PALYNOLOGICAL CHARACTERIZATION OF THE ENDEMIC ASTEROIDEAE FROM THE ARCHIPELAGO OF MADEIRA

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With 6 figures and 2 tables

ABSTRACT. Twenty-one endemic taxa of the *Asteroideae*, 15 of which are Madeiran and 6 Macaronesian, were analysed. A palynological study of these taxa is presented. Eleven characters of pollen grains, including morphology and sporoderm sculpture were recorded by optical and scanning microscopy. The results were statistically analysed and used to characterise the pollen of endemic *Asteroideae*. The principal pollen features are discussed and endemic *Asteroideae* pollen types characterised. Among the endemic *Asteroideae*, different pollen models – echinate and microechinate – are observed, the latter corresponds to the *Artemisia* pollen type. Based on specific biometrics and morphological characters, the echinate pollen is subdivided into *Argyranthemum*, *Carlina*, *Helichrysum* and *Senecio* types. This study represents the first systematic approach to a palynological study of the flora of Madeira.

KEY WORDS: *Asteroideae* endemics, Pollen morphology, *Anthemideae*, *Inuleae*, *Cynareae*, *Senecioneae*, *Calenduleae*.

RESUMO. Vinte e um endemismos da flora da Madeira, da sub-família *Asteroideae*, Asteraceae, dos quais 15 são endemismos exclusivos do arquipélago e 6 endemismos macaronésicos, foram estudados do ponto de vista palinológico. Neste estudo foram analisados 11 caracteres polínicos, incluindo a morfologia polínica e a escultura da esporoderme, através das microscopias óptica e electrónica de varrimento. Os resultados, após tratamento estatístico, foram

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utilizados para caracterizar os pólenes dos endemismos das *Asteroideae*. As principais características polínicas são analisadas e os tipos polínicos presentes entre *Asteroideae* endémicas apresentados. Dois modelos polínicos, definidos com base na ornamentação da esporoderme, estão presentes entre as espécies estudadas – equinado e microequinado. Este último corresponde ao tipo polínico da *Artemisia*, a única espécie endémica das *Asteroideae* microequinada. Os pólenes equinados das restantes espécies foram agrupados em 4 tipos polínicos – tipos *Argyranthemum*, *Carlina*, *Helichrysum* e *Senecio*, tendo por base as características específicas da biometria polínica, a ornamentação e ultra-estrutura da esporoderme. Este estudo representa a primeira análise polínica sistemática das Asteroideae endémicas da flora da Madeira.

INTRODUCTION

The family *Asteraceae* is arranged in two subfamilies *Asteroideae* and *Lactucoideae* (HEYWOOD & HUMPHRIES, 1977; CRONQUIST, 1981; CRONQUIST, 1988) assembling 13 tribes, of which the *Lactuceae* represent the *Lactucoideae*, and the remaining tribes placed in the *Asteroideae* (CRONQUIST, 1977; CRONQUIST, 1981). This classification system is widely accepted, because of the stability of the taxonomic characters. Other systems of *Asteraceae* classification based on molecular criteria have also been proposed, including division of the group into three subfamilies – *Asteroideae*, *Lactucoideae* and *Barnadesioideae* (BREMER *et al*., 1992; JANSEN *et al*., 1992). This work raise questions about the status and interrelationships between tribes (BREMER *et al*., 1992).

The *Asteraceae* is the largest group in the flora of Madeira with 136 species; among them 27 Madeiran and 5 Macaronesian are endemics (VIEIRA, 1992; PRESS, 1994). The *Asteroideae* is represented by 10 tribes, 5 of which – *Anthemideae, Cardueae, Calenduleae, Inuleae, Senecioneae* – have a total of 21 endemics (PRESS, 1994). The Asteraceae rate of endemics is 23.5% of the number of class species from them 15.5% belongs to the *Asteroideae*. Despite several previous studies of these taxa, there have been no analyses of palynological data (HUMPHRIES, 1976; FRANCISCO-ORTEGA *et al*., 1995).

Pollen morphology is often used in Asteraceae taxonomy along with other morphological or molecular criteria to better understand its phylogenetic relationships (SKVARLA *et al*., 1977; BOLICK, 1978; CRONQUIST, 1981; ANDERBERG, 1989; ANDERBERG, 1996). Pollen morphology has used to define the taxonomic position of several taxa of the Asteraceae (NORDENSTAM & El-GHAZALY, 1977; SKVARLA *et al*., 1977; BOLICK, 1978; DIEZ, 1987). Pollen features analysed in such studies include the size, shape, presence and number of apertures, thickness and sculpture of exine, or

thickness of intine (ERDTMAN, 1966; SKVARLA & TURNER, 1966). These features have been successfully applied to *Asteroideae* pollen analysis in previous accounts (PERSON, 1974; HEYWOOD & HUMPHRIES, 1977; TURNER & POWELL, 1977; ROWLEY *et al*., 1980; CANTO, 1987; TORMO & UBERA, 1987; VALLÉS *et al*., 1987; ANDEBERG, 1996; CÂMARA *et al*., 1998).

