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Silica bodies and hooked papillae in lemmas of *Melica* species (Gramineae: Pooideae)

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Melica (sensu lato) is a genus with approximately 80 species distributed in the temperate regions of both hemispheres. The genus has been better studied morphologically than anatomically, but morphological patterns have led to conflicting subdivisions either into sections, or by segregation of the genus *Bromelica*. The lemma epidermis is examined here under scanning electron microscopy (SEM) for 40 species of *Melica* to see if it exhibits characters of systematic significance. Silica bodies and hooked papillae are reported in the lemma for the first time in the genus. Patterns of variation are evident within four structures that terminate in points: prickles, hooks, hooked papillae and macro-hairs. Fourteen qualitative characters for lemma epidermis are used in phenetic analyses. The presence or absence of macro-hairs conflicts with some other patterns, but gives some support to the classification of Papp. Characters associated with the split of the clusters were micro-hairs (straight and geniculate) and the distribution and frequency of prickles in both costal and intercostal zones. As a conclusion, *Melica* is not a coherent taxonomic grouping and a simple segregation of *Bromelica* from *Melica* genus is rejected. © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, **141**, 447–463.

ADDITIONAL KEYWORDS: anatomy – *Bromelica* – grasses – hooks – macro-hairs – Meliceae – micropapillae – phenetic analyses – Poaceae – prickles.

INTRODUCTION

Anatomical studies of the leaf-blade of the Gramineae have confirmed that some epidermal features can help to elucidate taxonomic relationships (Prat, 1932, 1936; Brown, 1958; Metcalfe, 1960; Palmer & Tucker, 1981; Ellis, 1986). Both anatomical studies of the leaf-blade and lemma epidermis have been important in the classification of broad groups within grasses, particularly subfamilies and tribes (Brown, 1958; Ellis, 1986). Structures that have proved of taxonomic significance include: silica cells and silica bodies (Metcalfe, 1960; Ellis, 1979; Palmer & Tucker, 1981), and the pattern, type and distribution of papillae in the lemma epidermis (Clark & Gould, 1975; Shaw & Smeins, 1981; Thomasson, 1986). Epidermal structures of the lemma have been used in the identification of fossil grasses by Thomasson (1980, 1984). He found that presence of hooks, the shape of the long-cells and presence of cork cells are useful in both fossil and living grasses, as in the tribes Stipeae, Paniceae and Oryzeae.

Scanning electron microscopy (SEM) has been extremely useful for examining the three-dimensional structure of both the leaf-blade and lemma epidermis of grasses (Clark & Gould, 1975; Terrell & Wergin, 1979; Palmer & Tucker, 1981, 1983; Hilu, 1984; Palmer & Gerbeth-Jones, 1986; Dávila & Clark, 1990). Most of the anatomical studies using both light microscopy and SEM techniques are based on broad surveys of the grasses of restricted geographical regions (Torres, 1980; Terrell & Wergin, 1981; Aiken & Lefkovitch, 1984), or representative taxa of major groups such as subfamilies (Prat, 1932, 1936; Brown, 1958), tribes (Decker, 1964; Palmer & Tucker, 1981, 1983; Renvoize, 1983; Palmer, Gerbeth-Jones & Hutchison 1985; Palmer & Gerbeth-Jones, 1986, 1988; Valdés-Reyna & Hatch, 1991) or some genera

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(Metcalfe, 1960; Clark & Gould, 1975; Terrell & Wergin, 1979, 1981; Shaw & Smeins, 1981; Hilu, 1984; Thomasson, 1986). It has been usual to study only one, two or a few species in a genus to be examined, especially in the larger genera (Soderstrom, 1967).

One of the largest grass genera in the tribe Meliceae is *Melica*, with approximately 80 species. *Melica* species are distributed in temperate regions throughout the world, except Australia. They are found in shady woodlands on dry stony slopes. The genus has been divided on the basis of morphological features into sections (Nyman, 1882; Scribner, 1885; Ascherson & Graebner, 1900; Boyle, 1945; Hempel, 1970, 1971, 1973; Hitchcock, 1935). Other authors considered subgenera, for example Thurber 1880), Papp (1928, 1932, 1937), Camus (1944) and Caro (1969). A few authors recognized the subgenus *Bromelica* as a separate genus (Farwell, 1919; Nicora, 1973; Torres, 1980; Muñoz, 1983–84). Only one author, Bernhardi (1800), recognized *Beckeria* as a separate genus. Several of these systems conflict with others, as illustrated graphically in Figure 1 for South American species, and summarized under the 'Papp' and 'Hempel' schools in Table 1.

Melica has been mostly studied morphologically and anatomical studies are rather few. Prat (1936) studied anatomical features across the whole family in order to propose a classification. In this study *Melica* showed anatomical features that appeared to be festucoid, but Prat excluded it from the Festuceae because its chromosomes are in multiples of nine and those of Festuceae are seven. The classic anatomical survey by Metcalfe (1960) unfortunately included only three species: *M. altissima* L., *M. ciliata* L. and *M. uniflora* Retz. Parry & Smithson (1966) studied the silica bodies in the inflorescences of 31 British grasses in which included *M. uniflora*. Their results are not very clear because they did not give in detail in which species the silica bodies were present. As a result the presence of silica bodies in *M. uniflora* is ambiguous. Torres (1980), included 17 species in her revision of the genus in Argentina. She suggested three species groups on the basis of adaxial rib sizes and presence of adaxial sclerenchyma. Unfortunately she did not

