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**Epidermal studies in *Euphorbia* subsect. *Galarraei* (*Euphorbiaceae*):
E. squamigera and its allies**

Abstract

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The epidermis of 7 closely related and often misinterpreted species of *Euphorbia* subsect. *Galarraei* (*E. squamigera*, *E. clementei*, *E. margalidiana*, *E. paniculata*, *E. bivonae*, *E. melitensis*, and *E. nereidum*) were investigated under the light microscope and scanning electron microscope. Epidermis and stomata cell dimensions, epidermis and stomata cell density, stomatal type, anticlinal wall thickening, papilla type, and trichome length and ornamentation were studied. High intraspecific variability was observed in some characters. Trichome ornamentation supports the union of *E. atlantis* var. *villosa* and *E. clementei* var. *villifolia* in a single taxon: *E. clementei* subsp. *villosa*.

Introduction

The *Euphorbia squamigera* complex is formed of 7-12 species (Vindt 1953; Greuter & al. 1986). We recognize 7 species: *E. clementei* Boiss. with subsp. *clementei*, subsp. *faurei* (Maire) Vicens & al. and subsp. *villosa* (Faure & Maire) Vicens & al.; *E. squamigera* Loisel.; *E. margalidiana* Kuhbier & Lewej.; *E. paniculata* Desf. with subsp. *paniculata*, subsp. *welwitschii* (Boiss. & Reut.) Vicens & al. and subsp. *monchiquensis* (Franco & P. Silva) Vicens & al.; *E. nereidum* Jahand. & Maire; *E. bivonae* Steud. with subsp. *bivonae* and subsp. *tunetana* Murb.; and *E. melitensis* Parl. They form a group of closely related taxa on which controversial opinions are held regarding their variability and taxonomic delimitation. Leaf epidermal features have proved useful taxonomic markers in *Euphorbia* (Vindt 1960; Raju & Rao 1987; Simon & Blanché 1988; Molero & Rovira 1992; Benedí & Orell 1993; Simon 1993). The little information there is on the cuticular and epidermal structures of the above-mentioned species is found in Vindt's (1960) study of taxa from Morocco, plus some data in Sehgal & Paliwal (1974). Light (LM) and scanning electron microscopy (SEM) of foliar cuticle and epidermis of these species have been carried out in order to fill this gap and to use the results to better understand the taxonomic relationships.

Materials and methods

Fresh plants of thirty populations were collected in different parts of the Iberian Peninsula, the Balearic Islands, Morocco and Tunisia. Vouchers were deposited in the herbarium of the Facultat de Farmàcia, Universitat de Barcelona (BCF). Ten herbarium specimens were obtained from the herbaria of Real Jardín Botánico de Madrid (MA), the Conservatoire et Jardin botaniques de la Ville de Genève (G), the Institut de Botanique, Montpellier (MPU), and the Muséum Requier (AV). We thus could study each species throughout its geographical range. A list of specimens investigated follows.

E. clementei subsp. *clementei*. – **Hs:** Málaga: inter Ronda et Atajate (locus classicus), 30S UF65, 20 May 1990, *Blanché & Vicens* (BCF 38608). **Lu:** Algarve: S. Bras de Alportel versus S. Romão, 29S NB91, 18 May 1990, *Blanché & Vicens* (BCF 38610). **Ma:** Kenitra: Zäer, from Rabat to Rommani, 29S QT12, *Molero & Vicens* (BCF 38612). **Al:** Aurès: Wilaya Batna, Dj. Chelia, 6/40E-35/18N, 7 June 1984 *Podlech* (G 284076). Tizi Ouzou: Djurjura, Djebel Aizer, 13 June 1980, *Dubuis* (MPU Herb. Dubuis).

E. clementei subsp. *faurei*. – **Ma:** Oujda: Taforalt, Djebel Metchich, 30S WD54, 20 May 1991, *Molero & Vicens* (BCF 38611).

E. clementei subsp. *villosa*. – **Ma:** Meknès: Azrou, Ras el Ma, 30S TC90, 1 June 1991, *Molero & Vicens* (BCF 38613). **Al:** Oran: Bossuet, 21 Apr. 1927, *Faure* (G).

E. squamigera. – **Ga:** Var: env. de Toulon, *Robert* (AV). **Bl:** Balears: Mallorca, Cala Bóquer, 31S EE01, 29 Mar. 1991, *Vicens* (BCF 38614). **Hs:** València: Xeresa, 30S YJ42, 4 Apr. 1990, *Molero & Vicens* (BCF 38616). Alacant: Montgó de Dènia, 31S BC59, 20 Mar. 1989, *Simón* (BCF 38618). Murcia: Sierra Espuña, 30S XG28, 5 June 1991, *Molero & Vicens* (BCF 38619); Cartagena, Peña Blanca, 30S XG76, 8 Apr. 1990, *Molero & Vicens* (BCF 38620). Almería: Turrillas, 30S WF69, 6 Apr. 1990, *Molero & Vicens* (BCF 38621). Granada: Vélez de Benaudalla, 30S VF57, 6 June 1991, *Molero & Vicens* (BCF 38622); Orjiva, 30S VF68, *Benedí* (BCF 38623). Málaga: entre Cómpeta i Frigiliana, 30S VF17, 22 May 1990, *Blanché & Vicens* (BCF 38624). **Ma:** Oujda: Debdou, 30S VC96, 22 May 1991, *Molero & Vicens* (BCF 38625). Agadir: Tizi-n-Test, versant S, 29R NQ61, 30 May 1991, *Molero & Vicens* (BCF 38626); Tizi-n-Test, versant N, 29R NQ62, 30 May 1991, *Molero & Vicens* (BCF 38627); Tizi-n-Test prope Ijoukak, 29R NQ72, 30 May 1991, *Molero & Vicens* (BCF 38628).