This paper compares the pollen of the endemic *Asteroideae* from Madeira, whose features may contribute to a better understanding of pollen morphology in these species and the *Asteroideae* in general.

MATERIAL AND METHODS

Pollen of 21 taxa of *Asteroideae* endemic from the Archipelago of Madeira was studied (Table 1). The samples were collected *in situ* or from herbarium collections of MADS, MADJ and COI. Voucher specimens of the field samples have been deposited in the Madeira University Herbarium – numbers 0030 to 0041 and 0049 to 0099.

The pollen was acetolysed according to ERDTMAN'S modified technique (1960). Acetolysed pollen was mounted in glycerine jelly (REITSMA, 1969) and the glass slides deposited in the Palinotheca of the Madeira University. Eleven characters including – polar (P) and equatorial (E) axes, exine thickness at the pole (Ex. P) and equator (Ex. E) or spines height (AE) and basis width (BE) and spines number in polar view (Z) – have been analysed. At least 20 pollen grains were measured in each sample. Pollen samples from herbarium vouchers and field specimens have been compared for each taxa. For scanning electron microscopy (SEM) acetolysed pollen grains were coated with gold. The pollen was examined and photographed in a JEOL, model JSM-5400.

Statistical analysis of data included a minimum display, median values calculation. The SYSTAT software sub. pro. ANOVA and Microsoft EXCEL version 5.0 Copyright © 1984-94 were used in the parameter analysis. For all biometrical parameters presented below the validity of a minimum display has been confirmed.

We followed terminology proposed by ERDTMAN (1966) and PUNT *et al*. (1994).

RESULTS

This study uses generic pollen features to compare endemic *Asteroideae* within different tribes. The characterisation of the various pollen types was achieved based on morphological and biometrics features. The statistical validity of the samples was tested through variance analysis of biometrics parameters at the different taxonomic levels – species, genera and tribes. A concise description of pollen grains is given below.

TABLE 1 - Pollen characterisation of the endemic *Asteroideae* of the Archipelago of Madeira. Table present the studied taxa, their distribution among *Asteroideae* tribes and MADJ voucher specimen numbers.

N.º	Taxa	Herbarium Collection
	Anthemideae	
1.	*Argyranthemum dissectum* (Lowe) Lowe	MADJ-R.3568
2.	*Ar. haematomma* (Lowe) Lowe	MADJ-R.3576
3.	*Ar. pinnatifidum* (L. f.) Lowe subsp. *pinnatifidum* Rustan	MADJ-R.3567
4.	*Ar. pinnatifidum* (L. f.) Lowe subsp. *montanum* Rustan	MADJ-R.8033
5.	*Ar. pinnatifidum* (L. f.) Lowe subsp. *succulentum* (Lowe) Humphries	MADJ-R.3578
6.	*Ar. thalassophilum* (Svent.) Humphries	MADJ-R.4668
7.	*Artemisia argentea* L'Héritier	MADJ-R.3595
	Calenduleae	
8.	*Calendula maderensis* DC.	MADJ-R.2712
	Cynareae	
9.	*Carduus squarrosus* (DC.) Lowe	MADJ-R.2524
10.	*Carlina salicifolia* (L. f.) Cavanilles var. *salicifolia*	MADJ-R.7951
11.	*C. salicifolia* (L. f.) Cavanilles var. *inermis* Lowe	MADJ-R.3627
12.	*Cheirolophus massonianus* Lowe	MADJ-R.8305
13.	*Cirsium latifolium* Lowe	MADJ-R.3621
	Inulaeae	
14.	*Helichrysum devium* J. Y. Jonhson	MADJ-R.3716
15.	*H. melaleucum* Rchb.ex Holl	MADJ-R.3720
16.	*H. monizii* Lowe	MADJ-R.3736
17.	*H. obconicum* DC.	MADJ-R.8211
18.	*Schizogyne sericea* (L. f.) Schultz Bip.	MADJ-R.8801
19.	*Phagnalon hansenii* Quaiser & Lack	MADJ-R.2889
	Senecioneae	
20.	*Pericallis aurita* (L'Heritier) B. Nord	MADJ-R.3777
21.	*Senecio incrassatus* Lowe.	MADJ-R.3801

