

MORPHOLOGICAL SEED STUDIES OF SOUTHWEST AFRICAN *ANDROCYMBIUM* (COLCHICACEAE)

NÚRIA MEMBRIVES¹, JOAN PEDROLA -MONFORT¹ & JULI CAUJAPÉ-CASTELLS²

¹ Estació Internacional de Biologia Mediterrània-Jardí Botànic Marimurtra. Passeig Karl Faust, 10. 17300 - Blanes. Girona. Apdo. Correos 112. España (nuriamem@jazzfree.com; jpedrola@grn.es).

² Jardín Botánico Canario «Viera y Clavijo». Apdo. 14 de Tarifa Alta. 35017 Las Palmas de Gran Canaria, islas Canarias. España (julicaujape@granca.step.es).

Recibido: Agosto 2000.

Palabras clave: *Androcymbium*, Colchicaceae, morfología seminal, filogenia, África.

Key words: *Androcymbium*, Colchicaceae, seed morphology, phylogeny, Africa.

SUMMARY

Macromorphological and micromorphological seed characteristics are described in 32 populations belonging to 19 taxa of the genus *Androcymbium* distributed in Southwest Africa. The heterogeneity shown in the seed characteristics in Southwest African species is compared with the uniformity described previously in the Northern African congeners. The principal seed characteristics are evaluated in the taxonomic classification of the genus, and their evolution is considered under a recent cladistic analysis from morphological data. According to this phylogeny, all seed characters studied show complex patterns of parallelisms and reversals in the evolution of the genus.

RESUMEN

Se describen las características macromorfológicas y micromorfológicas de las semillas de 32 poblaciones pertenecientes a 19 taxones del género *Androcymbium* distribuidas en Sudáfrica Occidental. La heterogeneidad observada en las características seminales en las especies sudafricanas se compara con la uniformidad descrita previamente en los congéneres norteafricanos. Las principales características seminales se evalúan en la clasificación taxonómica del género y la evolución de estos caracteres se analiza en un reciente análisis cladista a partir de datos morfológicos. Según esta filogenia, todos los caracteres seminales estudiados presentan complejos patrones de paralelismos y reversiones en la evolución del género.

INTRODUCTION

The genus *Androcymbium* Willd. (Colchicaceae) is represented by about 50 species (ARNOLD & WET, 1993; MÜLLER-DOBLIES & MÜLLER-DOBLIES, 1998; PEDROLA-MONFORT *et al.*, 1999a, 1999b, 2000) with a disjunct distribution in Africa (Fig. 1A). The genus has been historically divided into three sections: *Androcymbium*, *Erythrostictus*, and *Dregeocymbium* (KRAUSE, 1920). Most of the species belong to section *Androcymbium* and are distributed in South Africa, either in the western (about 40 species) and in the eastern (seven species) region. Only two species are ascribed to section *Dregeocymbium* (*A. dregei* and *A. exiguum*). These distribute in Southwest Africa and Namibia. Seven species belong to section *Erythrostictus* and occur mainly in Northern Africa (four in the Mediterranean basin and two in the Canary Islands), and only one of them (*A. roseum*), occurs in Southern Africa. MÜLLER-DOBLIES & MÜLLER-DOBLIES (1998) published a new supraspecific classification of section *Androcymbium* where they propose its segregation into two subsections with eight series and four subseries. Recently, MEMBRIVES (2000) proposes a new generic classification under phylogenetic tenets based on the cladistic analysis of morphological and reproductive traits.

Given that seed morphology has been shown to be a conservative character in many plant species (DAVIS & HEYWOOD, 1963), it is generally inferred that it bears taxonomic value (STEBBINS, 1974; STuessy, 1990). Within the Colchicaceae, variability in seed size, colour, caruncula presence and in the microstructure of the external layer has been reported in some genera (BUXBAUM, 1936; NORDERSTAM, 1982; PEDROLA-MONFORT, 1993). In *Ornithoglossum*, the microstructure of the external layer is of proven taxonomic usefulness (NORDERSTAM, 1982). Previous surveys in the genus *Androcymbium* allowed species differentiation based on seed size alone (GREUTER, 1967; ROESSLER, 1974; SANTOS, 1977; REIFERBERGER, 1990; PEDROLA-MONFORT, 1993). Within section *Erythrostictus*, the shape of the cells of the internal layer showed inter-specific variability, with the Northern African *A. wysianum* and the Southern African *A. roseum* displaying rectangular cells, and the rest of species showing quadrangular cells (PEDROLA-MONFORT, 1993).

Our objectives are, first, to describe seed morphology and biometry in a broad representation of *Androcymbium* species distributed in Southwest Africa (Fig. 1B) in order to assess their value for taxonomic classification within the genus. And second, to assess the evolution of these traits in the frame of a recent cladistic analysis based on morphological data.

MATERIALS AND METHODS

We sampled 32 populations representing 19 taxa of genus *Androcymbium* distributed in Southwest Africa (Appendix 1; Fig. 1B), and the six species from Northern Africa already studied by PEDROLA-MONFORT (1993). Seeds were obtained from plants grown in culture except from those belonging to *A. cruciatum* and *A. volutare* which correspond to herbarium specimens (U. Müll-Doblies & D. Müll.-Doblies 80099n -Botanischer Garten und Botanisches Museum Berlin-

Dahlem- for *A. cruciatum*, and P. Goldblatt 6238 -Royal Botanic Garden, Kew- for *A. volutare*).

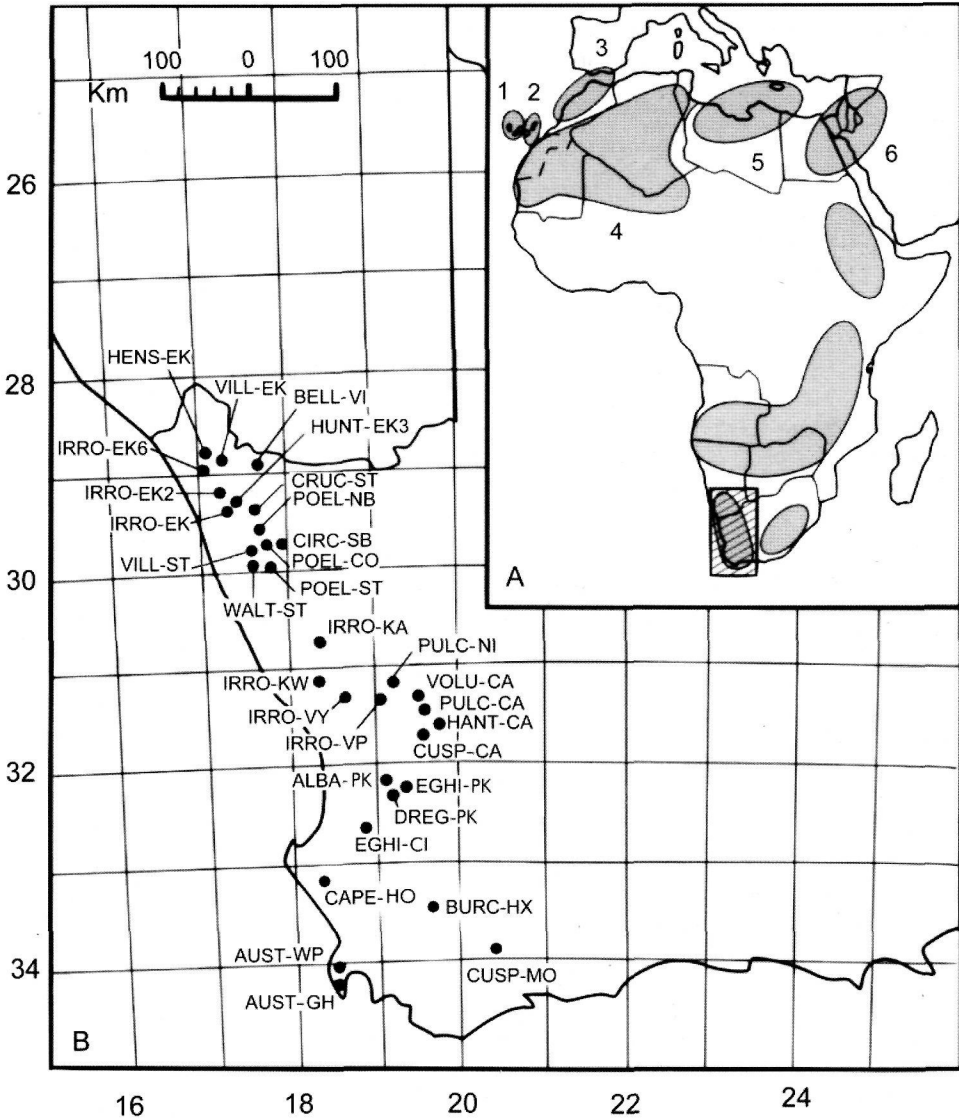


Figure 1.- A. Geographic distribution of genus *Androcymbium*. The numbers show the distribution of Northern African species (1: *A. hierrense*; 2: *A. psammophilum*; 3: *A. gramineum*; 4: *A. wyssianum*; 5: *A. rechingerii*; 6: *A. palaestinum*). B. Geographic distribution of the Southwest African populations studied. The abbreviations of the Southwest African populations are described in Appendix 1.