E. margalidiana. – **Hs:** Balears: Eivissa, Ses Margalides, 31S CD52, Jun. 1990, *Gradaille*, culta in horto botanico (BCF 38629); ibidem, 26 Aug. 1979, *Regueiro* (MA 250481).

E. paniculata subsp. *paniculata*. – **Hs:** Badajoz: Valdecaballeros, 30S UJ04, 15 May 1990, *Blanché & Vicens* (BCF 38630). **Lu:** Alto Alentejo: Marvão, 29S PD46, 16 May 1990, *Blanché & Vicens* (BCF 38633); Portoalegre, 29S PD36, 15 May 1990, *Blanché & Vicens* (BCF 38634). **Ma:** Rabat: Ain el Aouda, S de Rabat, 6 Apr. 1933, *Maire & Wilczek* (G). **Al:** Annaba: La Calle, route de Bone, 22 Apr. 1915, *Clavé* (G). **Tn:** Jendouba: Ain Draham, Apr. 1920, *Pitard* (G).

E. paniculata subsp. *monchiquensis*. – **Lu:** Baixo Alentejo: Odemira, 29S NB36, 17 May 1990, *Blanché & Vicens* (BCF 38635). Algarve: Monchique, 29S NB33, 18 May 1990, *Blanché & Vicens* (BCF 38636).

E. paniculata subsp. *welwitschii*. – **Lu:** Estremadura: Trejouce, 29S MC78, 3 May 1991, *Molero & Vicens* (BCF 38632).

E. nereidum. – **Ma:** Beni Mellal: Beni Mellal, 29S QR47, 1 June 1991, *Molero & Vicens* (BCF 38637).

E. bivonae subsp. *bivonae*. – **Al:** Alger: Bou-Zarea, supra hospitium militare, 3 Feb. 1867, *Paris* (MPU). **Tn:** Cap-Bon: Aïn-Oktor, 29 May 1992, *Molero, Vicens & Hakim* (BCF 38638). **Si:** Palermo: Palermo, *Zubierleimo* (G).

E. bivonae subsp. *tunetana*. – **Tn**: Sfax: Bou Hedma, Oued Cherchara, 32S ND61, 26 May 1992, *Molero, Vicens & Hakim* (BCF 38639). Gabès: Djebel Tebaga, 32S NC53, 22 May 1992, *Molero & Vicens* (BCF 38640).

E. melitensis. – **Me**: Gozo: Mistra Rocks, 33S VV39, 23 Apr. 1992, *Barceló & Vicens* (BCF 38641).

Light microscopy. – Upper caulinar (non-bracteal) leaves were cut and softened in chloral hydrate (saturated solution) or, when necessary, in Jeffrey's liquid (chromic acid 10 % and nitric acid 40 %, 1 : 1). Epidermal peels were washed, stained with Ruthenium Red and observed under the LM at a 400× magnification. Five optical fields from each specimen were drawn and studied.

Scanning electron microscopy. – Fresh leaves were fixed in glutaraldehyde 2.5 % in cacodylate buffer and stored in ethanol 50 %. Rectangular portions were dehydrated and critical point dried. Herbarium samples were air-dried. Both kinds of samples were sputtered and observed with a Hitachi S 2300 SEM at the electron microscopy service of the Universitat de Barcelona. Terminology for surface description follows Wilkinson (1979) and Barthlott (1990).

Results

Shape of cells (primary sculpture). – The cells are isodiametric in surface view, with a polygonal outline and straight or slightly curved anticlinal walls (Fig. 1 and 2). The outer periclinal walls are either simply domed, or domed and mamillate, or domed and strongly mamillate, or bearing cylindrical papillae (Fig. 3 and 4). The cell lumen protrudes into the papillae (Fig. 5.1). The number of cells per mm² is highly variable in *Euphorbia squamigera*; *E. clementei*, *E. squamigera*, *E. margalidiana*, *E. paniculata*, and *E. nereidum* have larger cells than *E. bivonae* and *E. melitensis*.

Relief of cell wall (secondary sculpture). – The surface of the outer periclinal walls is smooth, but the anticlinal walls present moniliform thickenings, more marked on the abaxial leaf surface. These thickenings are conspicuous under the LM. We also observed them under the SEM, on the inner surface of the wall of sectioned cells (Fig. 5.2), where they appear to be reinforcement structures.

Epicuticular waxes (tertiary sculpture). – Epicuticular waxes are easily washed off by organic solvents (ethanol, amyl acetate) as are used in critical point drying. We observed them only in a few samples from dry herbarium specimens. They are formed by crystalloids of wax in the shape of irregular vertical platelets of type III, according to the classification of Ameluxen & al. (1967) and Wilkinson (1979) (Fig. 5.3).