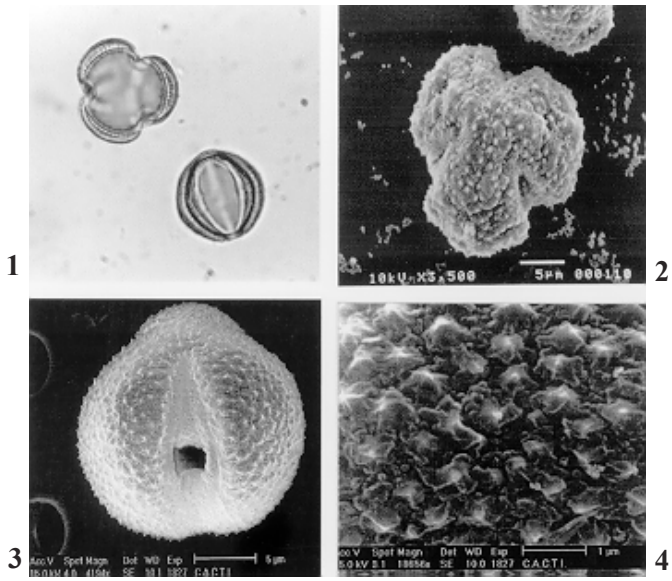

Fig. 1 - Microphotographs of *Artemisia argentea* L'Héritier pollen obtained by light microscope and scanning electron microscope. Light microscope: 1. polar view and equatorial view (x1000). Scanning microscope: 2. polar view, with an aspect of the mesocolpia. 3. an aspect of the apertural system, with the pore. 4. pollen sporoderm ornamentation – microspinules.

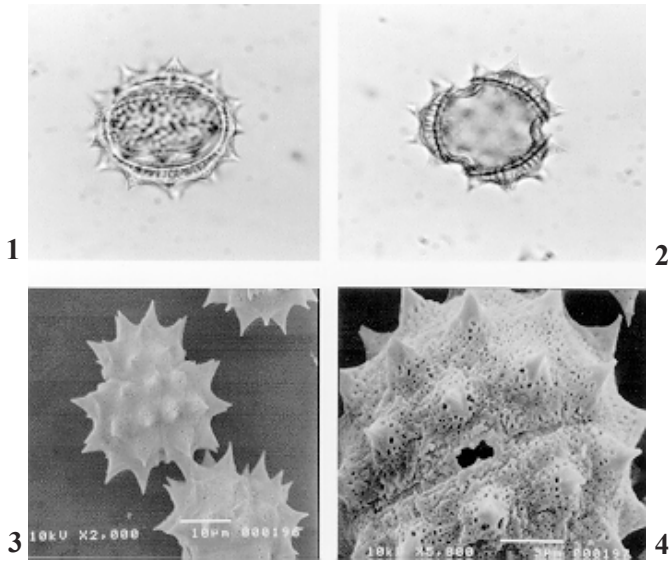

Fig. 2 - Microphotographs of *Argyranthemum haematomma* (Lowe) Lowe pollen obtained by light microscope and scanning electron microscope. Light microscope: 1. equatorial view (x1000). 2. polar view with an aspect of the colpus and spines (x1000). Scanning microscope: 3. pollen polar view with colpus. 4. an aspect of the apertural system, with pore, middle constriction and rugous tectate-perforate exine.

TABLE 2 - Pollen characterisation of endemic Asteroideae from the Archipelago of Madeira. Major biometric features of endemic Asteroideae pollen. The average values for each pollinic parameter are presented. P - polar axis; E - equatorial axis; ExE - equator exine thickness; AE - spine or spinules height. All measures are expressed in μm.

Taxa	P	E	P/E	Shape	ExE	AE	Ornamentation
Ar. dissectum	35.7±1.2	36.0±1.9	0.99±0.03 [0.97-1.03]	Oblate-spherical	9.5±0.5	4.4±0.5	Conical spines
Ar. haematomma	38.6±1.1	38.0±1.0	1.00±0.03 [0.92-1.03]	Spherical	9.2±0.6	4.7±0.6	Narrowed spines
Ar. pinnat. subsp. *succulentum*	36.3±0.8	35.3±0.8	1.03±0.03 [0.98-1.03]	Prolate-spherical	9.2±0.4	4.5±0.5	Narrowed spines
Ar. pinnat. subsp *montanum*	35.9±1.0	34.9±0.6	1.03±0.03 [1.01-1.07]	Prolate-spherical	8.7±0.4	4.1±0.4	Conical spines
Ar. pinnat. subsp *pinnatifidum*	39.3±0.8	39.2±1.4	1.00±0.03 [0.97-1.10]	Spherical	8.9±0.6	4.4±0.5	Conical spines
Ar. thalassophilum	35.2±1.0	35.3±1.0	0.99±0.04 [0.96-1.03]	Oblate-spherical	9.4±0.6	3.8±0.4	Broadly-base spines
A. argentea	24.0±1.0	25.8±1.0	0.93±0.03 [0.90-0.98]	Oblate-spherical	3.9±0.3	0.6±0.2	Micropsinules
Cal. maderensis	58.8±1.8	56.4±2.2	0.99±0.06 [0.89-1.08]	Oblate-spherical	10.1±0.7	6.3±0.8	Narrowed spines
Ca. squarrosus	52.0±2.1	52.3±2.1	1.00±0.09 [0.88-1.14]	Spherical	9.7±0.8	4.6±0.6	Broadly-base spines
C. salic. var. *salicifolia*	57.7±1.4	57.7±1.3	1.0±0.07 [0.93-1.11]	Spherical	12.8±1.0	2.6±0.5	Broadly-base spinules

TABLE 2 (Cont.)