Macromorphological traits.- Following previous studies within the Colchicaceae (NORDERSTAM, 1982; PEDROLA-MONFORT, 1993), we studied seed shape, diameter, colour, and caruncula presence/absence. Morphological observations and biometrical measurements were carried out in a binocular lens. Seed diameter was obtained by pooling 50 measurements of each of five individuals per population.

Micromorphological traits.- The seeds of the species of genus *Androcymbium* show two different layers that wrap the endosperm and form the testa (PEDROLA-MONFORT, 1993). Accordingly, the micromorphological descriptions of the seeds considered both the external and the internal layers. To observe the internal layer, the seeds were boiled during 10-15' and then the external cell layer was removed using a nail. Then, seeds were subjected to ultrasonic waves to remove cellular remains of the external layer. The studied traits were the shape of the cells in both layers. Observations were carried out using the Scanning Electron Microscope (SEM) at the University of Valencia (Spain).

RESULTS

The irregularities due to the pressure within the capsula notwithstanding, the seeds of genus *Androcymbium* are always globose (Figs. 4-8) except in *A. cuspidatum* (Fig. 7C), where they show a slightly elliptical shape. Seed diameter was mostly around 1.5 mm (Table 1, Fig. 2) and varied between 0.7 mm in *A. dregei* and 3.5 mm in *A. burchellii* subsp. *pulchrum*. The seed colour varied among light brown, brown, brown-reddish and black (Table 1).

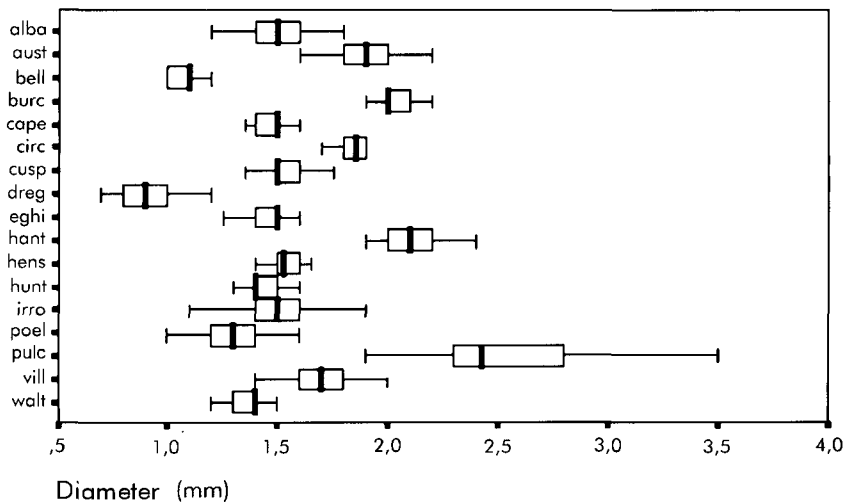


Figure 2.- Seed diameter in *Androcymbium*. The boxes show the median, the quartiles and the extreme values. In all cases, the names of species are coded with the first four letters.

Population	Seed color	Seed diameter	CAR	EXT	INT
<i>Section Androcymbium</i>					
ALBA-PK	Brown-reddish	(1.20) 1.52 (1.80)	P	Reticulate (II)	Quadrangular
AUST-GH	Brown-reddish	(1.50) 1.92 (2.50)	A	Mosaic (IV)	Rectangular
AUST-WP	Brown-reddish	(1.30) 1.79 (2.40)	A	Mosaic (IV)	Rectangular
BELL-VI	Black	(1.00) 1.07 (1.20)	A	Mosaic (III)	Indifferenced
BURC-HX	Brown	(1.80) 2.07 (2.60)	A	Rough	Quadrangular
CAPE-HO	Brown	(1.35) 1.49 (1.60)	P	Reticulate(II)	Quadrangular
CIRC-SB	Black	(1.70) 1.84 (1.90)	P	Mosaic (III)	Rectangular
CUSP-CA	Brown	(1.50) 1.62 (1.90)	A	Reticulate (I)	Quadrangular
CUSP-MO	Brown	(1.20) 1.45 (1.70)	A	Reticulate (I)	Quadrangular
EGHI-CI	Brown	(1.30) 1.51 (1.70)	A	Mosaic (IV)	Rectangular
EGHI-PK	Brown	(1.20) 1.41 (1.60)	A	Mosaic (IV)	Rectangular
HANT-CA	Brown-reddish	(1.90) 2.14 (2.40)	P	Mosaic (II)	Quadrangular
HENS-EK	Brown-reddish	(1.30) 1.52 (1.65)	P	Mosaic (I)	Quadrangular
HUNT-EK3	Black	(1.30) 1.44 (1.60)	A	Mosaic (I)	Indifferenced
IRRO-EK	Black	(1.20) 1.43 (1.60)	P	Mosaic (III)	Variable
IRRO-EK2	Black	(1.50) 1.74 (1.90)	P	Mosaic (II)	Variable
IRRO-EK6	Black	(1.50) 1.69 (1.90)	P	Mosaic (II)	Variable
IRRO-KA	Black	(1.20) 1.49 (1.80)	P	Mosaic (I)	Variable
IRRO-KW	Black	(1.10) 1.33 (1.60)	P	Mosaic (I)	Variable
IRRO-VP	Brown-reddish	(1.30) 1.49 (1.70)	P	Mosaic (I)	Variable
IRRO-VY	Black	(1.20) 1.39 (1.60)	P	Mosaic (I)	Variable
POEL-CO	Black	(1.00) 1.25 (1.50)	A	Mosaic (I)	Rectangular
POEL-NB	Black	(1.20) 1.42 (1.60)	A	Mosaic (I)	Rectangular
POEL-ST	Black	(1.20) 1.26 (1.40)	A	Mosaic (I)	Rectangular
PULC-CA	Brown	(1.90) 2.30 (2.80)	A	Rough	Quadrangular
PULC-NI	Brown	(2.20) 2.76 (3.50)	A	Rough	Quadrangular
VILL-EK	Black	(1.40) 1.58 (1.80)	P	Mosaic (III)	Rectangular
VILL-ST	Black	(1.60) 1.83 (2.00)	P	Mosaic (III)	Rectangular
VOLU-ST	?	?	A	Mosaic (II)	Quadrangular
WALT-ST	Black	(1.00) 1.35 (1.70)	A	Mosaic (I)	Quadrangular
<i>Section Erythroctictus</i>					
CRUC-CA	?	?	A	Rough	Quadrangular
<i>Section Dregeocymbium</i>					
DREG-PK	Light brown	(0.70) 0.94 (1.20)	A	Reticulate (I)	Quadrangular

Table 1.- Macromorphological seed characteristics of genus *Androcymbium*. CAR: caruncula (P=present; A=absent). Seeds are measured in mm. EXT: Microstructure of the external layer; INT: Cell morphology of the internal layer. The abbreviations of the populations are described in Appendix 1.

In species *A. albanense* subsp. *clanwilliamense*, *A. capense*, *A. circinatum*, *A. hantamense*, *A. henssenianum*, *A. irroratum*, and *A. villosum*, the raphe develops in a caruncula (Table 1; Figs. 4A,E; 5C; 6A,C; 7E,G), a phenomenon that has also been reported in other genera of the Liliales like *Erythronium*, *Gagea*, *Uvularia*, *Colchicum*, *Hermodactylus*, and *Patersonia* (DAHLGREN, 1985). The width of this caruncula-like raphe is never higher than 1 mm.