Stomata. – The distribution of the stomata on the abaxial leaf surface is always regular. On the adaxial surface, the stomata may be distributed regularly or irregularly. In *Euphorbia clementei* subsp. *villosa* and some populations of *E. squamigera* stomata show a regular distribution on the adaxial face but are less numerous than on the abaxial face (hypoamphistomatic distribution). In eastern Algerian populations of *E. clementei* subsp. *clementei* the distribution of stomata is regular adaxially, and their number is higher than on

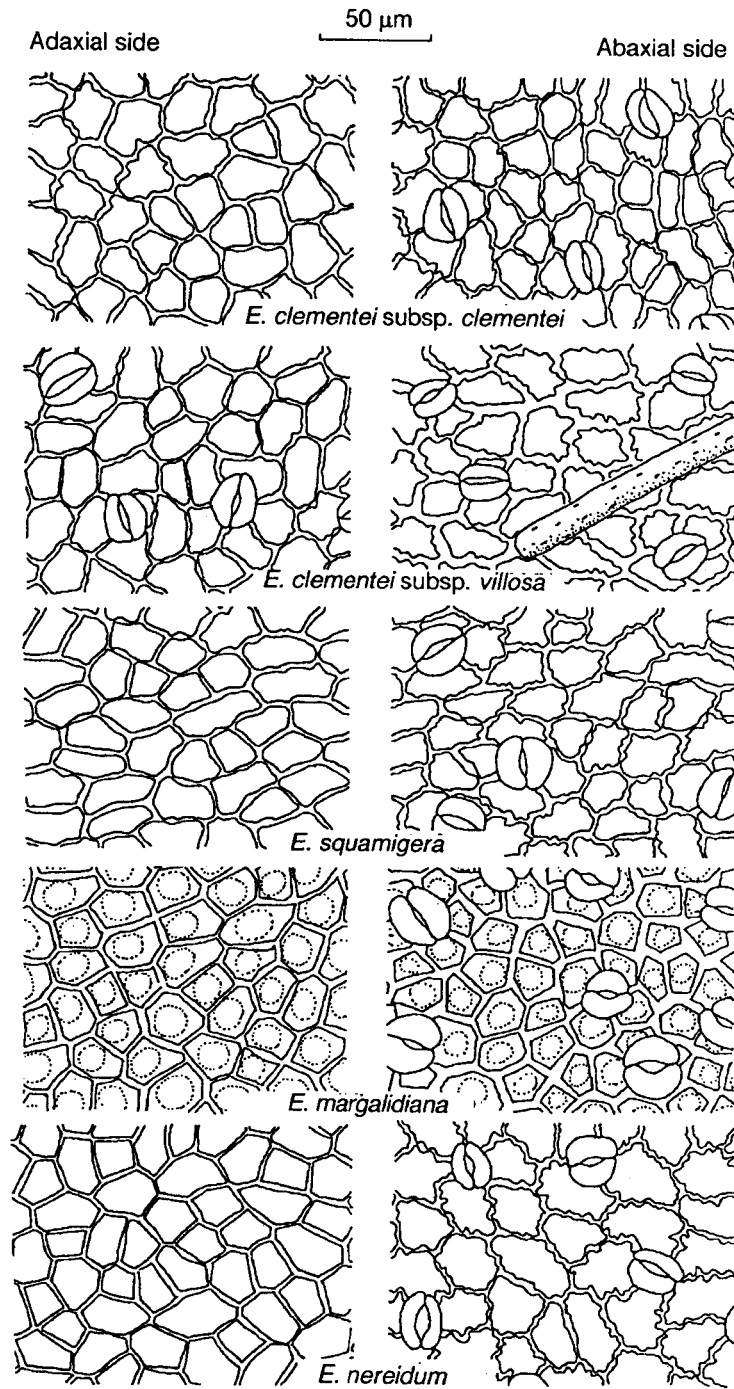


Fig. 1. Adaxial (left) and abaxial (right) face of leaf epidermis, in light microscopy, of *Euphorbia clementei* subsp. *clementei* and subsp. *villosa*, *E. squamigera*, *E. margalidiana*, and *E. nereidum*.