Taxa	P	E	P/E	Shape	ExE	AE	Ornamentation
C. salic. var. *inermis*	57.0±2.0	57.7±2.0	0.99±0.05 [0.93-1.07]	Oblate-spherical	11.6±0.6	2.1±0.4	Broadly-base spinules
Ch. massonianus	63.9±5.9	70.8±5.9	0.90±0.02 [0.89-0.91]	Oblate-spherical	12.1±0.7	5.4±0.7	Broadly-base spines
Ci. latifolium	64.8±3.7	65.8±3.3	0.98±0.08 [0.89-1.09]	Oblate-spherical	14.5±1.3	6.3±0.8	Broadly-base spines
H. devium	29.3±0.9	28.7±1.2	1.02±0.03 [1.00-1.07]	Prolate-spherical	6.6±0.5	3.5±0.5	Conical spines
H. melaleucum	25.3±2.1	25.7±0.5	1.00±0.03 [0.97-1.04]	Spherical	5.8±0.5	3.3±0.5	Conical spines
H. monizii	29.1±1.1	29.5±1.5	0.99±0.06 [0.93-1.07]	Oblate-spherical	6.3±0.5	2.2±0.4	Broadly-base spinules
H. obconicum	26.3±0.9	26.4±1.2	0.99±0.08 [0.86-1.09]	Oblate-spherical	5.6±0.8	3.0±0.3	Conical spinules
P. aurita	32.1±0.9	32.1±0.9	1.0±0.05 [0.94-1.10]	Spherical	6.8±0.4	5.8±0.5	Narrowed spines
Ph. hansenii	29.0±0.8	29.1±1.0	0.99±0.02 [0.97-1.01]	Oblate-spherical	7.1±0.6	3.2±0.4	Conical spines
Sch. sericea	36.2±1.0	36.8±1.1	0.98±0.03 [0.94-1.00]	Oblate-spherical	7.9±0.6	4.2±0.4	Broadly-base spines
S. incrassatus	30.9±0.6	31.7±1.0	0.96±0.02 [0.94-0.99]	Oblate-spherical	6.6±0.6	3.1±0.4	Conical spinules

POLLEN DESCRIPTION

Anthemideae tribe

This tribe is represented by 7 endemic taxa (see Table 1): 4 species and 3 subspecies. Pollen grains of these taxa show the following features: Pollen has echinate or microechinate ecaveate (non-caveate). This feature is the principal difference between *Artemisia argentea* L'Héritier and the remaining *Anthemideae* taxa pollen. The exine sculpture in *A. argentea* pollen is microechinate, without micro-perforations and with microspinules, averaging 0.5 μm wide and from 0.4 to 0.6 μm height, irregularly arranged (Table 2, Fig. 1). The pollen of *Argyranthenum* differs in having an echinate ornamentation with spines > 4 μm and an average of 12 spines in equatorial plane (Table 2, Fig. 2). Spines are uniformly arranged, with an average distance between them of 7.4 μm to 10.0 μm. Spines have narrowed or slightly conical shapes (Table 2), average basis width 4.7-5.7 μm and height of 3.7-4.7 μm, with micro-perforations, columellae extending, to $^{1}/_{2}$ or $^{2}/_{3}$ of their height. The pollen shape of endemic *Anthemideae* varies between oblate-spherical and prolate-spherical shapes, circular or subcircular in equatorial view. The pollen are three- zonocolporate, 3-lobed in polar view, with prominent mesocolpia, average mesocolpium length 15.7 μm for *A. argentea* and 22.0 μm for *Argyranthenum pinnatifidum* (L. f.) Lowe subsp. *pinnatifidum* Rustan. The P and E values vary between 24.0 ± 1.0 μm and 25.8 ± 1.0 μm for *A. argentea* and 39.3 ± 0.8 μm and 39.2 ± 1.4 μm for *A. pinnat*. subsp. *pinnatifidum*. The exine has an average thickness of 7.4-9.1 μm at the pole and 8.7-9.5 μm at the equator, nexine average thickness 1-2 μm, and sexine of 4-5 μm. Tectate-perforate exine, irregularly micro-perforate, with lumina < muri (Fig. 2). However, the values for pollen wall in the *A. argentea* are 2.5 μm of exine thickness at the pole and 3.9 μm at the equator, nexine average thickness 1 μm, and sexine less than 3 μm. The aperture system is composed by the ectoaperture and endoaperture. The ectoaperture is a colpus with acute ends. In the ectoaperture of *Argyranthenum* pollens, near the endoaperture, the sexine is thicker, protuberant and very irregular. The endoaperture is an endocolpus with acute ends, with or without middle constriction. The endoaperture in *A. argentea* is usually a pore and easily visible. The pores are average of 2.9 μm in length and 1.2 μm width.

Endemic *Argyranthenum* pollens can be distinguished by their sizes (Table 2) or specific exine characters, *i. e*. spine shapes and exine ornamentation.