The external layer is rough in *A. austrocapense*, *A. bellum*, *A. burchellii* subsp. *burchellii*, *A. burchellii* subsp. *pulchrum*, *A. circinatum*, *A. cruciatum*, *A. dregei*, *A. eghimocymbion*, *A. gramineum*, and *A. villosum* (Figs. 5G; 6; 7A; 8) and smooth in the rest of species studied. Cell shape and disposition as analyzed in the SEM revealed three distinct patterns of microstructure in the external layer (Table 1):

a) Type mosaic. It features cells with walls within the cell surface. It is observed in most species studied and four subtypes can be distinguished. Mosaic I is characterized by a smooth pavement with regular, polygonal cells with 5-6 faces of different size that have sharp edges and a thin cell wall (Figures 4; 5B). It was observed in *A. henssenianum*, *A. huntleyi*, *A. irroratum* (populations IRRO-KA, IRRO-KW, IRRO-VP and IRRO-VY), *A. poeltianum*, and *A. walteri*. Mosaic II is characterized by a smooth pavement with regular cells, blunt edges and a thick cell wall (Fig. 5D,F). It was observed in *A. hantamense*, *A. volutare*, and *A. irroratum* (populations IRRO-EK2 and IRRO-EK6). Mosaic III is characterized by an irregular rough pavement with differently sized polygonal cells with 5-6 faces arranged in different levels, sharp edge and a thin cell wall (Figs. 5H; 6B,D). It was observed in *A. bellum*, *A. circinatum*, *A. irroratum* (population IRRO-EK), and *A. villosum*. Mosaic IV is characterized by a smooth pavement with irregular cells with rounded or elliptical edges and undifferentiated cell walls (Fig. 9F,H). It was observed in *A. austrocapense* and *A. eghimocymbion*.

b) Type reticulate. It features an external layer micromorphology with walls overtaking the cell surface. Two subtypes were observed among the studied species. Reticulate I is characterized by irregular polygonal cells (Fig. 4B,D) and was observed in *A. cuspidatum* and *A. dregei*. Reticulate II corresponds to a supareticulate structure with a thin reticle on top of the thick reticle underneath (Fig. 7F,H) and was observed in *A. albanense* subsp. *clanwilliamense*, and *A. capense*.

c) Type rough. It features irregular pavement without clear cell edges (Fig. 8) and was described in *A. burchellii* subsp. *burchellii*, *A. burchellii* subsp. *pulchrum*, *A. cruciatum*, and in all the Northern African species of the genus.

The surface of the internal layer showed a rough surface in *A. bellum* and *A. huntleyi*, where the cell edges cannot be precisely delimited (Fig. 9A, table 1). In contrast, the rest of species showed a smooth or almost smooth wall (Fig. 9B,C,D), where the edges of the cells in the internal layer are well delimited and group the species in three general types: 1) quadrangular cells in *A. albanense* subsp. *clanwilliamense*, *A. burchellii* subsp. *burchellii*, *A. burchellii* subsp. *pulchrum*, *A. capense*, *A. cruciatum*, *A. cuspidatum*, *A. dregei*, *A. gramineum*, *A. hantamense*, *A. henssenianum*, *A. rechingerii*, *A. volutare* and *A. walteri* (Fig. 9B); 2) rectangular cells in *A. eghimocymbion*, *A. austrocapense*, *A. circinatum*, *A. poeltianum*, *A. villosum*, and *A. wyssianum* (Figs. 9C); and 3) irregular cells (generally quadrangular tending to rectangular) in *A. hierrense*, *A. irroratum*, *A. palaestinum*, and *A. psammophilum* (Fig. 9D).

DISCUSSION

Seed morphology in the species of *Androcymbium* shows a remarkable inter-specific heterogeneity, while it behaves quite uniformly at the intra-specific level except for the seven studied populations of *A. irroratum*. On the one hand, population IRRO-EK shows a rough external layer, whereas the rest show a smooth external layer. On the other hand, seeds of population IRRO-VP are brown-reddish, and the rest of conspecific populations are black (Table 1).

Seed size in the South African taxa (Table 1) is similar to that of the North African congeners (Table 2) and, of which *A. palaestinum* and *A. rechingerii* show the smallest seeds (averaging 1.6 mm), and *A. hierrense* shows the biggest seeds, with an average of 2.3 mm (ARDANUY, 1997). Remarkably, seed size in genus *Androcymbium* is small as compared with other genera of the Colchicaceae like *Colchicum*, *Merendera*, *Bulbocodium*, *Ornithoglossum*, and *Gloriosa* (NORDERSTAM, 1982; GIBERT, *unpubl.*).

Taxa	Seed diameter	CAR	EXT	INT
<i>A. gramineum</i>	1.75 ± 0.20	A	Rugose	Quadrangular
<i>A. hierrense</i>	2.26 ± 0.29	A	Rugose	Irregular
<i>A. palaestinum</i>	1.60 ± 0.12	A	Rugose	Irregular
<i>A. psammophilum</i>	1.75 ± 0.23	A	Rugose	Irregular
<i>A. rechingerii</i>	1.60 ± 0.15	A	Rugose	Quadrangular
<i>A. wyssianum</i>	1.93 ± 0.26	A	Rugose	Rectangular

Table 2.- Macromorphological seed characteristics of Northern African species of genus *Androcymbium* (from PEDROLA-MONFORT, 1993). CAR: caruncula (P=present; A=absent). EXT: Microstructure of the external layer; INT: Cell morphology of the internal layer. The diameter of the seeds are measured in mm.

The caruncula might act as a nourishing reward and, therefore, it could be related to seed dispersal mechanisms. All South African species studied show dehiscent capsule. Hence, seed dispersal can be carried out individually, indicating that dispersal agents could be influencing the distribution of individuals in populational space. In contrast, some of the species distributed in North Africa feature a dehiscent capsule and, consequently, the dispersal unit is the whole stock of seeds per individual. A study in a stand of *A. gramineum* revealed that this is a paramount factor in determining the spatial distribution of individuals in neighbourhoods of genetically related individuals (CAUJAPÉ-CASTELLS & PEDROLA-MONFORT, 1997).

A close relationship between *A. wyssianum* (distributed in Northern Africa) and *A. roseum* (distributed in Southern Africa) was inferred by PEDROLA-MONFORT (1993) from the observation of rectangular cells in the internal layer of the seeds in both species. This fact led to the consideration that *A. wyssianum* and *A. roseum* might be the same species or were closely related. This also indicated that *A. roseum*, distributed in South Africa, could be of paramount importance to under-

stand the dispersal path of the genus into North Africa. Recent studies allowed us to observe additional seed material and indicate that the cells in the internal layer of *A. hierrense*, *A. palaestinum*, and *A. psammophilum* (which were defined as quadrangular in PEDROLA-MONFORT, 1993) show variable morphologies (Table 2).

A recent phylogeny based on cpDNA RFLPs (CAUJAPÉ-CASTELLS *et al.*, 1999) groups *A. gramineum*, *A. palaestinum*, and *A. rechingerii*, and the species *A. hierrense*, *A. psammophilum*, and *A. wyssianum* in different clades. This topology is well supported and hints at the possibility that the present distribution of the North African species might be accounted for by the existence of two different dispersal lines starting in South Africa (CAUJAPÉ-CASTELLS *et al.*, *in mss.*). The shape of the cells in the internal layer might support this hypothesis under the consideration that the species that exhibit rectangular cells (*A. roseum* and *A. wyssianum*, and with variability *A. hierrense*, *A. psammophilum*, and *A. palaestinum*) could be more primitive than *A. gramineum* and *A. rechingerii*, whose cells tend to be quadrangular. The morphological variability observed in the cells of the internal layer of South African species makes it difficult to substantiate this hypothesis.

Taxonomic implications

None of the seed characters allows to support the classification of the genus in three sections (*Androcymbium*, *Dregeocymbium* and *Erythrostictus*). All of the seed characters examined (size, shape, colour, presence/absence of caruncula, type of external and internal layer) show variability in the 17 taxa of section *Androcymbium* included in this study. Therefore, seed characters cannot be used as an indicator of sectional taxonomic category in the genus *Androcymbium*.

The only representative studied of section *Dregeocymbium* (*A. dregei*) shows two seed traits that differentiate it from the rest of species: a small seed size (almost always < 1 mm) and the brown light colour of the external cover. This species had been included in section *Erythrostictus* by previous authors (MÜLLER-DOBLIES & MÜLLER-DOBLIES, 1990). The seed traits exclusive of *A. dregei* in the genus are not shared by the rest of species within section *Erythrostictus* (PEDROLA-MONFORT, 1993; ARDANUY, 1997), which have bigger and darker seeds. From the studied species, only *A. bellum* and some individuals of populations IRRO-KW and POELCO, present a seed diameter that overlaps only partially with the range observed in *A. dregei*. However, their seeds are black.