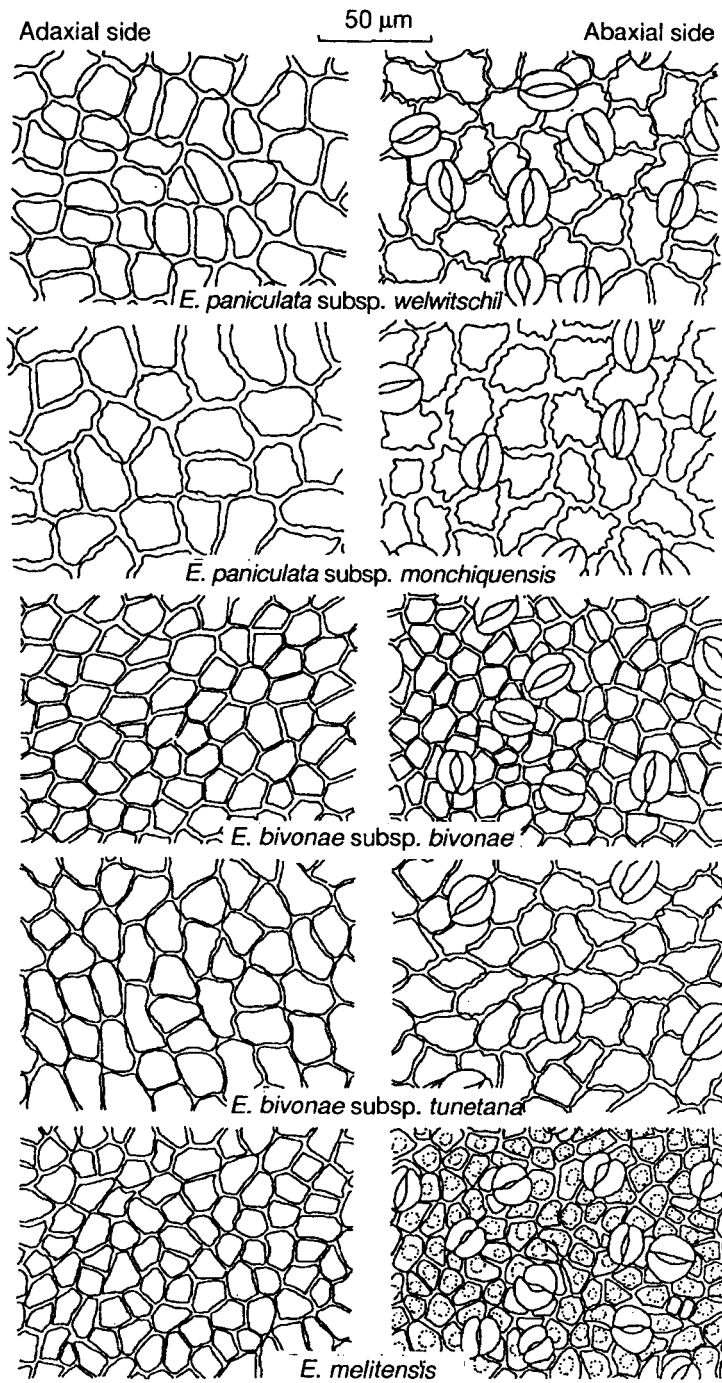


Fig. 2. Adaxial (left) and abaxial (right) face of leaf epidermis, in light microscopy, of *Euphorbia paniculata* subsp. *welwitschii* and subsp. *monchiquensis*, *E. bivonae* subsp. *bivonae* and subsp. *tunetana*, and *E. melitensis*.

Table 1. Stomatal features of adaxial (ad) and abaxial (ab) foliar epidermis [average \pm standard deviation / (total range)]: stomatal frequency, cell frequency, stomatal index, guard cell (GC) length. When stomata are sometimes lacking (0) adaxially, averages are based only on populations where they are present (data summarized from Vicens 1994).

<i>Euphorbia</i>		stomata/mm ²	cells/mm ²	stomatal/cells (%)	GC length (mm)
<i>clementei</i> subsp.	ad	109 \pm 15 (0/88-132)	1333 \pm 221 (1154-1736)	7.5 \pm 0.8 (0/5.9-8.5)	32.8 \pm 3.3 (0/27.3-38.6)
<i>clementei</i>	ab	174 \pm 8 (255-374)	1315 \pm 315 (868-1978)	11.1 \pm 3.9 (4.3-17.9)	30.8 \pm 3.7 (25.0-36.4)
– subsp. <i>faurei</i>	ad	–	769 \pm 44 (703-835)	–	–
	ab	73 \pm 15 (44-88)	809 \pm 49 (725-879)	8.2 \pm 1.7 (5.1-9.9)	38.6 \pm 3.2 (34.1-45.5)
– subsp. <i>villosa</i>	ad	51 \pm 16 (33-77)	1135 \pm 107 (989-1286)	4.3 \pm 1.4 (2.5-7.2)	34.3 \pm 4.9 (27.3-45.5)
	ab	114 \pm 20 (77-154)	993 \pm 114 (868-1187)	10.3 \pm 1.2 (8.1-12.0)	35.8 \pm 4.8 (27.3-43.2)
<i>squamigera</i>	ad	43 \pm 15 (0/22-66)	1044 \pm 254 (560-1791)	4.2 \pm 1.5 (0/1.7-7.0)	35.0 \pm 3.0 (0/29.5-40.9)
	ab	123 \pm 75 (44-307)	1036 \pm 372 (582-2451)	10.3 \pm 2.6 (4.6-16.2)	33.1 \pm 4.7 (22.7-47.7)
<i>margalidiana</i>	ad	–	1291 \pm 161 (1055-1549)	–	–
	ab	97 \pm 28 (55-143)	1210 \pm 205 (967-1626)	7.4 \pm 1.7 (4.1-9.7)	36.3 \pm 3.1 (25.0-38.6)
<i>paniculata</i> subsp.	ad	–	1172 \pm 164 (846-1516)	–	–
<i>paniculata</i>	ab	197 \pm 52 (99-297)	1173 \pm 230 (736-1835)	14.4 \pm 2.7 (9.5-20.5)	30.9 \pm 2.5 (25.0-36.4)
– subsp. <i>mon-</i>	ad	–	1120 \pm 213 (879-1549)	–	–
<i>chiquensis</i>	ab	197 \pm 42 (143-253)	1119 \pm 135 (923-1286)	14.9 \pm 2.1 (10.7-17.5)	35.1 \pm 2.1 (25.0-40.9)
– subsp. <i>wel-</i>	ad	–	919 \pm 88 (802-1044)	–	–
<i>witschii</i>	ab	145 \pm 25 (110-176)	905 \pm 92 (791-1022)	13.7 \pm 1.1 (12.2-15.5)	35.0 \pm 1.5 (34.1-38.6)
<i>nereidum</i>	ad	–	1356 \pm 91 (1253-1516)	–	–
	ab	138 \pm 15 (121-165)	1099 \pm 47 (1044-1165)	11.2 \pm 1.3 (9.4-13.3)	30.0 \pm 1.7 (27.3-34.1)
<i>bivonae</i> subsp.	ad	–	1864 \pm 560 (989-2582)	–	–
<i>bivonae</i>	ab	172 \pm 57 (88-264)	2289 \pm 714 (1297-3253)	7.0 \pm 1.2 (5.1-9.6)	33.0 \pm 5.1 (25.0-40.9)
– subsp. <i>tune-</i>	ad	–	1422 \pm 98 (1297-1593)	–	–
<i>tana</i>	ab	172 \pm 57 (88-170)	1516 \pm 177 (1264-1824)	7.4 \pm 1.0 (6.2-9.2)	30.8 \pm 3.4 (25.0-36.4)
<i>melitensis</i>	ad	–	2873 \pm 163 (2681-3121)	–	–
	ab	358 \pm 31 (302-396)	3110 \pm 219 (2835-3396)	10.3 \pm 0.8 (9.1-11.2)	27.3 \pm 1.4 (25.0-29.5)