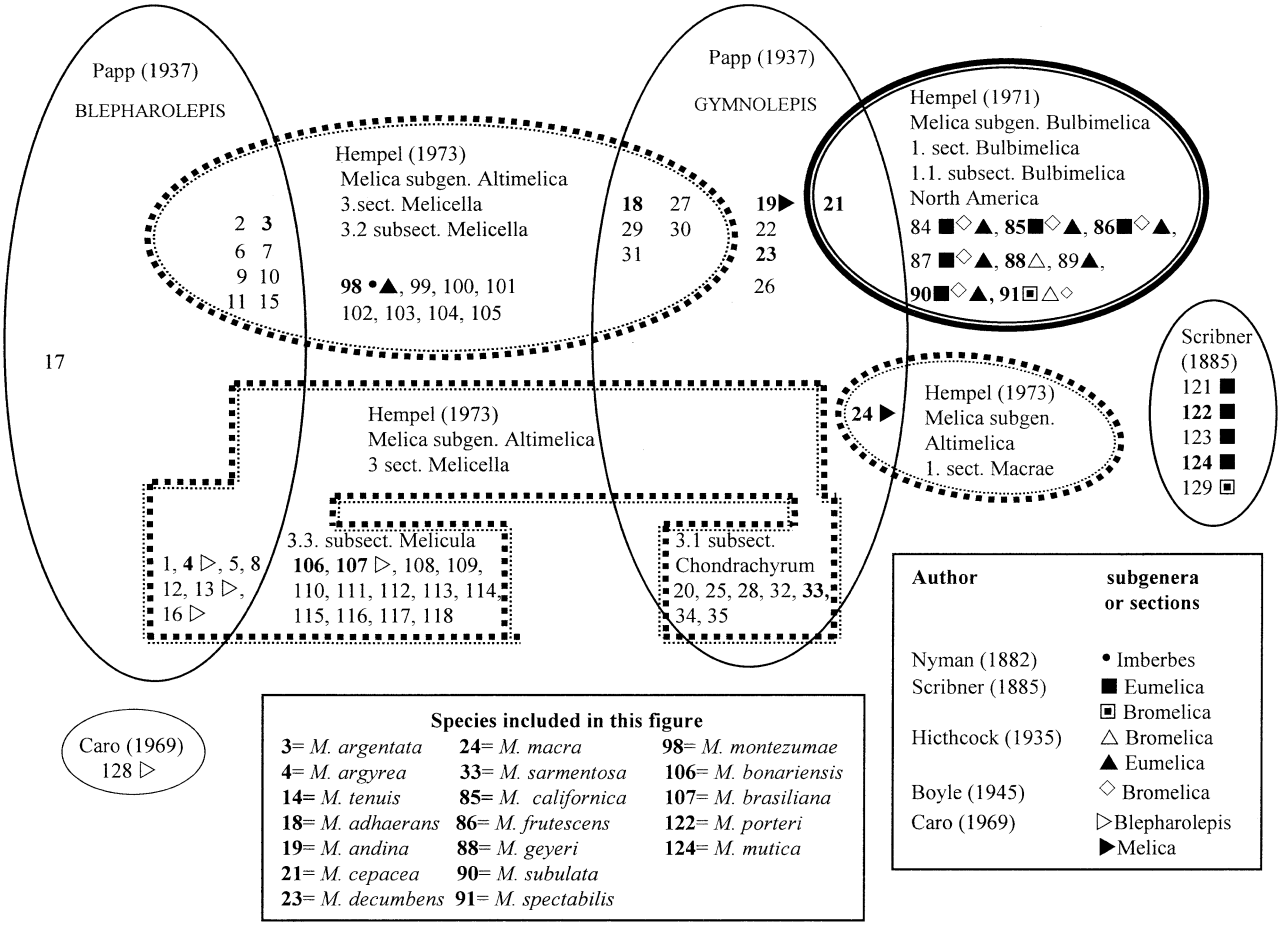


Figure 1. *Melica*: subgenera and sections considered by various authors. South America.

Table 1. (a) *Melica* – the 'Papp' school. (b) *Melica* – the 'Hempel' school

(a)

Bernhardi (1800)	Nyman (1882)	Ascherson & Graebner (1900)	Papp (1928)	Caro (1969)	Characteristics
Melica	**Imberbes**	**Eumelica**	Gymnolepis	Melica	Absence of hairs in the lemma/lateral compression
Beckeria	**Barbatae**	**Beckeria**	Blepharolepis	Blepharolepis	Presence of hairs in the lemma/dorsal compression

(b)

Thurber (1880)	Scribner (1885)	Farwell (1919)	Hitchcock (1935)	Camus (1944)	Boyle (1945)	Hempel (1970)	Hempel (1971)	Hempel (1973)	Nicora (1973)	Torres (1980)	Muñoz (1983–84)	Morphological features
Melica	–	*Melica*	**Eumelica**	Melica Husnotchloa	**Eumelica**	Melica: **Melica Beckeria Cupani Penicillaris**	Melica: **Uniflorae**	Altimelica: **Altimelica Macrae Melicella**	Melica	Melica	Melica	1–2 fertile florets/spikelets with broad shape/ presence of rudimentary florets/spikelet disarticulation below glumes
Bromelica	**Bromelica Eumelica Glyceriae**	*Bromelica*	**Bromelica**	–	**Bromelica**	–	Bulbimelica: **Bulbimelica Bromelica**	–	*Bromelica*	*Bromelica*	*Bromelica*	3–8 fertile florets/spikelets with narrow shape/ absence of rudimentary florets/spikelet disarticulation above glumes

Italic = genus; Roman = subgenus; bold = sections

include any species of the *Bromelica* group because she considered it a separate genus. In contrast Thomasson (1986) studied the lemma epidermal features in the 17 North American *Melica* species including some *Bromelica*. He concluded that *Melica* is a natural and uniform group, and is not necessarily divided into sections or groups. His results displayed lemma epidermal features that were homogeneous in the *Melica* species that he studied. These species share characteristics such as presence of hooks and prickles, and absence of both silica cells and macrohairs (except in *M. montezumae* Piper and *M. subulata* (Griseb.) Scribn.).

The purpose of the present study was to survey epidermal features of the lemma of 40 *Melica* species using SEM to see if they provided information of taxonomic value. The information will be used for classificatory and phylogenetic purposes.

MATERIAL AND METHODS

Species selected for this study

As a result of screening of floras and monographic treatments we have compiled a list of 84 species in the genus *Melica*. We analysed the groups of subgenera considered by Papp (1928, 1932, 1937) and Hempel (1970, 1971, 1973) by displaying them graphically in Figure 1 and added sections considered for other authors such as Nyman (1882), Scribner (1885), Ascherson & Graebner (1900), Boyle (1945), Caro (1969) and Hitchcock (1935). Even though the groupings of these authors disagree in part, we were able to select 40 species of *Melica* in such a way that there are some species for each of the groupings of all these authors (Tables 1a and 1b). This ensures that our sample both covers the groupings of these competing systems, and covers the whole range of forms defined in early studies. They also encompass the full geographical range of the genus (Table 2).

Studies were performed on herbarium specimens obtained from the following Herbaria (herbarium codes according to Holmgren *et al.*, 1990):

BAA, Herbario, 'Gaspar Xuárez', Facultad de Agronomía, Universidad de Buenos Aires, Argentina. **E**, Herbarium, Royal Botanic Garden, Edinburgh, UK. **ENCB**, Herbario, Escuela Nacional de Ciencias Biológicas, Departamento de Botánica, Instituto Politécnico Nacional, México. **ICN**, Herbário, Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. **K**, Herbarium, Royal Botanic Gardens, Kew, UK. **LP**, Herbario, División Plantas Vasculares, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina. **MEXU**, Herbario Nacional, Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, México. **NY**, Herbarium, New York Botanical Garden, New York, USA. **PRE**, National Herbarium, Botanical Research Institute, Pretoria, South Africa. **RNG**, Herbarium, School of Plant Sciences, The University of Reading, Reading, UK. **SGO**, Herbario, Sección Botánica, Museo Nacional de Historia Natural, Santiago, Chile. **SI**, Herbario, Instituto de Botánica Darwinion, San Isidro, Buenos Aires, Argentina. **SPN**, Herbarium, Biological Sciences Department, Southampton University, Southampton, UK. **TI**, Herbarium, Botanical Gardens, University of Tokyo, Tokyo, Japan. **UC**, Herbarium, Department of Botany, University of California, Berkeley, California, USA.

Standard SEM technique

The epidermis of the lemma was surveyed following the standard scanning electron microscope (SEM) preparation technique and using a HITACHI S-450 microscope. Lemmas were removed from the first and second florets of mature spikelets from dried herbarium specimens. They were mounted on small brass discs (12.5 mm diam.) with double-coated scotch-tape so as to observe the abaxial surface. The specimens were sputter-coated with gold-palladium (60% Au/40% Pd). Samples were examined under the SEM. Photographs were taken with Ilford FP4 6X/black and white roll film. Photographs were taken of general view, costal and intercostal zones, micropapillae, prickles, hooks, hooked papillae and silica bodies. Photographs were also taken of some macro-hairs and stomata.

Surveying the epidermal features of the lemma

Melica uniflora was used as the basis for initial selection of anatomical characters of the lemma. The anatomical characters were chosen on the basis of the previous descriptors used by various authors (Palmer & Tucker, 1981, 1983; Thomasson, 1986; Valdés-Reyna & Hatch, 1991; Watson & Dallwitz, 1992). Four new characters were added: (1) hooked papillae present or absent, (2) distribution of hooked papillae, (3) barb types of the prickles, and (4) macro-hairs straight or twisted. The anatomical terminology used follows Ellis (1979).