Androcymbium cruciatum has been included historically within section *Erythrostictus* (Appendix 1). This species shares the absence of caruncula with the North African species (belonging to this section), and differst from them in the external layer type. MEMBRIVES (2000) argues for the inclusion of *A. cruciatum* in a new monotypic section based on morphological traits.

The species *A. bellum* was segregate from section *Erythrostictus* and include it in section *Androcymbium* by MÜLLER-DOBLIES & MÜLLER-DOBLIES (1998). This species shares with other species in section *Erythrostictus* the absence of caruncula and the roughness of the testa's external layer. However, the seeds of *A. bellum* show a smaller size and a rougher internal layer than the others (PEDROLA-MONFORT, 1993). According to seed traits, *A. bellum* is most similar to *A. huntleyi* (that belongs to section *Androcymbium*) than the other species of section *Erythros-*

tictus. Both of them share seed colour and diameter, the absence of caruncula, mosaic external layer and rough internal layer, and they only differ in the size and shape of the cells in the external layer.

Only 15 of the 34 taxa classified within section *Androcymbium* (Appendix 2) by MÜLLER DOBLIES & MÜLLER DOBLIES (1998) were included in our study. The two subsections of these authors are not supported by any of the studied characters. Subsection *Gradatocymbium* includes the species *A. albanense*, *A. poeltianum*, *A. henssenianum*, and *A. cuspidatum*, that differ in most of the studied traits (seed shape, colour, caruncula's presence, type of external layer and shape of the cells of the internal layer). Neither does subsection *Androcymbium* share any of the studied seed traits. For instance, *A. irroratum* and *A. eghimocymbium* (series *Eghimocymbia*) differ in seed colour, presence/absence of caruncula, type of mosaic and the shape of the internal layer cells (Table 1).

A cladistic analysis of genus *Androcymbium* based on morphological and reproductive data (MEMBRIVES, 2000) concludes that none of the seed traits analysed is monophyletic (Fig. 3) and shows that caruncula presence appeared three times in the evolution of the genus. First in *A. henssenianum*, then in *A. hantamense* and *A. capense*, and finally in *A. irroratum*, *A. albanense* subsp. *clanwilliamense*, *A. villosum*, and *A. circinatum*. Furthermore, this character would have undergone a reversal in *A. volutare*, *A. walteri*, *A. bellum*, and *A. poeltianum*. When the evolution of the microstructural patterns of the external layer is analysed, the result is that none of the four types behaves as a monophyletic trait either. Rough forms appear at the base of the morphological phylogenetic tree as primitive external layer microstructures, and then again in the terminal clade formed by *A. burchellii* subsp. *burchellii* and *A. burchellii* subsp. *pulchrum*. Reticulate types appear three times in that phylogeny: in the clade made up by *A. dregei* and *A. exiguum*, in *A. cuspidatum* and in *A. crispum*. Suprareticulate types appear independently in species from two distinct clades (*A. capense* and *A. albanense* subsp. *clanwilliamense*). Mosaic types appear three times also: in *A. henssenianum* and *A. huntleyi*, in *A. melanthioides* and *A. hantamense*, and in the clade that groups *A. eghimocymbium*, *A. austrocapense*, *A. irroratum*, *A. villosum*, *A. circinatum*, *A. volutare*, *A. walteri*, *A. bellum*, and *A. poeltianum*.

Given that none of the seed traits analysed in the genus *Androcymbium* are good indicators of phylogenetic relatedness (MEMBRIVES, 2000), they have no usefulness as taxonomic descriptors of supra-specific classification under a phylogenetic perspective. Therefore, we can conclude that the seed characters considered do not indicate either phylogenetic taxonomic assemblages, or morphological groupings like the historical classification in three sections (KRAUSE, 1920), or the MÜLLER-DOBLIES & MÜLLER-DOBLIES (1998) proposal.

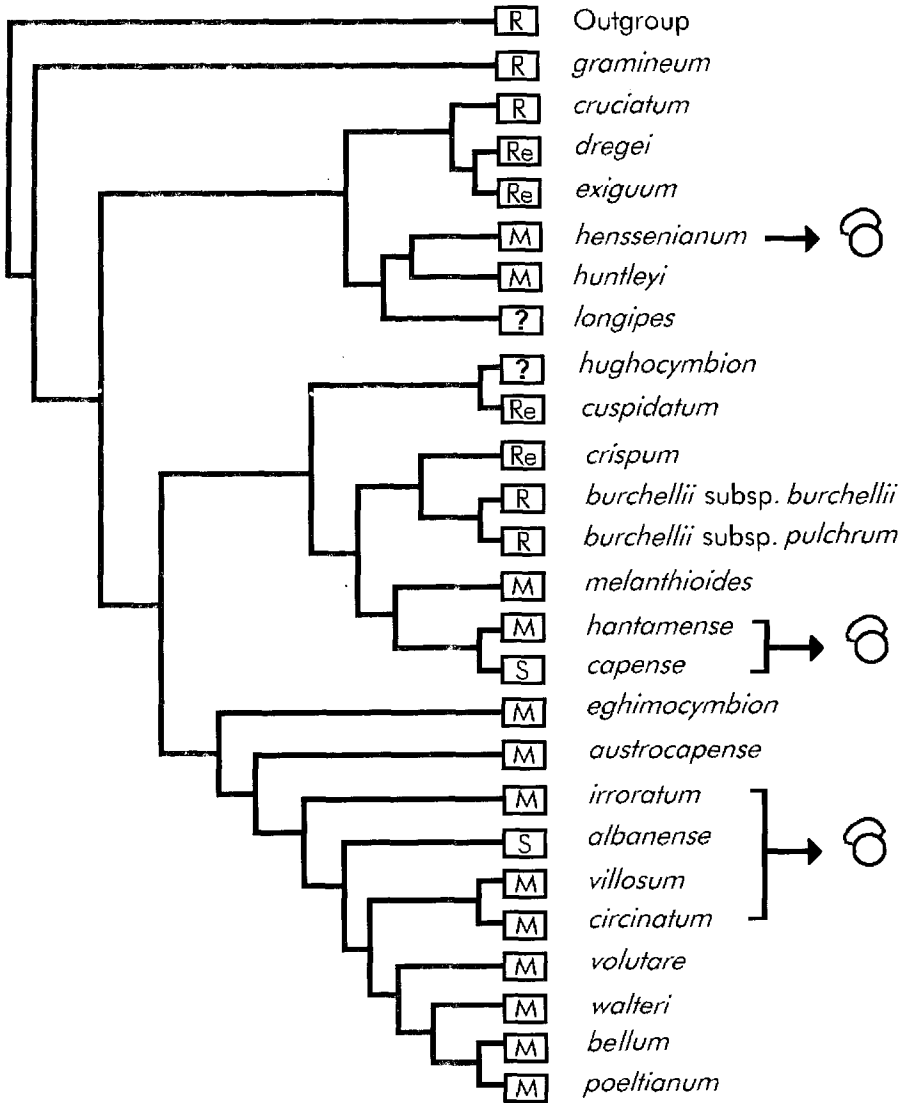


Figure 3.- Phylogenetic tree of genus *Androcymbium* from morphologic and reproductive data (MEMBRIVES, 2000). The species with seminal data unknown have been excluded. The evolution of the external layer seed microstructure (squares at the end of the branches) and the presence/absence of caruncula (where the presence of caruncula is represented by a picture of the seed with a developed raphe) is represented in the tree. Types of microstructure: R=rough; Re=reticulate; S=suprareticulate; M=mosaic; ?=unknown data.

ACKNOWLEDGEMENTS

We thank Isabel Mateu-Andrés for the facilities given to undertake this study and for her suggestions in the classification of cell patterns. Amparo Ardanuy provided for the welfare of the material in cultivation. The Karl Faust Foundation gave financial support for both the expedition to South Africa that allowed us to collect the analysed samples and the subsequent investigations in conservation genetics of *Androcymbium* carried out in the "Estació Internacional de Biologia Mediterrània-Jardí Botànic Marimurtra".