Calenduleae tribe

This tribe is represented by one endemic species (see Table 1) with the following pollen features: Pollen is echinate with oblate-spherical shape, sub-elliptic in equatorial view. P and E axes with sizes average between 58.8 ± 1.8 μm and 56.4 ± 2.2 μm,

respectively (Table 2, Fig. 3) Mesocolpia average length 32.3 ∝m. Exine with an average thickness of 10.3 ∝m at the pole and 10.1 ∝m at the equator. Nexine and sexine thickness similar 5 ∝m. Tectate-perforate exine, caveae, lumina much smaller than muri, smooth and slightly micro-perforated view. Displayed in equatorial plane, 17 narrowed spines with micro-perforations at their basis. Ectoaperture has a colpus with acute ends, endoaperture as an endocolpus without middle constrictions, depressed exine at the margins of colpus with columelae.

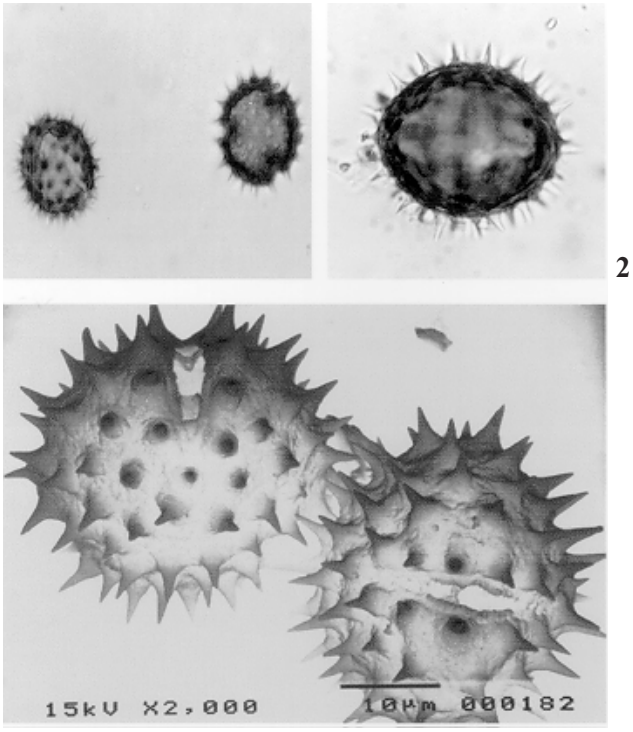

Fig. 3 - Microphotographs of *Calendula maderensis* DC. pollen obtained by light microscope and scanning electron microscope. Light microscope: 1. & 2. equatorial and polar views (x1000). Scanning microscope: 3. pollen aspect with the view of apertural system, spines and the spines ornamentation.

Cynareae tribe (= *Cardueae*)

This tribe is represented by 3 endemic species and 2 varieties (see Table 1) with the following pollen features: Pollen has echinate with oblate-spherical, spherical or prolate-spherical shapes, three-zonocolporate with circular or sub-elliptic shape in equatorial view. P and E axes with sizes average between 52.0-64.9 ∝m and 57.7-65.8 ∝m, respectively (Table 2, Fig. 4). Despite this *Carduus squarrosus* (DC.) Lowe shows

the smallest pollen and *Cirsium latifolium* Lowe the largest pollen, with sizes of 52.0 ± 2.1 μm (P) and 57.7 ± 2.2 μm (E), and 64.8 ± 3.7 μm and 65.8 ± 3.3 μm, respectively. Average mesocolpia length 30.0-40.8 μm. Exine average thickness 9.9-13.8 μm at the pole and 9.7-14.5 μm at the equator. *Carlina* varieties can be distinguished by their exine thickness at the pole or equator – 12.1 and 12.8 μm for *Carlina salicifolia* (L. f.) Cavanilles var. *salicifolia* or 11.1 and 11.6 μm for *Carlina salicifolia* (L. f.) Cavanilles var. *inermis* Lowe. Nexine thickness is larger than sexine. Average nexine of 6.0 μm for *Carlina* varieties, 5.0 μm for *C. squarrosus*, 6.0-7.0 μm for *Cheirolophus massonianus* Lowe and 8.0 μm for *C. latifolium*. Sexine thickness with an average of 3.0-6.0 μm. Reticulate exine, ecaveate or caveate (*Carduus squarrosus* (DC.) Lowe), lumina ≥ muri. However, exine shows irregularly displayed scabrae in the pollen of *Carlina*, a generally smooth view in *C. squarrosus* or a rugous view in pollens of *C. massonianus* and *C. latifolium*. Exine ornamentation represented by broadly based spines or spinules. *Carlina* pollen has 17 flatted spinules displayed in equatorial plane, without micro-perforations. *C. squarrosus* shows 15 non-microperforated flatted spines, while *C. latifolium* and *C. massonianus* have 14 flatted spines with micro-perforations in half of their height. The aperture system is composed by an ectoaperture with elliptic colpus and an endoaperture with endocolpus with (*C. squarrosus*) or without (other taxa) middle constriction. Pores are circular surrounded by rugous nexine in *Carlina* and *C. massonianus* pollen or by extremely rugous and depressed nexine, with regular displayed scrabae across the ectocolpus in *Ca. squarrosus*. Pollen of *Ci. latifolium* shows pores surrounded by depressed and granular nexine with the margins of ectocolpus with scabrae.