Analyses performed

Phenetic analyses were applied to the 40 species selected to represent the *Melica* genus. The MultiVariate Statistics Package (MVSP; Kovach, 1995) for the

Table 2. Species of *Melica* examined

Taxon	Collector/Number	Herbarium	Country of origin
Melica adhaerans Hack.	A.L. Cabrera 12099	LP	Argentina
M. altissima L.	C. Zahariadi s/n	RNG	Russia
M. andina Hauman	J. Semper 4320	LP	Argentina
M. argentata E. Desv.	O. Zöllner 9738	SGO	Chile
M. argyrea Hack.	A. Burkart 6819, 20455	SI	Argentina
M. aristata Thurb. ex Bol.	H.S. Yates 5833	UC	USA
M. bahuinii All.	A. Meebold s/n	K	France
M. bonariensis Parodi	E. Cano 2713	BAA	Argentina
M. brasiliana Ard.	S. Miotto s/n	ICN	Brazil
M. californica Scribn.	D.D. Keck & J. Clausen 5269	UC	USA
M. cepacea (Phil.) Scribn.	O. Boelcke 10817	BAA	Argentina
M. ciliata L.	J.O. Wright 56	RNG	Yugoslavia
M. cupani Guss.	P. Purse 2197	K	Iran
M. decumbens Thunb.	L. Smook 3306	PRE	South Africa
M. frutescens Scribn.	R. Moran 20552	ENCB	Mexico
M. geyeri Munro	H.S. Yates 227	UC	USA
M. harfordii Bol.	J.P. Tracy 6243	UC	USA
M. imperfecta Trin.	R. Moran 20669	ENCB	Mexico
M. macra Nees	Ragonese 43	BAA	Argentina
M. magnolii Gren. & Godr.	E. Ellman & E. Nelmes 42	RNG	Spain
M. minuta L.	H.J.M. Bowen 2424	RNG	Greece
M. montezumae Piper	C.G. Pringle 846	MEXU	Mexico
M. mutica Walter	A. Ruth 474	NY	USA
M. nitens (Scribn.) Nutt. ex Piper	A.J. Clemens 110	NY	USA
M. nutans L.	R. Camoletto 2011	RNG	Italy
M. onoei Franch. & Sav.	M. Togashi 7457	TI	Japan
M. penicillaris Boiss. & Bal.	J. Dörflerwien 2571	E	Turkey
M. persica Kunth	Rawi 21914	K	Iraq
M. picta K. Koch	C. Zahariadi s/n	RNG	Russia
M. porteri Scribn.	C.G. Pringle 2040	MEXU	Mexico
M. racemosa Thunb.	L. Smook 5559	PRE	South Africa
M. sarmentosa Nees	G. Hatschbach 1490	BAA	Argentina
M. secunda Regel	R.R. Stewart 22372	K	India
M. smithii (Porter ex A. Gray) Vasey	W.N. Suksdorf 11728	UC	USA
M. spectabilis Scribn.	N. Wavly 368	UC	USA
M. subulata (Griseb.) Scribn.	J.B. Davy 5405	UC	USA
M. tenuis Hack. & Arechav.	J. Valls et al. 3079	LP	Brazil
M. torreyana Scribn.	E. Lodge 251	UC	USA
M. transilvanica Schur	B.H. Kononob s/n	RNG	Russia
M. uniflora Retz.	Bromfield 139	SPN	UK

IBM PC and compatible computers was used to perform the analyses.

Gower's mixed data coefficient was used to generate the similarity matrix and this was then used to perform the cluster analyses. The Unweighted Pair Group Average Method (UPGMA) was the clustering method used.

RESULTS

A list of 14 qualitative characters was defined and used to score comparative epidermal features. It includes nine binary and five multistate characters (Table 3). They were used to build a data matrix (Table 4) on which we could perform the phenetic analyses.

ANATOMICAL DESCRIPTION OF LEMMA EPIDERMIS IN *MELICA*

Our terminology and the format of description are adapted from Ellis (1979) and Palmer & Tucker (1981). A summary of selected anatomical features is shown in Table 5. Typical epidermal features of the lemma are illustrated in Figures 5 and 6.

Table 3. Epidermal characters of the lemma used in the phenetic analyses

1	Intercostal long-cell outline straight, not undulate (0); outline loose, wide U-shaped curves of shallow amplitude (1); outline loose, V-shaped curves of deep amplitude (2); outline tight, deep convolutions of omega (Ω) shape (3).
2	Intercostal long-cell shape square and rectangular (0); rectangular (1).
3	Distribution of the hooked papillae in the costal zone (0); all lemma (1).
4	Frequency of the hooked papillae in the intercostal zone inapplicable (0); infrequent (1/1, a hooked papilla present only after two or more long-cells) (1); frequent (1/1, a hooked papilla present at both ends of each long-cell) (2).
5	Frequency of the hooked papilla in the costal zone is infrequent (1/1, a hooked papilla present only after two or more long-cells) (0); frequent (1/1, a hooked papilla present at both ends of each long-cell) (1).
6	Prickle types (barb shape in relation to base) with barb developed basally from the apex of the base (0); barb developed from the apex of the base but slightly raised (1); barb not developed from the apex of the conical base but raised (2); barb with recurved point not developed from the apex of the base (3).
7	Distribution of prickles in the costal zone (0); all lemma (1).
8	Frequency of the prickles in the intercostal zone is inapplicable (0); infrequent (1/1, a prickle present only after two or more long-cells) (1).
9	Frequency of the prickles in the costal zone is infrequent (1/1, a prickle present only after two or more long-cells) (0); frequent (1/1, a prickle present at both ends of each long-cell) (1).
10	Hooks are absent (0); present (1).
11	Macro-hairs are absent (0); present (1).
12	Macro-hairs inapplicable (0); straight (1); geniculate or twisted (2).
13	Frequency of macro-hairs is inapplicable (0); infrequent (1/1, a micro-hair present only after two or more long-cells) (1); frequent (1/1, a micro-hair present at both ends of each long-cell) (2).
14	Stomata were not observed (0); observed (1).

Long-cells

The long-cells are elongated axially (parallel with the long axis of the leaf or lemma) and relatively narrow. The relative lengths and shapes of the axial and transverse anticlinal walls determine cell shapes. Intercostal long-cells are rectangular in all *Melica* species; usually they are three or more times longer than wide. Infrequent square intercostal cells are distributed between the rectangular long-cells in a small number of species such as *M. adhaerans* Hack., *M. andina* Hauman, *M. bahuinii* All., *M. ciliata*, *M. decumbens* Thunb., *M. frutescens* Scribn., *M. montezumae*, *M. porteri* Scribn., *M. tenuis* Hack. & Arechav. and *M. transilvanica* Schur. Intercostal long-cell outlines fall into four types (Fig. 2), following Metcalfe & Chalk (1979) classification: (1) outline straight (not undulate) is the most frequent condition found (Fig. 7), (2) outline loose, wide U-shaped curves of shallow amplitude is found in *M. altissima*, *M. argyrea* Hack., *M. cepacea* (Phil.) Scribn., *M. macra* Nees (Fig. 8), *M. minuta* L., *M. onoei* Franch. & Sav., *M. sarmentosa* Nees and *M. smithii* (Porter ex A. Gray) Vasey, (3) outline loose, V-shaped curves of deep amplitude is present in only one species, *M. uniflora* (Fig. 9), and (4) outline tight, deep convolutions of omega shape (Ω), this shape is exhibited in *M. brasiliana* Ard., *M. californica* Scribn., *M. mutica* Walter, *M. nutans* L., *M. penicillaris* Boiss & Bal., *M. picta* K. Koch (Fig. 10) and *M. racemosa* Thunb.