REFERENCES

- ARDANUY, A., 1997.- Estudis bàsics per la gestió agronòmica i la conservació de sis espècies endèmiques del gènere *Androcymbium* Willd. Treball fi de carrera. Universitat de Girona.
- ARNOLD, T.H. & B.C. DE WETT, 1993.- Plants of southern Africa: Names and Distribution. *Memoirs of the botanical survey of South Africa* No. 62. pp. 131.
- BUXBAUM, F., 1936.- Die Entwicklungslinien der Lilioideae. I. Die Wurmbaeoideae. *Bot. Archiv* 38: 213-293.
- CAUJAPE-CASTELLS, J. & J. PEDROLA-MONFORT, 1997.- Space-time patterns of genetic structure within a stand of *Androcymbium gramineum* (Cav.) McBride (Colchicaceae) *Heredity* 79: 341-349.
- R.K. JANSEN, J. PEDROLA-MONFORT & N. MEMBRIVES, 1999.- Chloroplast DNA Restriction Site Phylogeny of the Genus *Androcymbium* (Colchicaceae) *Syst. Bot.* 24(4): 581-597.
- DAHLGREN, R., H.T. CLIFFORD & P.F. YEO, 1985.- *The families of the Monocotyledons: Structure, Evolution, and Taxonomy*. Springer-Verlag. Berlin.
- DAVIS, P.H. & V.H. HEYWOOD, 1963.- *Principles of Angiosperm Taxonomy*. Ed. Olivier. Edinburg.
- GREUTER, W., 1967.- Contributiones floristicae Austro-Aegeae. *Candollea* 22(2): 233-253.
- KRAUSE, K., 1920.- Revision der Gattung *Androcymbium* Willd. *Notizbl. Bot. Gart. Berlin* 7: 512-526.
- MEMBRIVES, N., 2000.- Biologia evolutiva del gènere *Androcymbium* (Colchicaceae) a Sudàfrica Occidental. Tesis Doctoral. Universitat de Barcelona.
- MÜLLER-DOBLIES, U. & D. MÜLLER-DOBLIES, 1990.- Zur Kenntnis der Gattung *Androcymbium* (Colchicaceae) im südlichen Afrika: 2. *Androcymbium exiguum* hat doch Artwert. *Willdenowia* 19:453-470.
- & D. MÜLLER-DOBLIES, 1998.- De Liliifloris Notulae. 6. De decuria prima specierum novarum generis *Androcymbium* sect. *Androcymbium* (Colchicaceae) in Africa Australi s.l. Praeterea novitates de huius sectionis nonnullarum specierum distributione (praesertim aucta speciminibus STEllenbosensibus i.a. collectis a botanico vero E. G. H. OLIVERO) *Fedd. Reper.* 109 (7-8): 551-572.
- NORDERSTAM, B., 1982.- A monograph of the genus *Ornithoglossum* (Liliaceae). *Opera Botànica* 64: 1-51.
- PEDROLA-MONFORT, J., 1993.- *Biologia poblacional del complexe Androcymbium gramineum* (Cav.) McBride (Colchicaceae). Tesis Doctoral. Universitat de València.
- N. MEMBRIVES, J.M. MONTERRAT & J. CAUJAPE-CASTELLS, 1999a.- A new species from the Western of South Africa: *Androcymbium huntleyi* (Colchicaceae) *Fontqueria* 53: 1-2.
- N. MEMBRIVES & J.M. MONTERRAT, 1999b.- Two new *Androcymbia* (Colchicaceae) from Western South Africa. *Fontqueria* 54(2): 7-9.
- N. MEMBRIVES, J. M. MONTERRAT & J. CAUJAPE-CASTELLS, 2000.- Systematic relationships of some species of the genus *Androcymbium* Willd. (Colchicaceae) in Western South Africa. *Bot. Macaronésica*, 24: 107-126.
- REIFERBERGER, U., 1990.- *Androcymbium hierrense* Santos ssp. *macrosperrum* Reifenberger ssp. nov. Liliaceae., ein neuer Endemit der insel La Gomera. *Vierea* 18: 251-259.
- ROESSLER, H., 1974.- Die Gattung *Androcymbium* Willd. (Liliaceae) in Südwestafrika. *Mitt. Bot.*

München 11: 545-566.

SANTOS, A. 1977.- *Androcymbium hierrensis* spec. nova para la flora canaria. Ed. Funchal. Pp: 53-59.

STEBBINS, G. L., 1974. *Flowering Plants. Evolution above the species level*. Harvard University Press. Cambridge. Massachusset.

STUESSY, T. F., 1990.- *Plant Taxonomy*. Columbia University Press. New York.

Appendix 1. - Sampled populations and localities of genus *Androcymbium* studied in Southwest Africa. Abb: abbreviations of the population and locality.

Population	Abb.	Locality
<i>Section Androcymbium</i>		
<i>A. albanense</i> subsp. <i>clanwilliamense</i>	ALBA-PK	3219AA (WUPPERTAL) Clanwilliam-Wuppertal Road. Km 10
<i>A. austrocapense</i>	AUST-GH	3418AC (SIMONSTOWN) Road to the Cape of Good Hope
<i>A. austrocapense</i>	AUST-WP	3418AD (SIMONSTOWN) Wheal's Point. Cape Point Reserve
<i>A. bellum</i>	BELL-VI	2817DC (VIOOLSDRIFT) Steinkopf to Vioolsdrift Road. Km 40
<i>A. burchellii</i> subsp. <i>burchellii</i>	BURC-HX	3319BC (WORCESTER) Worcester to Towsrivier Road. Near Hexrivierpass
<i>A. burchellii</i> subsp. <i>pulchrum</i>	PULC-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km from the deviation to Kreitzberg
<i>A. burchellii</i> subsp. <i>pulchrum</i>	PULC-NI	3118AA (CALVINIA) Wild Flowers Reserve of Nieuwoudtville
<i>A. capense</i>	CAPE-HO	3318AB (CAPE TOWN) Malmesbury to Hopefield Road. Km 49
<i>A. circinatum</i>	CIRC-SB	2917DB (SPRINGBOK) 3 km W of Springbok
<i>A. cuspidatum</i>	CUSP-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km from the deviation to Kreitzberg
<i>A. cuspidatum</i>	CUSP-MO	3320CD (MONTAGU) Near Montagu-Badskloof. W side of the gorge.
<i>A. eghimocymbion</i>	EGHI-CI	3218DB (CLANWILLIAM) N-7 Road in the Piketberg Pass to Citrusdal
<i>A. eghimocymbion</i>	EGHI-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road. Km 28
<i>A. hantamense</i>	HANT-CA	3119DA (CALVINIA) Calvinia to Ceres Road, 7 km from the deviation to Kreitzberg
<i>A. henssenianum</i>	HENS-EK	2817CC (VIOOLSDRIFT) Eksteenfontein to Modderfontein Road
<i>A. huntleyi</i>	HUNT-EK3	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 20 km from the first entry to Eksteenfontein
<i>A. irroratum</i>	IRRO-EK	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 6 km from the first entry to Eksteenfontein
<i>A. irroratum</i>	IRRO-EK2	2917AD (SPRINGBOK) Springbok to Port Nolloth Road, 15 km from the first entry to Eksteenfontein
<i>A. irroratum</i>	IRRO-EK6	2817CC (VIOOLSDRIFT) Eksteenfontein to Modderfontein Road, first turn
<i>A. irroratum</i>	IRRO-KA	3018CB (KAMIESBERG) Bitterfontein to Kliprand Road.
<i>A. irroratum</i>	IRRO-KW	3118BC (VANRHYNSDORP) Vredental to Koekenaap Road, 100 from the train station
<i>A. irroratum</i>	IRRO-VP	3119AC (CALVINIA) Vanrhynspass
<i>A. irroratum</i>	IRRO-VY	3118AD (VANRHYNSDORP) Vrendental to Vanrhynsdorp Road.
<i>A. poeltianum</i>	POEL-CO	2917DB (SPRINGBOK) Springbok to Concordia Road.
<i>A. poeltianum</i>	POEL-NB	2917DB (SPRINGBOK) Springbok to Nababeep Road.
<i>A. poeltianum</i>	POEL-ST	2917DC (SPRINGBOK) Road from Steinkopf to Springbok, 5 km
<i>A. villosum</i>	VILL-EK	2817CC (VIOOLSDRIFT) 1 km S of Eksteenfontein
<i>A. villosum</i>	VILL-ST	2917BC (SPRINGBOK) 3 km S of Steinkopf, parallel to N7.
<i>A. volutare</i>	VOLU-CA	3119BC (CALVINIA) Perdekraal Farm
<i>A. walteri</i>	WALT-ST	2917DC (SPRINGBOK) Road from Steinkopf to Springbok. Km 5
<i>Section Erythrosticktus</i>		
<i>A. cruciatum</i>	CRUC-ST	2917BC (SPRINGBOK) 5 km SSW of Steinkopf, parallel to N7.
<i>Section Dregeocymbium</i>		
<i>A. dregei</i>	DREG-PK	3219AA (WUPPERTAL) Clanwilliam to Wuppertal Road. Km 28

Appendix 2.- Taxonomic classification for section *Androcymbium* proposed by MÜLLER-DOBLIES & MÜLLER-DOBLIES (1998).

