* to assess whether the present sectional classification should be modified.

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