Short-cells and silica bodies

Short-cells are usually nearly isodiametric and are always shorter than the long-cells. They occur in axial rows in pairs, or they may be solitary, according to the species. Furthermore, the short-cells in the costal and intercostal zones are usually arranged and distributed differently. Short-cells have been generally classified either as silica cells or cork cells. Silica cells are more or less completely filled with a single silica-body. They assume very characteristic forms when the grass leaf is mature, a feature of considerable value for diagnostic and taxonomic purposes. Silica bodies are discrete deposits of hydrated silica present in the epidermal cells. They are more frequent in the costal zones than the intercostal zones. Silica bodies are not common in the lemma of *Melica* and in our sample we observed them in the costal zone of only five species: *M. californica* (Fig. 11). *M. cepacea*, *M. nutans*, *M. onoei* and *M. picta*. Silica bodies observed are axially elongated and dumb-bell shaped, that is, relatively short and infrequent in the costal zone, except in *M. californica* and *M. onoei*, where they are common and arranged in a single row.

Micropapillae

Micropapillae are variously shaped protrusions from the outer walls of long and short epidermal cells (Fig. 3a). They occur mostly on the long-cells, particularly in the intercostal zone and are found in all *Melica* species. They are circular or rounded in outline, smaller than hooks or prickles, thin-walled and inflated, of different sizes (Fig. 12). There are more than 20 micropapillae on each cell, irregularly arranged and present in many or all intercostal

Table 4. Data matrix of anatomical characters of the epidermis of the lemma in *Melica*

Taxon	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. *Melica adhaerans*	0	0	0	0	0	2	0	0	0	1	0	0	0	0
2. *Melica altissima*	1	1	0	0	1	1	0	0	1	0	0	0	0	1
3. *Melica andina*	0	0	0	0	1	2	0	0	0	1	0	0	0	0
4. *Melica argentata*	0	1	1	1	1	3	0	0	1	1	1	2	1	0
5. *Melica argyrea*	1	1	1	1	1	3	1	1	0	1	1	2	1	0
6. *Melica aristata*	0	1	1	2	1	0	0	0	0	0	0	0	0	1*
7. *Melica bahuinii*	0	0	1	2	1	2	1	1	1	1	1	2	1	0
8. *Melica bonariensis*	0	1	0	0	1	3	0	0	0	1	1	2	1	0
9. *Melica brasiliana*	3	1	0	0	1	3	0	0	0	0	1	2	1	1
10. *Melica californica*	3	1	1	2	0	1	1	1	1	0	0	0	0	1
11. *Melica cepacea*	1	1	1	2	1	2	1	1	1	0	0	0	0	1
12. *Melica ciliata*	0	0	1	1	1	1	1	1	1	0	1	2	2	1
13. *Melica cupani*	0	1	1	1	0	0	0	0	0	0	1	1	2	0
14. *Melica decumbens*	0	0	0	0	1	1	0	0	0	0	1	2	2	1
15. *Melica frutescens*	0	0	1	2	1	2	1	1	1	1	0	0	0	1
16. *Melica geyeri*	0	1	1	1	0	2	1	1	1	0	0	0	0	1*
17. *Melica harfordii*	0	1	1	2	1	0	0	0	1	0	1	1	1	0
18. *Melica imperfecta*	0	1	1	2	1	2	0	0	1	0	0	0	0	0
19. *Melica macra*	1	1	1	2	1	2	0	0	0	0	0	0	0	0
20. *Melica magnolii*	0	1	0	0	1	3	0	0	1	1	1	2	2	0
21. *Melica minuta*	1	1	1	1	1	3	0	0	0	0	0	0	0	0
22. *Melica montezumae*	0	0	0	0	1	1	0	0	1	0	1	2	1	1
23. *Melica mutica*	3	1	1	2	1	1	0	0	0	1	0	0	0	1
24. *Melica nitens*	0	1	0	0	1	2	0	0	1	0	0	0	0	1
25. *Melica nutans*	3	1	0	0	1	0	0	0	0	1	0	0	0	0
26. *Melica onoei*	1	1	1	2	0	0	0	0	0	0	0	0	0	0
27. *Melica penicillaris*	3	1	0	0	1	0	0	0	0	1	1	2	2	1
28. *Melica persica*	0	1	0	0	1	0	0	0	0	1	1	2	2	0
29. *Melica picta*	3	1	1	2	1	0	0	0	0	1	0	0	0	1
30. *Melica porteri*	0	0	1	1	0	1	0	0	1	1	0	0	0	1
31. *Melica racemosa*	3	1	1	2	1	0	0	0	0	1	1	2	2	0
32. *Melica sarmentosa*	1	1	1	2	1	2	0	0	1	0	0	0	0	0
33. *Melica secunda*	0	1	1	2	0	1	1	1	1	1	0	0	0	0
34. *Melica smithii*	1	1	1	2	1	0	1	1	1	0	0	0	0	0
35. *Melica spectabilis*	0	1	1	2	1	1	0	0	1	1	0	0	0	0
36. *Melica subulata*	0	1	1	2	1	1	0	0	0	0	1	1	1	1*
37. *Melica tenuis*	0	0	0	0	1	2	0	0	0	1	1	2	1	1
38. *Melica torreyana*	0	1	1	2	1	1	1	1	1	1	0	0	0	0
39. *Melica transilvanica*	0	0	0	0	1	3	0	0	1	0	1	2	2	0
40. *Melica uniflora*	2	1	1	2	1	1	0	0	0	0	0	0	0	0

*Data from Thomasson (1986)

long-cells. Small pits are observed in some of the long-cell surfaces of nine species: *M. argyrea, M. ciliata, M. harfordii* Bol., *M. imperfecta* Trin., *M. subulata, M. torreyana* Scribn., *M. montezumae, M. picta* and *M. tenuis*. These pits could be micropapillae which have collapsed as previously mentioned by Ellis (1979). This collapse could possibly have happened when the plants were dehydrated to make the herbarium specimens on which our observations were made.

Hooked papillae

A peculiar type of short-cell has been seen in all *Melica* species surveyed. They have a circular papillate base, conical outer periclinal wall and pointed apex which can be developed as a hook (Fig. 3b). We refer to

Table 5. Summary of selected epidermal features of the lemma in *Melica* species

Species	Silica bodies	Hooked papillae: distribution and frequency		Prickle types				Prickles: distribution and frequency		Hooks	Macro-hairs	Stomata
		Intercostal zone	Costal zone	1	2	3	4	Intercostal zone	Costal zone			
M. adhaerans	–	–	I			+		–	I	+	–	–
M. altísima	–	–	F		+			–	F	–	–	+
M. andina	–	–	F			+		–	I	+	–	–
M. argentata	–	I	F				+	–	F	+	+	–
M. argyrea	–	I	F				+	I	I	+	+	–
M. aristata	–	F	F	+				–	I	–	–	–
M. bahuinii	–	F	F			+		I	F	+	+	–
M. bonariensis	–	–	F				+	–	I	+	+	–
M. brasiliana	–	–	F				+	–	I	–	+	+
M. californica	+	F	I		+			I	F	–	–	+
M. cepacea	+	F	F			+		I	F	–	–	+
M. ciliata	–	I	F		+			I	F	–	+	+
M. cupanni	–	I	F	+				–	I	–	+	–
M. decumbens	–	–	F		+			–	I	–	+	+
M. frutescens	–	F	F			+		I	F	+	–	+
M. geyeri	–	I	I			+		I	F	–	–	–
M. harfordii	–	F	F	+				–	F	–	+	–
M. imperfecta	–	F	F			+		–	F	–	–	–
M. macra	–	F	F			+		–	I	–	–	–
M. magnolii	–	–	F				+	–	F	+	+	–
M. minuta	–	I	F				+	–	I	–	–	–
M. montezumae	–	–	F		+			–	F	–	+	+
M. mutica	–	F	F		+			–	I	+	–	+
M. nitens	–	–	F			+		–	F	–	–	+
M. nutans	+	–	F	+				–	I	+	–	–
M. onoei	+	F	I	+				–	I	–	–	–
M. penicillaris	–	–	F	+				–	I	+	+	+
M. persica	–	–	F	+				–	I	+	+	–
M. picta	+	F	F	+				–	I	+	–	+
M. porteri	–	I	I		+			–	F	+	–	+
M. racemosa	–	F	F	+				–	I	+	+	–
M. sarmentosa	–	F	F			+		–	F	–	–	–
M. secunda	–	F	I		+			I	F	+	–	–
M. smithii	–	F	F	+				I	F	–	–	–
M. spectabilis	–	F	F		+			–	F	+	–	–
M. subulata	–	F	F		+			–	I	–	+	–
M. tenuis	–	–	F			+		–	I	+	+	+
M. torreyana	–	F	F		+			I	F	+	–	–
M. transilvanica	–	–	F				+	–	F	–	+	–
M. uniflora	–	F	F		+			–	I	–	–	–