Section *Androcymbium*

Subsection *Gradatocymbium* U.Müll.-Doblies & D.Müll.-Doblies

Serie *Gradatocymbia* U.Müll.-Doblies & D.Müll.-Doblies

Subserie *Gradatocymbia*

A. longipes*, *A. natalense*, *A. decipiens

Subserie *Swazicymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. swazicum*, *A. burkei

Subserie *Leistnerocymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. leistneri*, *A. albanense* subsp. *albanense*, *A. poeltianum

Subserie *Pachystyla* U.Müll.-Doblies & D.Müll.-Doblies

A. henssenianum

Serie *Trifoliata* U.Müll.-Doblies & D.Müll.-Doblies

A. cuspidatum*, *A. kunkelianum*, *A. worsonense*, *A. hughocymbium

Subsection *Androcymbium*

Serie *Eghimocymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. eucomoides*, *A. undulatum*, *A. albomarginatum*, *A. vanjaarsveldii*, *A. scabromarginatum*, *A. irroratum*, *A. eghimocymbion

Serie *Myiocymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. circinatum*, *A. villosum*, *A. volutare

Serie *Therocymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. burchellii*, *A. latifolium

Serie *Melittocymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. capense*, *A. ciliolatum*, *A. hantamense*, *A. austrocapense*, *A. crispum

Serie *Androcymbium*

A. melanthioides*, *A. orienticapense*, *A. striatum

Serie *Schlechterocymbia* U.Müll.-Doblies & D.Müll.-Doblies

A. bellum

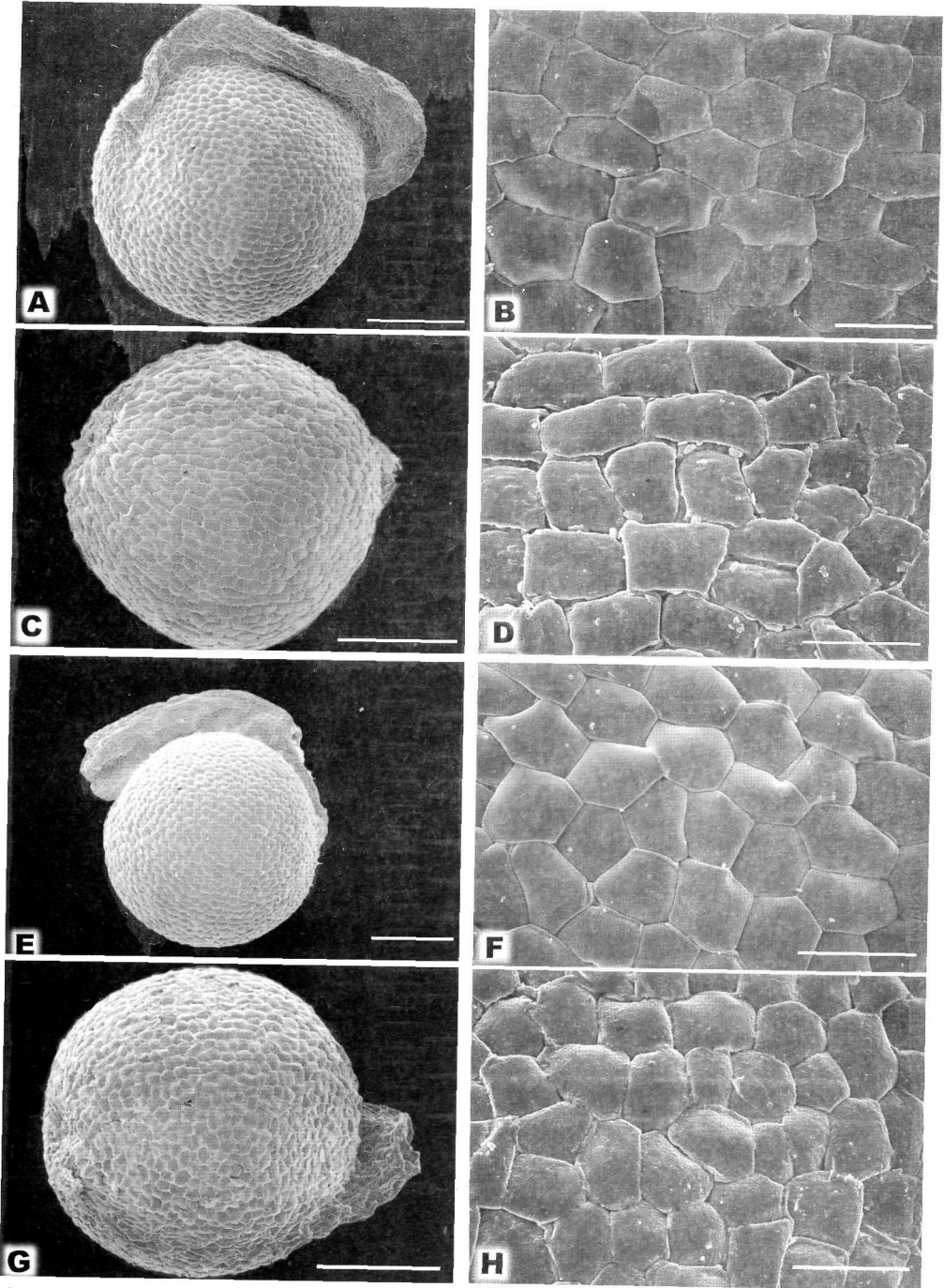


Figure 4.- Microstructure of seed external layer in *Androcymbium*. Type mosaic I. A,B. *A. henssenianum*. C,D. *A. huntleyi*. E,F. *A. irroratum* (IRRO-KW). G,H. *A. poeltianum*. A,C,E,G. Seed. The white lines indicate 500 μ m. B,D,F,H. Detail of the microstructure of the external layer. The white lines indicate 100 μ m.