the abaxial surface (epiamphistomatic distribution). In all other cases the distribution is irregular: stomata are distributed in strips on either side of the midvein of the leaf (hypostomatic distribution). In some populations of *E. squamigera* and *E. bivonae* we also found scarce, scattered stomata by the secondary veins.

The stomata are always anomocytic, which confirms the results of Vindt (1960) and Sehgal & Paliwal (1974), although Vindt (1960) found some paracytic stomata in *Euphorbia bivonae*.

The number of stomata per mm² is highly variable within each taxon. The stomatal index (number of stomata per total number of cells) is more constant (Table 1). Hygrophilous and mesophilous species, such as *Euphorbia paniculata* or *E. nereidum*, have a higher stomatal index than xerophytes as *E. bivonae*.

The length of guard cells was also measured (Table 1). Some populations stand out when average values are considered, but the extreme values overlap with those of other populations so that this character is of no taxonomic avail.

Table 2. Indumentum and cellular features of adaxial (ad) and abaxial (ab) foliar epidermis (data summarized from Vicens 1994): trichome length and density [average \pm standard deviation / (total range)], papillae shape (PS: 1, simple domes; 2, mamillate domes; 3, strongly mamillate domes; 4, cylindrical papillae), thickenings of anticlinal walls (TAW: – absent; + weak; ++ strong). When trichomes are sometimes lacking (0), averages are based only on populations where they are present.

<i>Euphorbia</i>		trichome length (mm)	trichomes/cm ²	PS	TAW
<i>clementei</i> subsp.	ad	–	–	1/2	+
	ab	–	–	1/2	+ / ++
– subsp. <i>faurei</i>	ad	–	–	1	+
	ab	–	–	1	++
– subsp. <i>villosa</i>	ad	0.83 \pm 0.21 (0.45-1.36)	549 \pm 314 (220-1026)	1/4	++
	ab	0.89 \pm 0.23 (0.55-1.41)	674 \pm 315 (206-1099)	2	++
<i>squamigera</i>	ad	0.67 \pm 0.23 (0/0.36-1.32)	1311 \pm 520 (0/733-2418)	1/2/3	+
	ab	0.52 \pm 0.15 (0/0.36-0.68)	4061 \pm 2530 (0/1245-7331)	1/2/4	+ / ++
<i>margalidiana</i>	ad	–	–	3	+
	ab	–	–	3	+
<i>paniculata</i> subsp.	ad	–	–	1/2	+ / ++
	ab	–	–	1/2	++
– subsp. <i>monchiquensis</i>	ad	–	–	1/2	+
	ab	–	–	1/2	+ / ++
– subsp. <i>welwitschii</i>	ad	–	–	1	+
	ab	–	–	1	++
<i>nereidum</i>	ad	–	–	2	–
	ab	–	–	2	+
<i>bivonae</i> subsp.	ad	–	–	2	– / ++
	ab	–	–	2	+ / ++
– subsp. <i>tunetana</i>	ad	–	–	1/2	+ / ++
	ab	–	–	1/2	+
<i>melitensis</i>	ad	–	–	2	+
	ab	–	–	2	+

Indumentum. – *Euphorbia squamigera* and *E. clementei* are the only species which can be hairy, with indumentum of simple, unicellular, 0.4 to 1.4 mm long trichomes (Table 2). The other taxa have glabrous leaves. In *E. squamigera*, they can be densely hairy or absolutely glabrous; usually the lower leaves of the stem (winter leaves) have higher trichome density than the upper ones (spring leaves), but this feature is very variable, even within a single population. The two subspecies of *E. clementei* can be distinguished by their indumentum: subsp. *clementei* is glabrous, except for the occasional presence of a few hairs – with smooth surface, similar to those of *E. squamigera* – on the leaf margin; subsp. *villosa* has densely hairy leaves with warty trichomes (Fig. 5.4).