+ = present, – = absent, F = frequent, I = infrequent

these as 'hooked papillae' (Figs 13 and 14). They can cover the surface of the lemma or to be present only in the costal zone. They can be frequent, such as when one hooked papilla is present at both ends of each long-cell, or infrequent, such as when a hooked papillae is present only after two or more long-cells. Hooked papillae are distributed over the entire lemma in most *Melica* species. Only 14 species have the distribution confined to the costal zone: *M. adhaerans*, *M. altissima*, *M. andina*, *M. bonariensis* Parodi,

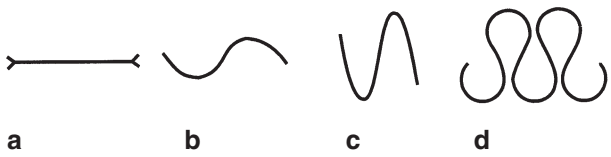


Figure 2. Basic patterns of anticlinal walls as seen in surface view (adapted from Metcalfe & Chalk, 1979). (a) Outline straight (not undulate). (b) Outline curved, wide U-shaped curves of shallow amplitude. (c) Outline curved, V-shaped curves of deep amplitude. (d) Outline tightly curved, deep convolutions of omega shape.

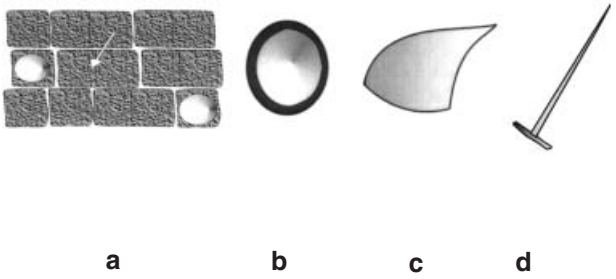


Figure 3. Lemma epidermal features. (a) Micropapillae. (b) Hooked papilla. (c) Prickle. (d) Macro-hair.

M. brasiliana, *M. decumbens*, *M. magnolii* Gren. & Godr., *M. montezumae*, *M. nitens* (Scribn.) Nutt. Ex Piper, *M. nutans*, *M. penicillaris*, *M. persica* Kunth, *M. tenuis* and *M. transilvanica*. Hooked papillae are frequently present in both costal and intercostal zones in most of the species with the exception of 11 species which have an infrequent distribution (Table 5).

Prickles

In grasses prickles are robust, pointed structures with swollen bases, arising directly from an integral part of the epidermis. They generally have thick, lignified walls (Fig. 3c). Prickles are usually larger than hooks and have elongate, oval or elliptical bases. They are found in both the costal and intercostal zones, but it is more common to find them in the costal zone. These prickles are present in all the *Melica* species. Four types of barb shape (Fig. 4) are considered in relation to the base as seen in lateral view: (1) barb developed basally from the apex of the base (Fig. 15), (2) barb developed from the apex of the base but slightly raised (Fig. 16), (3) barb not developed from the apex of the conical base but raised (Fig. 17), and (4) barb with recurved point not developed from the apex of the base (Fig. 18). The first three types are observed in approximately equal proportion in all *Melica* species. Additionally the fourth type is found in seven species only: *M. argentata* E. Desv., *M. argyrea*, *M. bonariensis*, *M. brasiliana*, *M. magnolii*, *M. minuta* and *M. transilvanica* (Table 5).

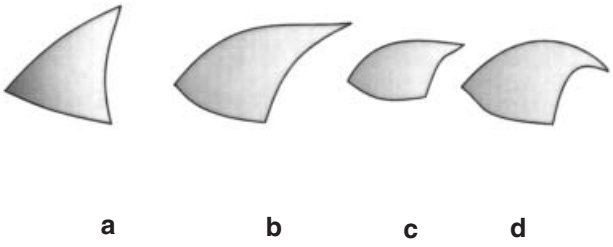


Figure 4. Types of barb shape in relation to the base as seen in lateral view (adapted from Ellis, 1979). (a) Barb developed basally from the apex of the base. (b) Barb developed from the apex of the base but slightly raised. (c) Barb not developed from the apex of the conical base but raised. (d) Barb with recurved point not developed from the apex of the base.

Prickles are principally distributed in the costal zone in most of grasses, but six species are found with an infrequent distribution: *M. californica*, *M. geyeri* Munro, *M. onoei*, *M. porteri*, *M. secunda* Regel and *M. adhaerans*. On the other hand, prickles are found in the intercostal zones with an infrequent distribution in just seven species: *M. argentata*, *M. argyrea*, *M. ciliata*, *M. cupani* Guss., *M. geyeri*, *M. minuta* and *M. porteri*

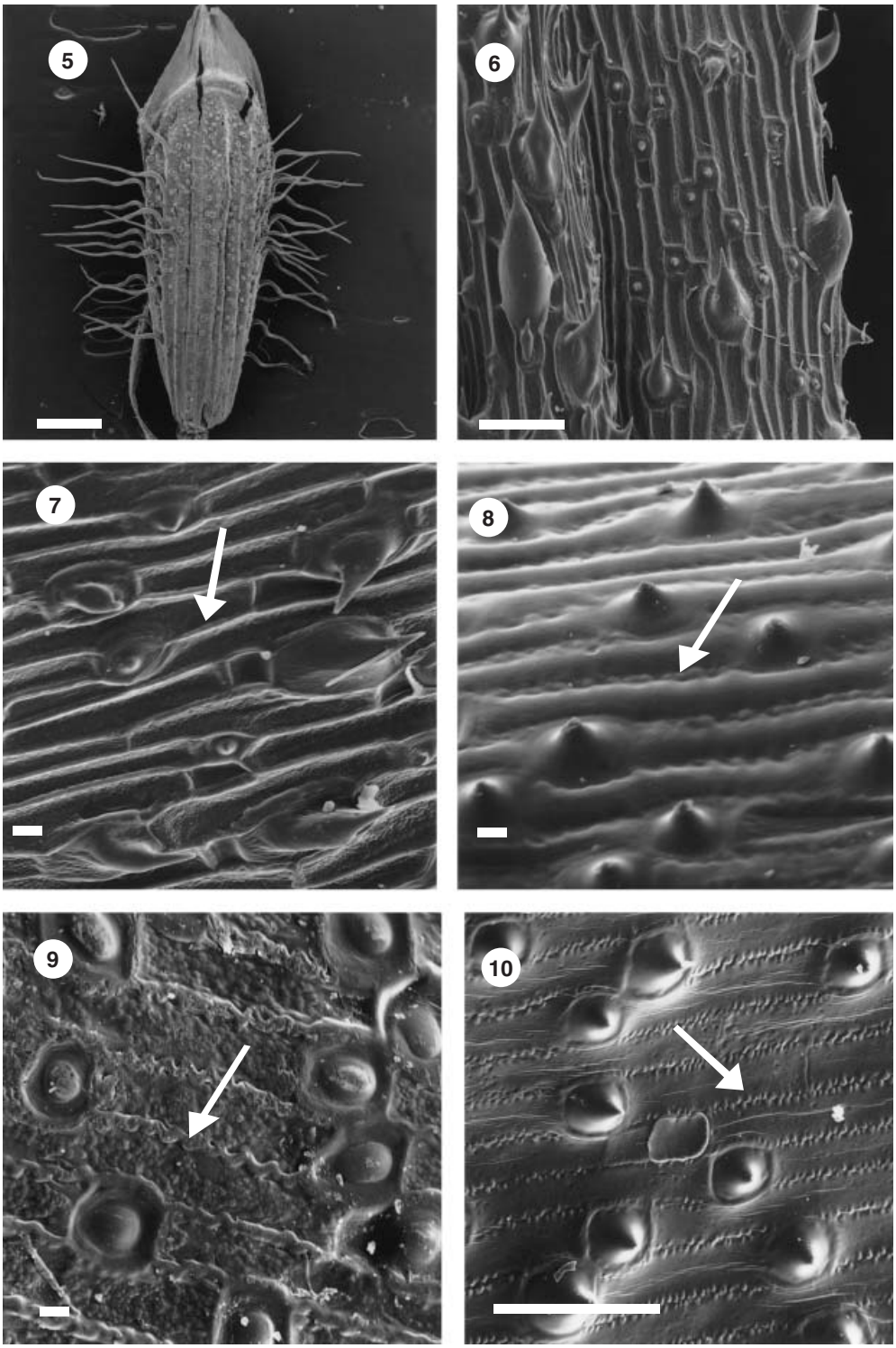
Prickles are orientated with the barb directed to the lemma apex in most *Melica* species. Five species are exceptional with the barb point orientated in both directions, towards and away from the lemma apex: *M. bahuinii* (Fig. 19), *M. ciliata*, *M. cupani*, *M. tenuis* and *M. transilvanica*. It is important to notice that *M. persica* is the only species with a barb point orientated away from the lemma apex. Prickles with a long barb are observed in *M. harfordii* and *M. nutans* (Fig. 20). There are prickles occur in two rows in *M. argentata*, *M. argyrea*, *M. magnolii*, *M. tenuis* and *M. transilvanica,* and in three rows just in *M. ciliata.*