Inulaeae tribe

This tribe is represented by 6 endemic species (see Table 1) with the following pollen features: Pollen is echinate with oblate-spherical, spherical or prolate-spherical shapes, three- zonocolporate, circular in equatorial plane (Fig. 5). P and E axes with sizes average between 25.3-36.1 μm and 25.7-36.8 μm. Despite this, *Schizogine sericea* (L. f.) Schultz Bip shows the pollen with the longest dimensions – 36.2 ± 1.0 μm and 36.8 ± 1.1 μm (Table 2). Average mesocolpia length 14.5-17.5 μm. Pollen is parasyncolpate with apocolpial field length of 10.0-11.1 μm for *Helichrysum* taxa, 12.0 μm for *Phagnalon hansenii* Quaiser & Lack and 15.0 μm for *S. sericea*. Exine average thickness has 5.6-6.7 μm at the pole and 5.6-7.1 μm at the equator. Nexine and sexine average thickness were different with 1-3 μm and 2-3.5 μm for *Helichrysum* taxa, ≤ 2 μm and 2-3 μm for *S. sericea* and 2 μm and > 2 μm for *P. hansenii*. Despite this nexine and sexine was the same thickness (2.5-3.0 μm) in *H. melaleucum* Rchb.ex Holl and *H. obconicum* DC pollen. Tectate-perforate exine, caveate, lumina ≤ muri, smooth view (*Helichrysum* and *Phagnalon* pollen) or rugous and irregularly micro-perforated

(*S. sericea*). The exine ornamentation has conical or broadly based spines and spinules. *H. monizii* Lowe and *H. obconicum* show 13 spinules displayed in equatorial plane with micro-perforations only at their basis. The remaining *Helichrysum* pollens have 12 (*H. devium*) or 13 (*H. melaleucum*) conical spines with micro-perforations only at their basis. Pollen of *S. sericea* shows 12 broadly based spines with microperforations in half of their height. Finally, *P. hansenii* shows 15 narrowed conical spines with micro-perforations in one third of their height. Aperture system composed by an ectoaperture with a large colpus, a mesoaperture which is difficult to see and an endoaperture with a elliptic endocolpus with (*P. hansenii*, *H. obconicum* and *H. monizii*) or without (remaining taxa) middle constriction. Pores of *P. hansenii* pollen are surrounded by irregular reticulate nexine.

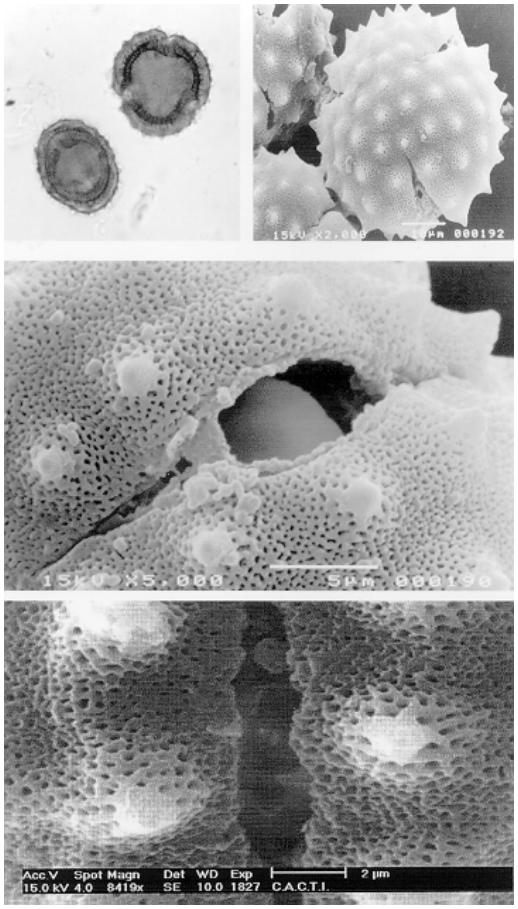

Fig. 4 - Microphotographs of *Carlina salicilofia* (L. f.) Cavanilles var. *salicifolia* pollen obtained by light microscope and scanning electron microscope. Light microscope: 1. polar and equatorial view (x1000). Scanning microscope: 2. pollen polar view with colpus. 3. & 4. Aspects of the apertural system and sporoderm ornamentation. Pore without constriction, reticulate exine.