Discussion

This study has shown that species with a wide distribution area are highly variable throughout their geographical range: this is the case of *Euphorbia squamigera*, ranging from

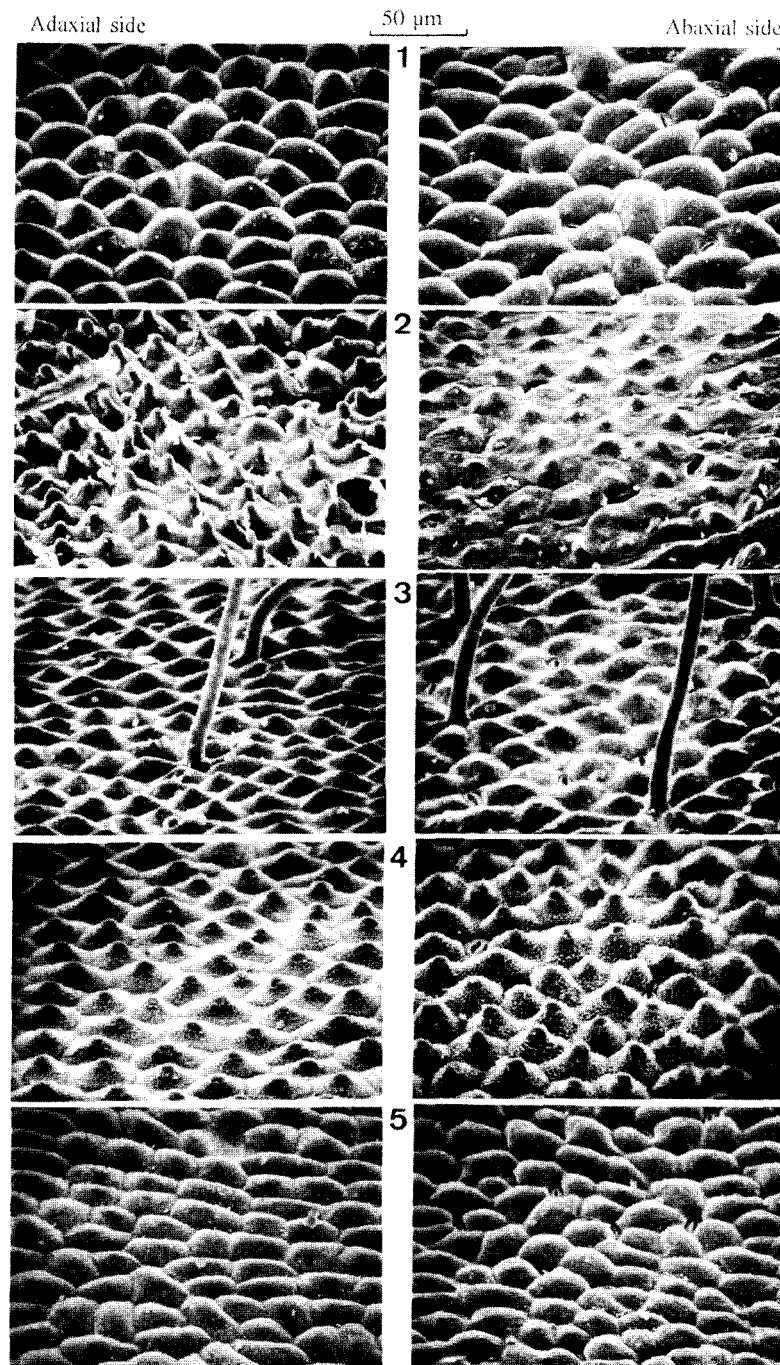


Fig. 3. Adaxial (left) and abaxial (right) face of leaf epidermis in scanning electron microscopy. – 1, *Euphorbia clementei* subsp. *clementei*. 2, *E. clementei* subsp. *villosa*. 3, *E. squamigera*. 4, *E. margalidiana*. 5, *E. paniculata* subsp. *welwitschii*.