Hooks

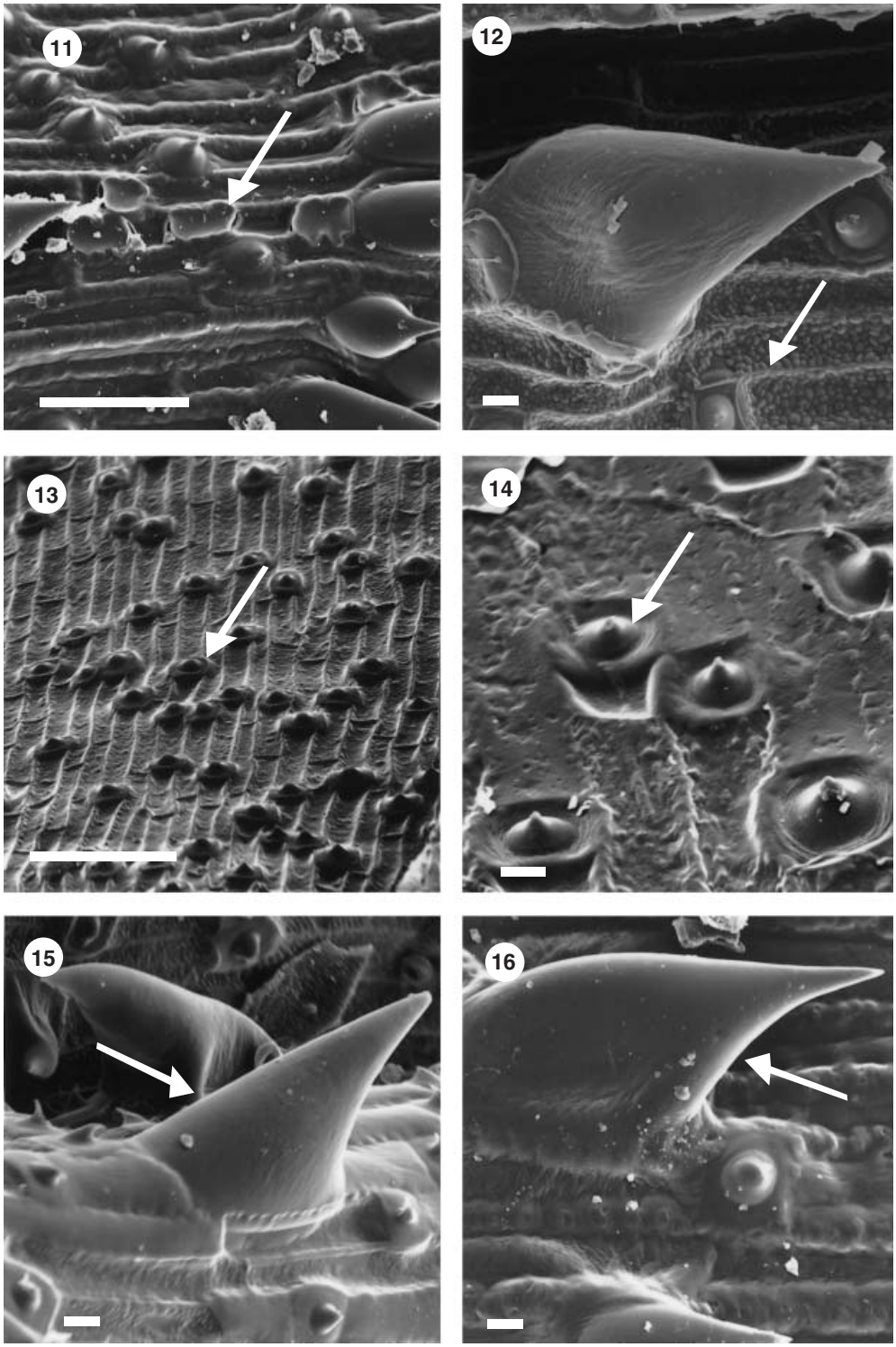
The hooks are smaller than prickles, they usually have circular bases, and are generally present in intercostal zones (Fig. 21). Hooks are rarely seen in half of the *Melica* species surveyed. They are distributed in the costal zone just in one species, *M. nutans*. Hooks have a barb point orientated towards the lemma apex in most of the species, as in most grasses. Hooks with a barb point orientated in both directions, towards and away from the lemma apex, are seen in *M. argentata* and *M. nutans*.

Macro-hairs

Macro-hairs (Fig. 3d) are much longer than micro-hairs, and are generally unicellular, although fine transverse walls partitions are sometimes present. The macro-hairs vary in length, in flexibility and in



Figures 5–10. SEM micrographs showing lemma epidermal features of *Melica* genus. Fig. 5. *M. argyrea*, a typical lemma epidermal features. Scale bar = 500 μm. Fig. 6. *M. andina*, a typical lemma epidermal features. Scale bar = 50 μm. Fig. 7. *M. andina*, intercostal long-cells outline straight. Scale bar = 5 μm. Fig. 8. *M. macra*, intercostal long-cells outline curved, wide U-shaped. Scale bar = 5 μm. Fig. 9. *M. uniflora* intercostal long-cells outline V-shaped. Scale bar = 5 μm. Fig. 10. *M. picta* intercostal long-cells outline deep convolution of omega shape. Scale bar = 50 μm.