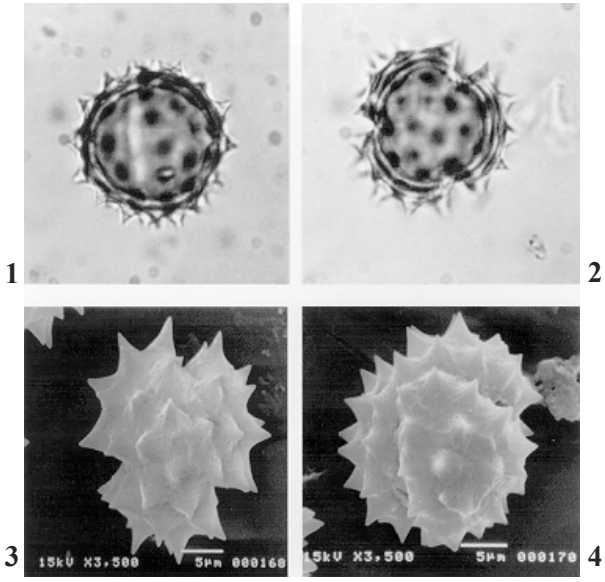

Fig. 5 - Microphotographs of *Helichrysum melaleucum* Rchb. ex Holl pollen obtained by light microscope and scanning electron microscope. Light microscope: 1. equatorial view (x1000). 2. polar view with the mesocolpia (x1000). Scanning microscope: 3. polar view with spines ornamention. 4. Aspects of the sporoderm ornamentation with smooth tectate-perforate exine.

Senecioneae tribe

This tribe is represented by 2 endemic species (see Table 1) with the following pollen features: Pollen is echinate with oblate-spherical or spherical shapes, three-zonocolporate, subcircular or circular in equatorial and polar views. P and E axes with sizes average between 30.9 ± 0.6 ∝m and 31.7 ± 1.0 ∝m for *Senecio incrassatus* Lowe, 32.1 ± 0.9 ∝m and 32.1 ± 0.9 ∝m for *Pericallis aurita* (L'Heritier) B. Nord (Table 2, Fig. 6). Average mesocolpia length 15.1 or 17.1 ∝m, respectively. However, pollen from *P. aurita* can be distinguish from *S. incrassatus* pollen by their parasyncolpate shape with apocolpial field length of 15.0 ∝m. Exine average thickness 6.2 ∝m at the pole and 6.6 ∝m or 6.8 ∝m at the equator. However, the nexine and sexine shows a similar thickness of 2.0-3.0 ∝m in the *S. incrassatus* pollen, but there thickness differs in *P. aurita* (nexine 1.0-2.0 ∝m, sexine < 3.0 ∝m). Tectate-perforate exine, caveate, lumina < muri and more or less smooth view. *S. incrassatus* pollen have 15 conical and irregularly micro-perforated spinules displayed in equatorial plane. *P. aurita* pollen shows 15 narrowed conical spines with micro-perforations till third of their height. The aperture system has composed by an ectoaperture as colpus with acute ends and an endoaperture as elliptic endocolpus with (*S. incrassatus*) or without (*P. aurita*) middle constriction.

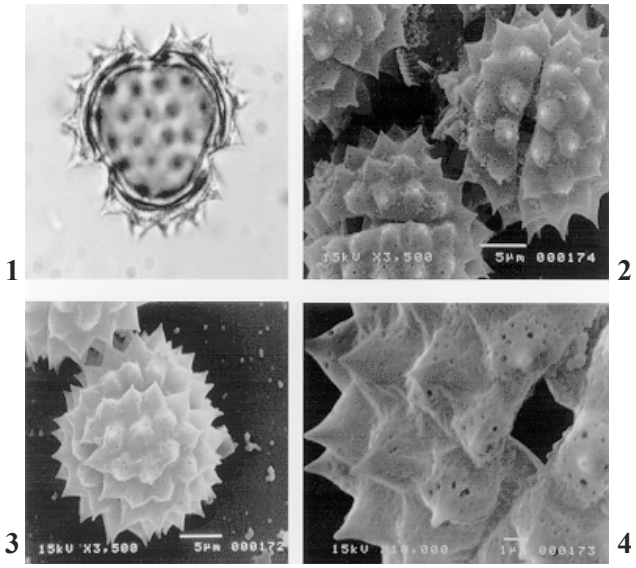

Fig. 6 - Microphotographs of *Senecio incrassatus* Lowe pollen obtained by light microscope and scanning electron microscope. Light microscope: 1. polar view with the mesocolpia (x1000). Scanning microscope: 2. apertural system without constrictions. 3. general pollen view, with the spines ornamentation. 4. tectate-perforate exine with smooth aspect.

Pollen types among the endemic *Asteroideae*

The presence of pollen grains with prominent spines or spinules and reduced micro-spinules indicates the existence of two major pollen models among the endemic *Asteroideae* – microechinate and echinate. These models can be represented by two taxa from *Anthemideae* tribe – *A. argentea* and *Ar. haematomma*. Microphotographs show details of the sporoderm ornamentation and shape of pollen of both taxa (Figs. 1 & 2). In spite of this, the endemic *Asteroideae* can be described as different pollen types.

Artemisia pollen type

This type is typical of the microechinate pollen. Among the endemic *Asteroideae*, *A. argentea* is the unique species representative of such a pollen type (Fig. 1). Ecaveate pollen has similarly to the Anthemoid type (BOLICK, 1991).

Argyranthenum pollen type

Argyranthenum type, which corresponds to the *Anthemis* (Anthemoid) type of Mediterranean flora, resembles the pollen of *Argyranthenum* endemics. The pollen of

A. haematomma can represent this type. Pollen has median sizes (P and E axes), ecaveate, endocolpus, without middle constriction, tectate-perforate exine, lumina < muri, 12 equatorial displayed spines (Fig. 2).