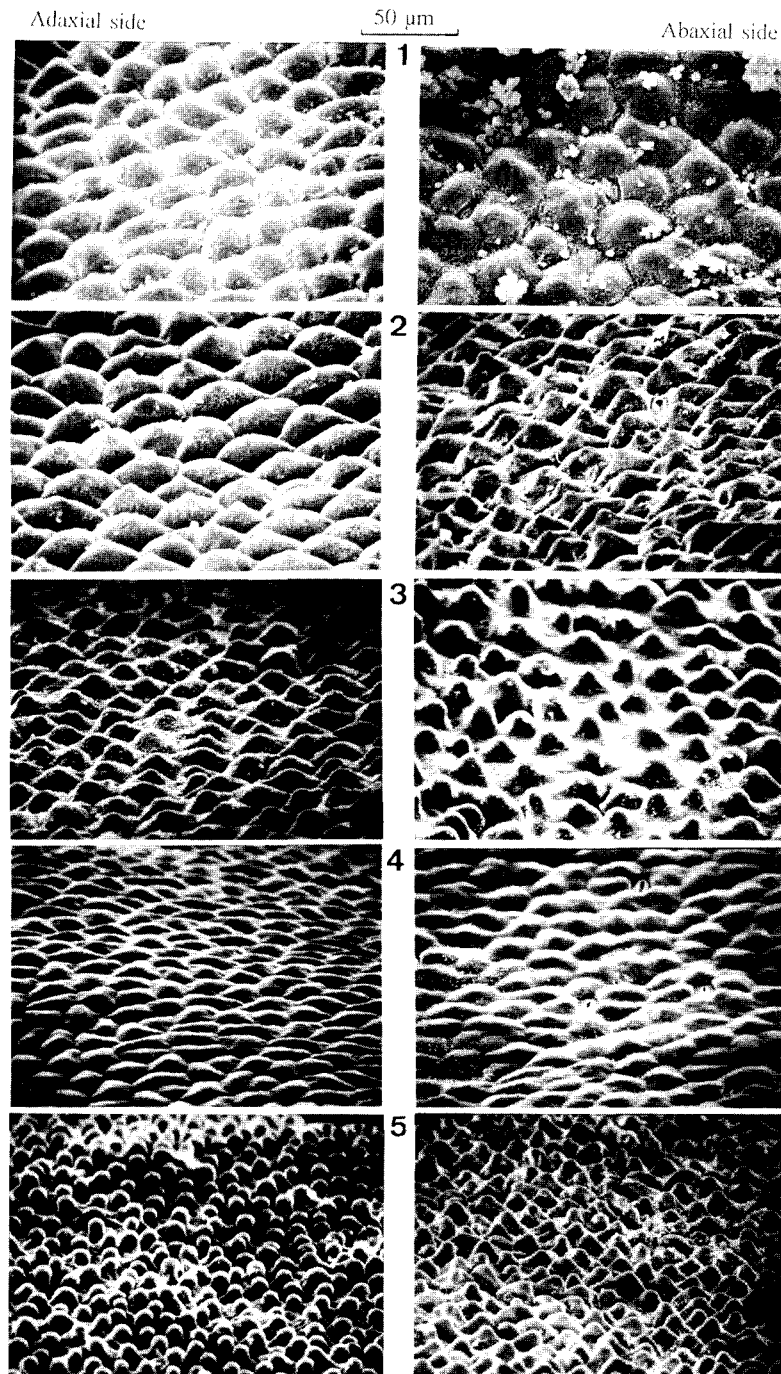


Fig. 4. Adaxial (left) and abaxial (right) face of leaf epidermis in scanning electron microscopy. – 1, *Euphorbia paniculata* subsp. *monchiquensis*. 2, *E. nereidum*. 3, *E. bivonae* subsp. *bivonae*. 4, *E. bivonae* subsp. *tunetana*. 5, *E. melitensis*.

the SE Iberian Peninsula to the Balearic Islands, Morocco and Algeria, which is variable with regard to indumentum, cell dimensions and stomata length; unfortunately, no pattern emerges on which taxonomic units might be established based on this variability.

Euphorbia clementei subsp. *clementei* is a widespread taxon which shows a stomatal distribution of two types: in populations from eastern Algeria the distribution of stomata is epimphistomatic while in the Iberian and Moroccan ones it is hypostomatic. The Algerian populations were named *E. atlantis* Maire (*E. atlantica* Coss. ex Boiss., non Pers.) by previous authors (Boissier 1862; Maire 1941; Vindt 1953) on the basis of features of the capsule. In spite of the differences in epidermis, we prefer to unite them with *E. clementei*, for three reasons: (a) we have not found any further discriminant characters, (b) epidermal features proved to be variable within species of this group (see *E. squamigera*), and (c) fruit characters do not seem to be very consistent and the above-cited authors have later revised their opinion (Vindt 1960; Maire in schedis, MPU).

Some high mountain populations of "*Euphorbia atlantis*" and *E. clementei*, growing at altitudes between 1200 and 2100 m, have hairy leaves; they were described, respectively, as

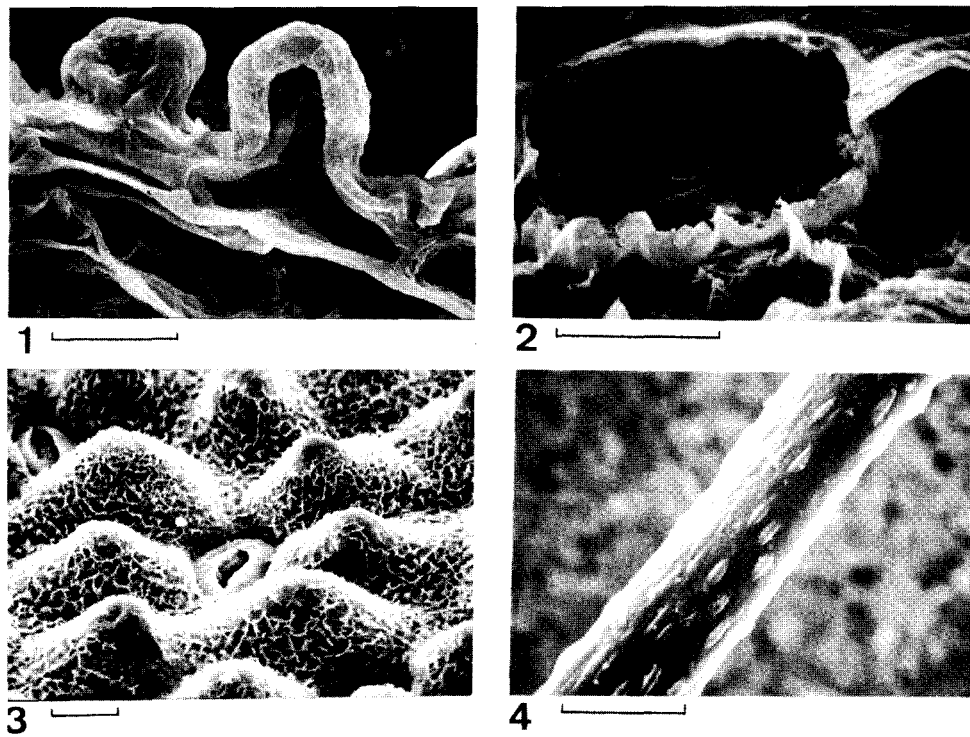


Fig. 5. Micromorphological details in scanning electron microscopy. – 1, Section of leaf epidermal papillae of *Euphorbia margalidiana*. 2, Inner surface of an epidermal cell, with thickenings, of *E. squamigera*. 3, Epicuticular waxes in *E. margalidiana*. 4, Warty trichome of *E. clementei* subsp. *villosa*. – Scale bar = 10 μ m.