Figures 11–16. SEM micrographs showing silica bodies, micropapillae, prickles and hooked papillae in lemma epidermal features of *Melica* genus. Fig. 11. *M. californica*, silica bodies. Scale bar = 50 μm. Fig. 12. *M. bahuinii*, long-cells with micropapillae. Scale bar = 5 μm. Fig. 13. *M. minuta*, hooked papillae. Scale bar = 50 μm. Fig. 14. *M. uniflora*, hooked papillae. Scale bar = 5 μm. Fig. 15. *M. cupani*, prickles with barb developed basally from the apex of the base. Scale bar = 5 μm. Fig. 16. *M. californica*, prickles with barb developed from the apex of the base but slightly raised. Scale bar = 5 μm.

the degree of cell-wall thickening. They may occur in the intercostal zones, but, on the whole, are more commonly found over the costal zones or at the leaf margin. Macro-hairs are present in just 17 *Melica* species. They cover the lemma in five species, and only *M. montezumae* has macro-hairs distributed in the middle lemma. Macro-hairs are densely distributed in ten species: *M. ciliata*, *M. cupani*, *M. decumbens*, *M. harfordii* (Fig. 22), *M. magnolii*, *M. penicillaris*, *M. persica*, *M. racemosa, M. subulata* and *M. transilvanica*. Macro-hairs with infrequent distribution are exhibited in seven species: *M. argentata*, *M. argyrea*, *M. bahuinii*, *M. bonariensis*, *M. brasiliana*, *M. montezumae* and *M. tenuis*. Two types of macro-hairs are found: (1) they are straight in three species: *M. cupani*, *M. harfordii* and *M. subulata*, (2) and they are geniculate or twisted in 14 species: *M. argentata, M. argyrea, M. bahuinii, M. bonariensis, M. brasiliana, M. ciliata, M. decumbens, M. magnolii, M. montezumae, M. penicillaris, M. persica, M. racemosa, M. tenuis* (Fig. 23) and *M. transilvanica*. Half of these *Melica* species exhibit silky long macro-hairs and the remainder are coarsely short macro-hairs.

Stomata

Stomata in grass leaves are confined to the intercostal zones and in some grasses from exposed or dry localities, they are sometimes restricted to the sides or bases of furrows in the leaf surface. Stomata are observed in 14 *Melica* species: *M. alissima*, *M. brasiliana*, *M. californica*, *M. cepacea*, *M. ciliata*, *M. decumbens*, *M. frutescens*, *M. montezumae*, *M. mutica*, *M. nitens* (Fig. 24), *M. penicillaris*, *M. picta*, *M. porteri* and *M. tenuis*.

Stoma shape

Grass stomata are paracytic; when fully mature, can be classified according to the shapes of the subsidiary cells. Two stomata types are found on the basis of the shapes of the subsidiary cells in surface view: (1) in the parallel-sided type subsidiary cells are rectangular in outline, it is the common shape found in *Melica* species, and (2) the dome-shaped subsidiary cells occur in *M. picta* only.

Frequency and distribution of stomata

Stomata in some *Melica* species are distributed throughout the intercostal zones in horizontal rows parallel to the long cell distribution. They can be in one row, as *M. nitens*, or in two rows, as *M. porteri*, or not in definite rows, as in the remaining *Melica* species. Stomata show infrequent distribution and they are surrounding by micropapillae, hooks, hooked papillae or prickles.

Interstomatal long-cells

The interstomatal long cells lie in the same axial, longitudinal rows as the stomata. Interstomatal long cells are rectangular in 14 species; walls are sinuous and thick in 11 species, and straight and thin in *M. cepacea*, *M. ciliata*, *M. decumbens*, *M. nitens* and *M. porteri*. Five species exhibit micropapillae on the interstomatal long-cells. These micropapillae are similar in shape and size to those on the long-cells in the intercostal zones.

Phenetic analyses

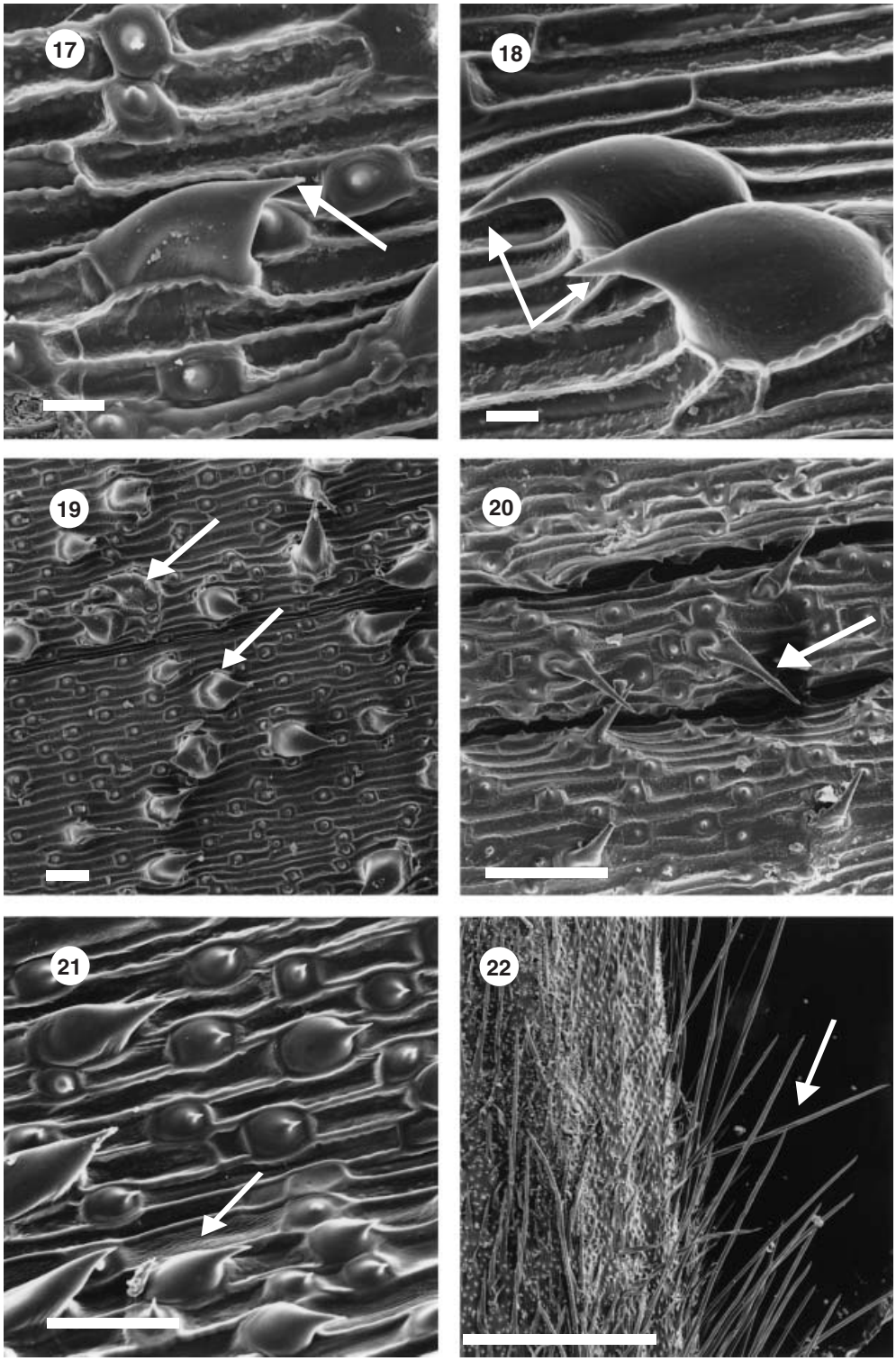
The results from the UPGMA clustering method show two main clusters marked as cluster A and B in Figure 26. The cluster A includes the 17 *Melica* species with presence of macro-hairs and includes two distinctive subclusters marked as subcluster AI and AII. The subcluster AI contains three species with macro-hairs straight, and the subcluster AII includes 14 species with geniculate or twisted macro-hairs. Cluster B groups the remaining 23 species in which macro-hairs are absent. Cluster B includes two subclusters: BI groups nine American species, and the subcluster BII includes ten mixed American-European-Asian species.