Carlina pollen type

Carlina type groups the pollen of *Cynareae* endemics and *C. maderensis*. Pollen of this type has large P and E sizes, ecaveate or caveate, reticulate exine, lumina ≥ muri, with verrucae in outer exine surface, 14-17 spines or spinules displayed in equatorial plane (Fig. 4).

Helichrysum pollen type

Helichrysum pollen type also resembles *S. sericea* pollen, but having tectate-perforate exine, caveate, lumina ≤ muri, 12 or 13 spines or spinules displayed in equatorial plane (Fig. 5).

Senecio pollen type

Senecio pollen type is also similar to *S. incrassatus*, *P. hansenii* and *P. aurita* pollen. This pollen type has middle P and E sizes, tectate-perforate exine, caveate, lumina ≤ muri. Fifteen spines or spinules are displayed in pollen equatorial plane (Fig. 6).

DISCUSSION

Pollen of the analysed endemic taxa have many features in common with other *Asteroideae* (DIEZ, 1987). The present study remains in agreement with the previous works on *Asteroideae* pollen (DIMON, 1971; SKVARLA *et al*., 1977; TORMO *et al*., 1984; TORMO & UBERA, 1987). The P/E ratio shows that the endemic *Asteroideae* pollen can vary between oblate-spherical and prolate-spherical shapes. This feature is similar to the pollen shapes of other European non-endemic *Asteroideae* (TORMO *et al*., 1984; DIEZ, 1987; TORMO & UBERA, 1987; pers. unpubl. data). Taking the P/E ratio and size, *A. argentea* is the endemic more distantly displaced from the remaining taxa, which can be determined by its wind pollination. Moreover, this plant and the *Carlina* endemics shown very distinct pollen sizes, having P and E average values that are equal to the upper limits of plant species from Iberian or Balearic flora (TORMO *et al*., 1984; TORMO & UBERA, 1987; VALLÉS *et al*., 1987).

The palynological analyses of the endemic *Asteroideae* reveal the existence of different pollen models and types determined by the variation of some morphometric features, especially the P and E sizes and exine ornamentation. The pollen models

observed among the endemic *Asteroideae* are the microechinate and echinate pollen. The existence of these pollen models was previously described (STIX, 1960; SKVARLA *et al*., 1977; HEYWOOD & HUMPHRIES, 1977; ROWLEY, 1981; TORMO & UBERA, 1987). However, the echinate pollen group appeared to be non-homogeneous, since there are data suggesting the existence of several pollen types (TORMO *et al*., 1984; DIEZ, 1987). These types are usually described based on morphological features and consequently they received taxonomic attention. The pollen data suggest five different pollen types among the endemic *Asteroideae* pollen. The pollen types are the *Artemisia* type, which corresponds to microechinate pollen, and the *Argyranthemum*, *Helichrysum*, *Senecio* and *Carlina* types corresponding to the echinate pollen. The *Artemisia* pollen type agrees with the earlier findings of STIX (1960). The *Argyranthemum* type corresponds to the *Anthemis* type proposed for the Mediterranean flora (TORMO & UBERA, 1987). The morphological features of *Argyranthemum* pollen are the same, but the pollen sizes of the endemics are larger. The *Senecio* type seems to be closely related to the *Senecio vulgaris* type described by DIEZ (1987). However, the DIEZ (1987) description of *Senecio vulgaris* type also includes, pollen from the genera *Carduus*, *Carlina* and *Cirsium*. However, our data show that such morphometric features as P and E sizes, exine tickness, nexine and sexine development, mesocolpia length and sporoderm structure, relate *S. incrassatus* pollen more closely with pollen from *P. hansenii* or *P. aurita* than to the pollen of endemic *Cynareae* from Madeira. For this reason we propose the *Carlina* type, which should included the *Cynareae* endemic pollen. This type corresponds to the *Carlina* type described before by TORMO *et al*. (1984). Since some morphometric features, such us the P and E sizes, exine tickness and mesocolpia length, of *C. maderensis* pollen are very similar to the *Carlina*, it was included in this type. However, *Calendula maderensis* pollen is also very similar to the one of *Calendula arvensis* which type was described before by DIEZ (1987) and can be pulled out of the *Carlina* type. Finally the *Helichrysum* type is closely similar to the *Inula* type described by SKVARLA *et al*. (1977).

CONCLUSIONS

This morphometric analysis of the pollen of endemic *Asteroideae* from Madeira revealed the existence of different pollen types. Five pollen types are described in order to characterise the endemic pollen morphological and biometric features. However, the continuous gradation of these features among the described endemic *Asteroideae* do not allow us to conclude that these pollen types are completely distinct from each other (SKVARLA & TURNER, 1966; SINGH & JOSIH, 1969). These data can, however, contribute to existing knowledge about *Asteroideae* palynology and help solve persisting problems of its taxonomy (SKVARLA *et al*., 1977; BREMER, 1987; BREMER *et al*., 1992; WAGENITZ, 1992).

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