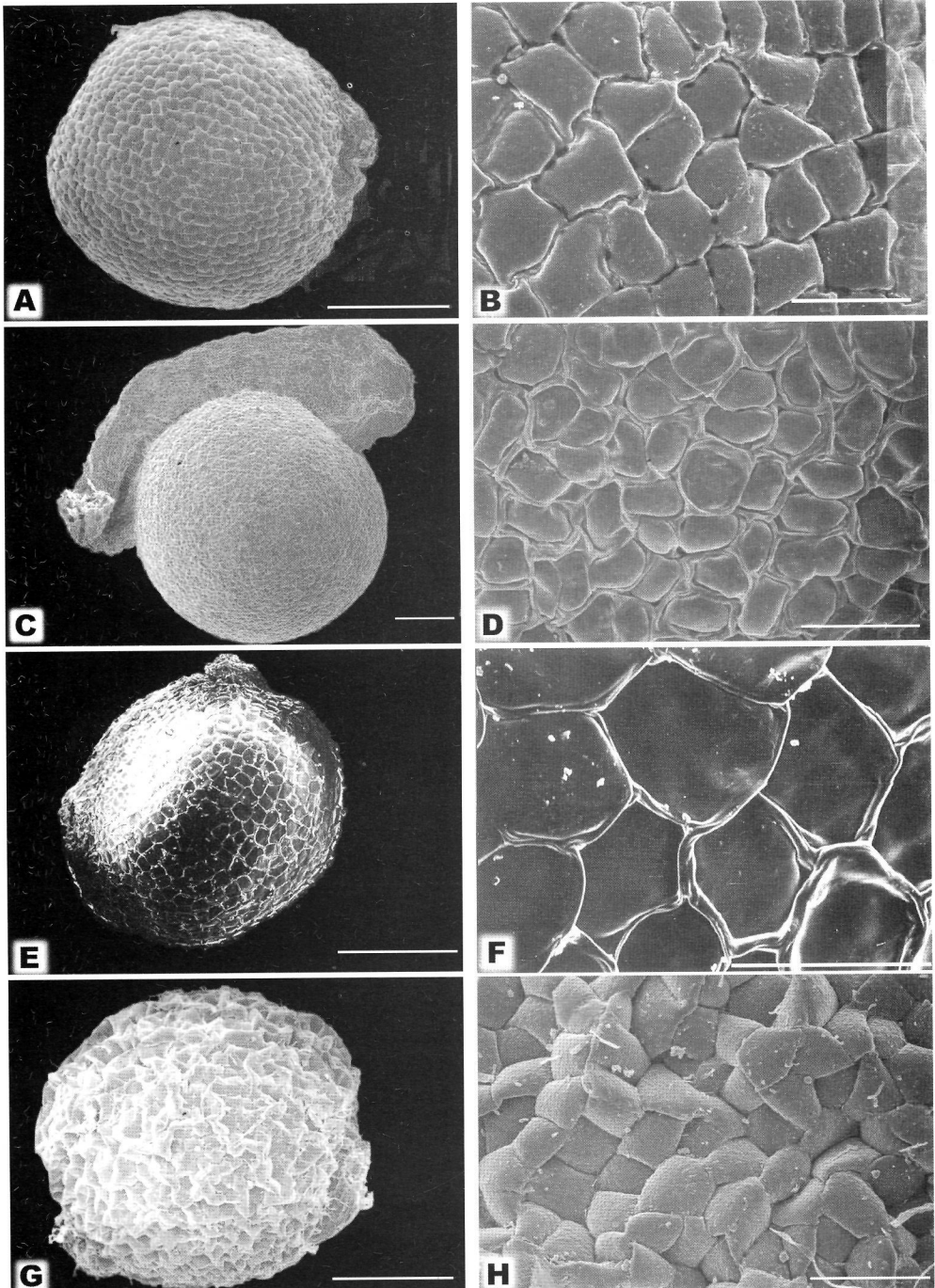


Figure 5.- Microstructure of seed external layer in *Androcymbium*. Type mosaic I. A,B. *A. walteri*. Type mosaic II. C,D. *A. hantamense*. E,F. *A. volutare*. Type mosaic III. G,H. *A. bellum*. A,C,E,G. Seed. The white lines indicate 500 μ m. B,D,F,H. Detail of the microstructure of the external layer. The white lines indicate 100 μ m

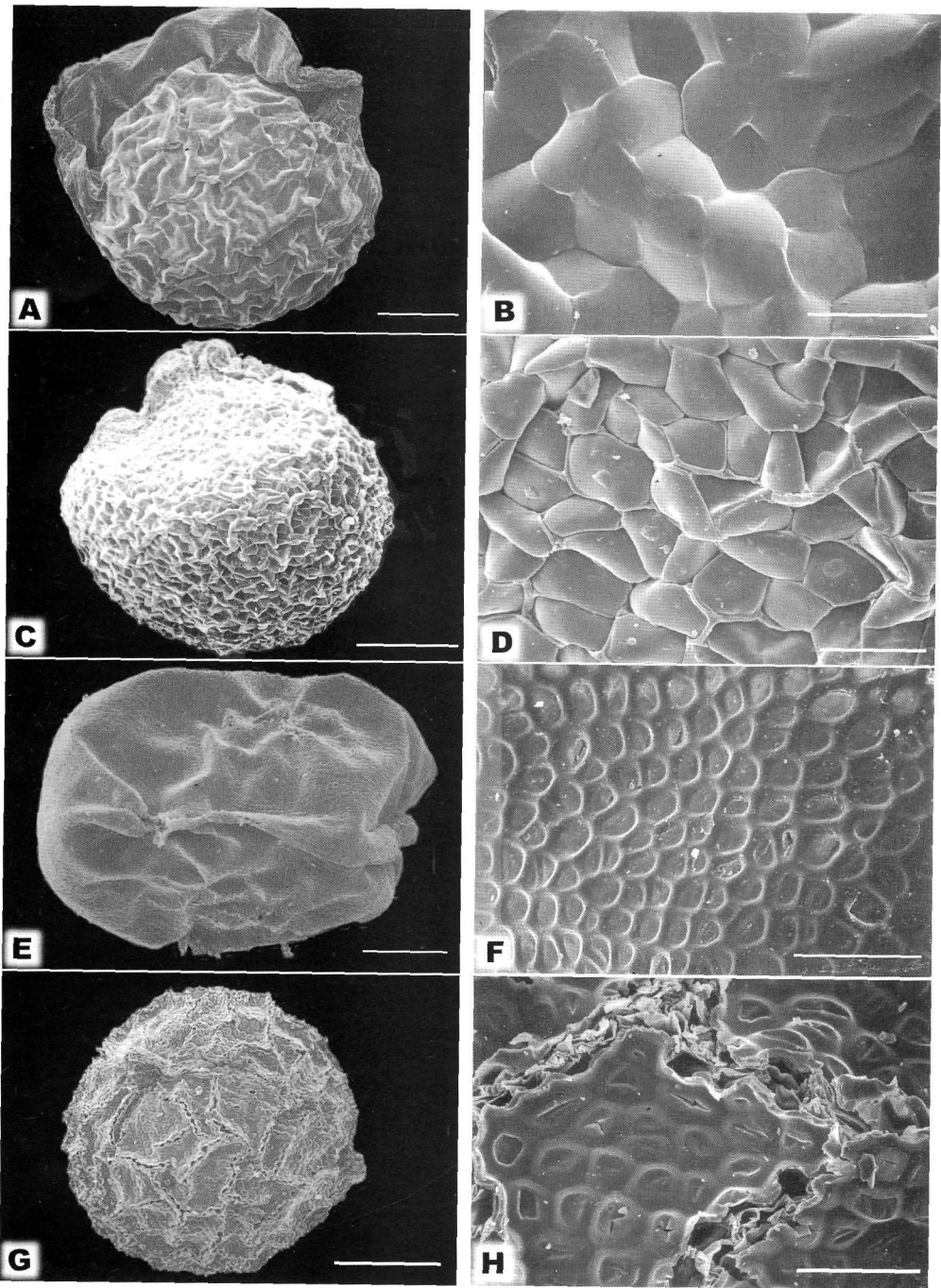


Figure 6.- Microstructure of seed external layer in *Androcymbium*. Type mosaic III. A,B. *A. circinatum*. C,D. *A. villosum*. Type mosaic VI. E,F. *A. austrocapense*. G,H. *A. eghimocymbion*. A,C,E,G. Seed. The white lines indicate 500 µm. B,D,F,H. Detail of the microstructure of the external layer. The white lines indicate 100 µm.