E. atlantica var. *villosa* Faure & Maire (Maire 1929) and *E. clementei* var. *villifolia* Maire (1935). They have identical, warty hairs, whereas typically *E. clementei* has smooth trichomes. Because of the altitudinal and ecological segregation and because the distinctive macro- and micromorphological features are conserved in cultivated plants, we have proposed to unite them in a new subspecies, *E. clementei* subsp. *villosa* (Vicens & al. 1996).

Euphorbia monchiquensis Franco & P. Silva and *E. welwitschii* Boiss. & Reut., both from the SW Iberian Peninsula, were discriminated against *E. paniculata* from North Africa by their foliar morphology. In our opinion, these differences are not relevant. Leaf epidermal characters are identical in all three taxa, which supports their union as subspecies of a single species (Vicens & al., 1996).

This study has also revealed that intraspecific variation may be influenced by ecological factors; for example, individuals of *Euphorbia margalidiana* collected in the field have more prominent papillae and thicker cuticles than individuals from the same population raised in a botanical garden.

Acknowledgements

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References

- Ameluxen, F., Morgenroth, K. & Picksak, T. 1967: Untersuchungen an der Epidermis mit dem Stereoscan-Elektronenmikroskop. – *Z. Pflanzenphysiol.* **57**: 79-95.
- Barthlott, W. 1990: Scanning electron microscopy of the epidermal surface in plants. – Pp. 69-94 in: Claugher, D. (ed.), *Scanning electron microscopy in taxonomy and functional morphology.* – Oxford.
- Benedí, C. & Orell, J. J. 1993: Contribució al estudio fitodermològic de *Chamaesyce* S. F. Gray (*Euphorbiaceae*). – *Collect. Bot. (Barcelona)* **22**: 39-48.
- Boissier, P. E. 1862: *Euphorbia*. – Pp. 1-188 in: Candolle, A. P. de (ed.), *Prodromus systematis naturalis regni vegetabilis* **15(2)**. – Paris.
- Greuter, W., Burdet H. M. & Long G. 1986: *Med-Checklist*, **3**. *Dicotyledones (Convolvulaceae-Labiatae)*. – Genève & Berlin.
- Maire, R. 1929: Contributions à l'étude de la flore de l'Afrique du Nord. Fascicule 16. – *Bull. Soc. Hist. Nat. Afrique N.* **20**: 171-220.
- 1935: Contributions à l'étude de la Flore de l'Afrique du Nord. Fascicule 23. – *Bull. Soc. Hist. Nat. Afrique N.* **26**: 184-234.
- 1941: Contributions à l'étude de la Flore de l'Afrique du Nord. Fascicule 31. – *Bull. Soc. Hist. Nat. Afrique N.* **32**: 202-216.
- Molero, J. & Rovira, A. 1992: *Euphorbia* L. subsect. *Esula* (Boiss. in DC.) Pax in the Iberian Peninsula. Leaf surface, chromosome numbers and taxonomic treatment. – *Collect. Bot. (Barcelona)* **22**: 121-181.

- Raju, V. S. & Rao, P. N. 1987: The taxonomic use of the basic stomatal type in the generic delimitation of *Chamaesyce* (*Euphorbiaceae*). – Feddes Repert. **98**: 137-142.
- Sehgal, L. & Paliwal, G. S. 1974: Studies on the leaf anatomy of *Euphorbia* VII. General conclusions and systematic considerations. – Phytomorphology **24**: 141-151.
- Simon, J. 1993: Estudis biosistemàtics en *Euphorbia* L. subsect. *Galarrhaei* (Boiss.) Pax (grup d'*E. flavicoma* i espècies afins) a la Mediterrània Occidental. – Thesis, University of Barcelona.
- & Blanché, C. 1988: Estudis biosistemàtics en el grup d'*E. verrucosa* s. l.: fitodermologia. – Pp. 205-209 in: Anonymous (ed.), Actes del Simposi Internacional de Botànica Pius Font i Quer, **2**, Fanerogàmia. – Lleida.
- Vicens, J. 1994: Estudis biosistemàtics en *Euphorbia* L. subsect. *Galarrhaei* (Boiss.) Pax a la Mediterrània Occidental: el complex d'*E. squamigera* i espècies afins. – Thesis, University of Barcelona.
- , Molero, J. & Blanché, C. 1996: Síntesis taxonómica del complejo de *Euphorbia squamigera* y especies afines (sect. *Helioscopia* Dumort.) en el Mediterráneo occidental. – Candollea **51**: 59-93.
- Vindt, J. 1953: Monographie des euphorbiacées du Maroc. Revision et systématique. – Trav. Inst. Sci. Chérifien. Sér. Bot. **6**: 1-228.
- 1960: Monographie des euphorbiacées du Maroc. Anatomie. – Trav. Inst. Sci. Chérifien, Sér. Bot., ser. 2, **19**: 1-340.
- Wilkinson, H. P. 1979: The plant surface (mainly leaf). – Pp. 97-165 in: Metcalfe, C. R. & Chalk, L., Anatomy of the dicotyledons, ed. 2, **1**. – Oxford.

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