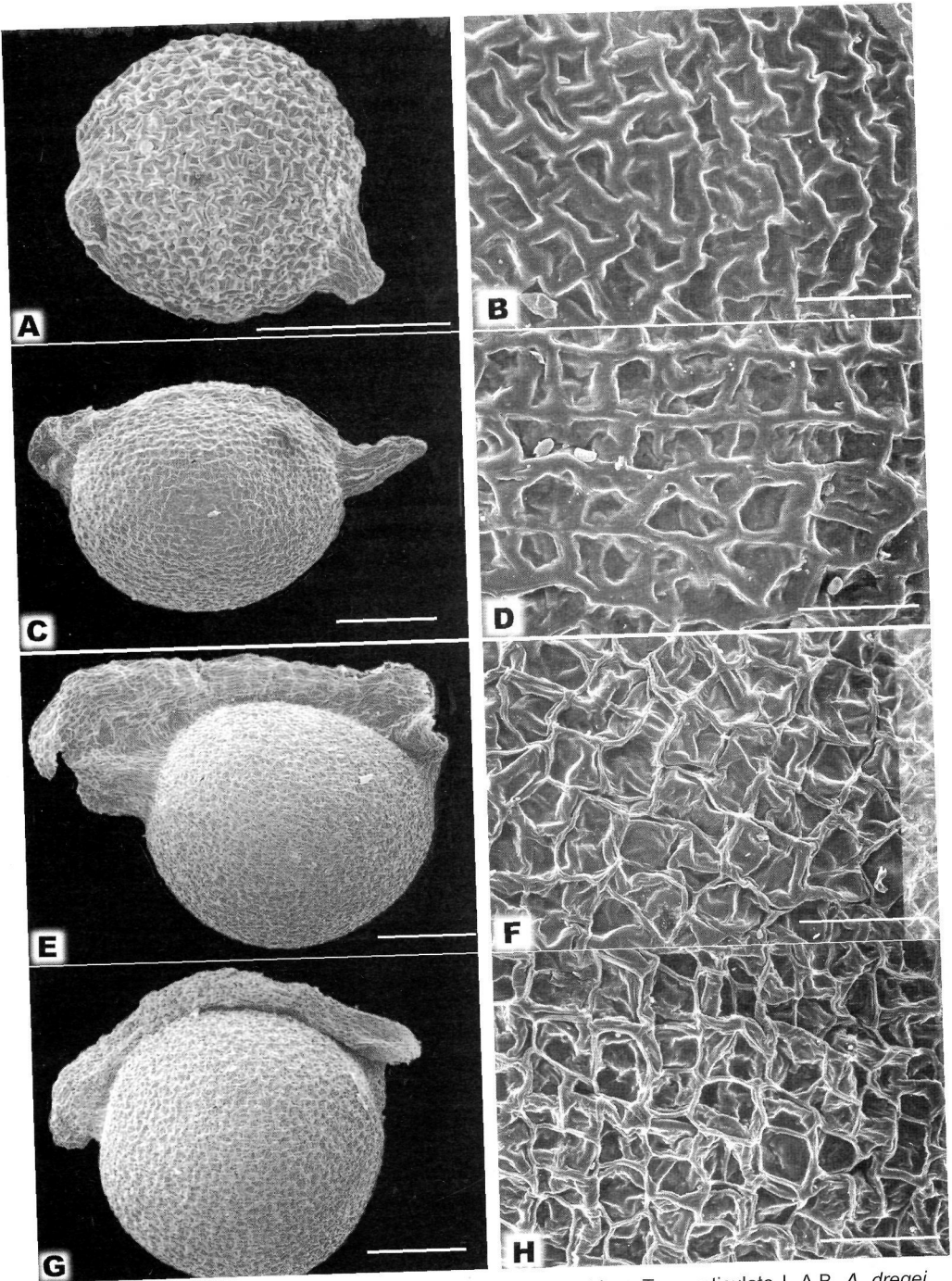


Figure 7.- Microstructure of seed external layer in *Androcymbium*. Type reticulate I. A,B. *A. dregei*. C,D. *A. cuspidatum*. Type reticulate suprareticulate. E,F. *A. albanense* subsp. *clanwilliamense*. G,H. *A. capense*. A,C,E,G. Seed. The white lines indicate 500 μ m. B,D,F,H. Detail of the microstructure of the external layer. The white lines indicate 100 μ m.

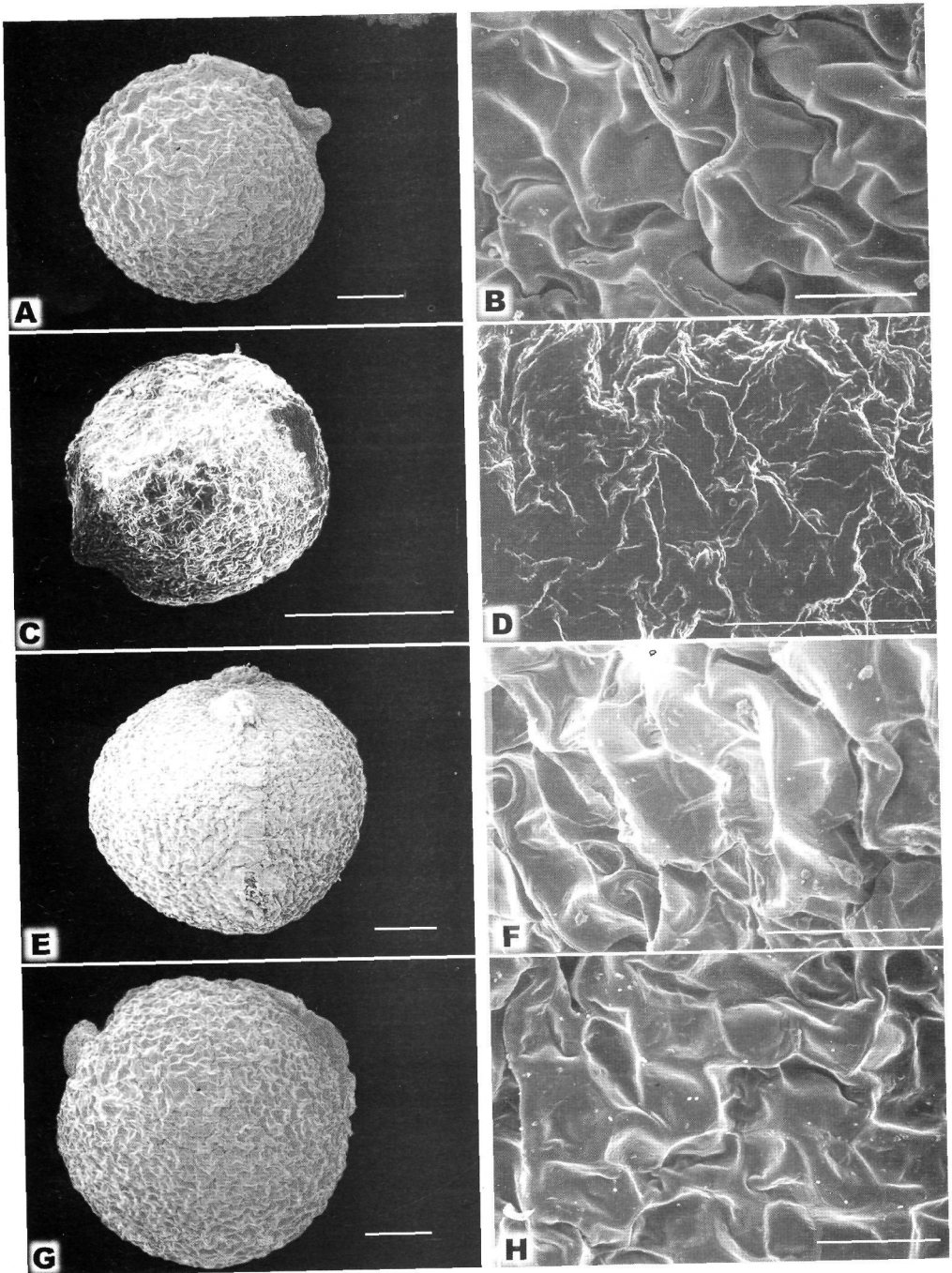


Figure 8. - Microstructure of seed external layer in *Androcymbium*. Type rough. A,B. *A. burchellii* subsp. *burchellii*. C,D. *A. cruciatum*. E,F. *A. gramineum*. G,H. *A. burchellii* subsp. *pulchrum*. A,C,E,G. Seed. The white lines indicate 500 μm . B,D,F,H. Detail of the microstructure of the external layer. The white lines indicate 100 μm .

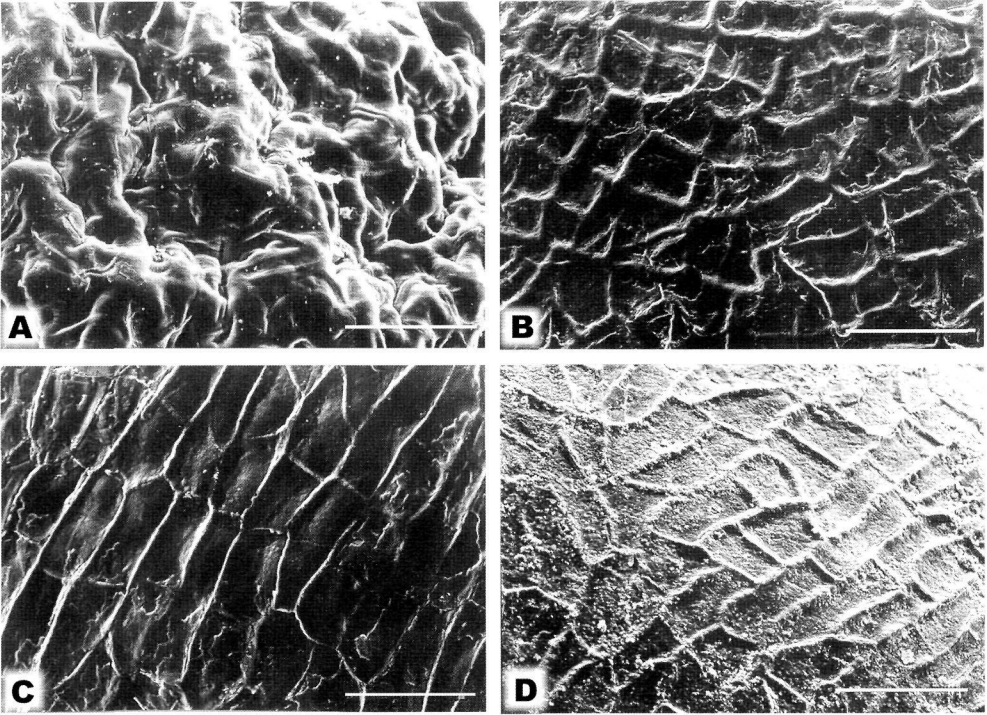


Figure 9.- Shape of the internal layer cells. A. Rough (*A. bellum*). B. Quadrangular polygonal (*A. henssenianum*). C. Rectangular polygonal (*A. austrocapense*). D. Irregular polygonal (*A. irroratum*). The white lines indicate 60 μ m.