Results from the UPGMA analysis thus give some support to Papp's subgenera on the basis of presence or absence of macro-hairs in the lemma. However these results leave open the question as to whether *Melica* should be positioned with a segregate genus *Bromelica* or subdivided into more than two groups.

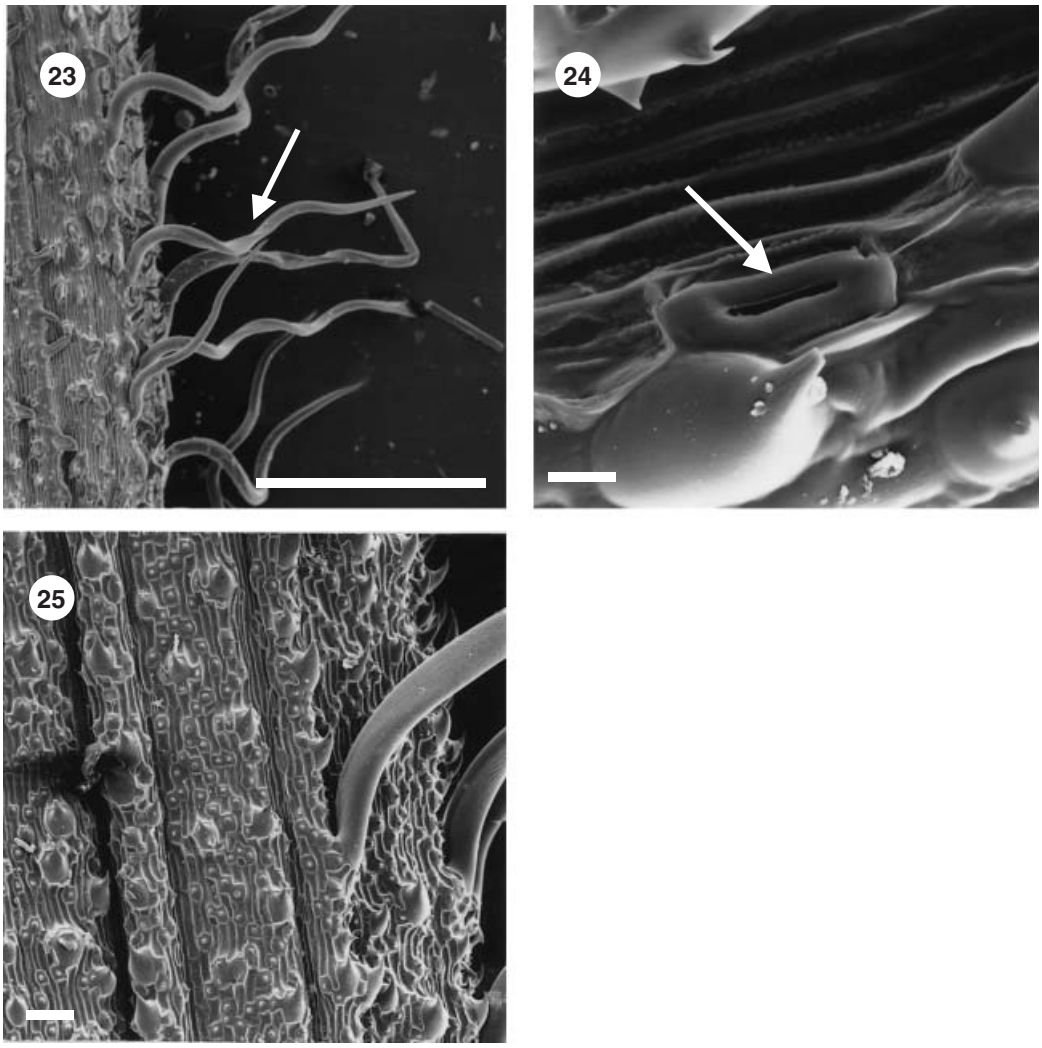
DISCUSSION

Epidermal features of the lemma in *Melica* show typical Pooideae anatomy from the leaf-blade such as long and narrow silica bodies, stomata absent or infrequent, subsidiary cells dome-shaped or parallel-sided cells, and the absence of micro-hairs (Gould & Shaw, 1983; Clayton & Renvoize, 1986; Watson & Dallwitz, 1992). Lemma epidermal features described by Thomasson (1986) in the North American *Melica* species are observed as well in the present study of 40 species worldwide: long cells rectangular and smooth to sinuous outlines; the types of pointed structures are: prickles, hooks, hooked papillae and macro-hairs. Prickles with long barbs in *M. harfordii* and *M. torreyana* previously cited by Thomasson (1986) are also observed in this study.

Our observations on stomata differ from those of Thomasson (1986). He found stomata in *M. aristata* Thurb. ex Bol., *M. geyeri*, *M. subulata*, *M. mutica* and *M. nitens*, but we observed stomata only in *M. mutica* and *M. nitens*. On the other hand stomata are seen in this study in four species: *M. californica*, *M. frutescens*, *M. montezumae*, and *M. porteri* which he did not



Figures 17–22. SEM micrographs showing prickles, hooks and macro-hairs in lemma epidermal features of *Melica* species. Fig. 17. *M. sarmentosa*, prickles with barb not developed from the apex of the conical base but raised. Scale bar = 5 μm. Fig. 18. *M. magnolii*, barb with recurved point not developed from the apex of the base. Scale bar = 5 μm. Fig. 19. *M. bauhinii*, prickles with a barb point orientated in both directions, towards and away from the lemma apex. Scale bar = 50 μm. Fig. 20. *M. nutans*, prickles with a long bar. Scale bar = 50 μm. Fig. 21. *M. frutescens*, hooks. Scale bar = 50 μm. Fig. 22. *M. harfordii*, macro-hairs straight. Scale bar 500 μm.



Figures 23–25. SEM micrographs showing macro-hairs and stomata in lemma epidermal features of *Melica* species. Fig. 23. *M. tenuis*, macro-hairs twisted/geniculate. Scale bar = 500 μm. Fig. 24. *M. nitens*, stoma. Scale bar 5 μm. Fig. 25. *M. montezumae*, a general view. Scale bar = 50 μm.

see. They exhibit a sparse distribution. They are not arranged in rows, with the exception of *M. nitens* (arranged in one row) and *M. porteri* (arranged in two rows). Most of the stomata are surrounded by hooked papillae or prickles.

Silica bodies are noted for the first time in the lemma epidermis of five *Melica* species: *M. californica*, *M. cepacea*, *M. nutans*, *M. onoei* and *M. picta*. Silica bodies are not included in the phenetic analyses because their absence or presence is uncertain in the remaining species.

M. montezumae shows lemma epidermal patterns different from the other species, as was previously mentioned by Thomasson (1986). Results obtained from the phenogram (Fig. 26) show *M. decumbens* as the species with the most similar anatomical features to *M. montezumae* (Fig. 25).

Results from this SEM study of selected *Melica* species has shown distinctive anatomical patterns of the lemma epidermis. Patterns of diversity are found within each of the three pointed structures: prickles, hooks and macro-hairs. Prickles exhibit the most diverse features such as the barb shape in relation to the base, distribution and frequency in both the intercostal and costal zones, arranged in one, two or three rows and barb point orientation to the leaf blade apex or in both directions towards and away from to the leaf apex.

Macro-hairs are as diverse as prickles, and we are able to propose two types of macro-hairs on the basis of appearance: straight macro-hairs and geniculate or twisted macro-hairs. Macro-hairs with a decumbent base are observed in only two species, *M. argyrea* and *M. bahuinii*.

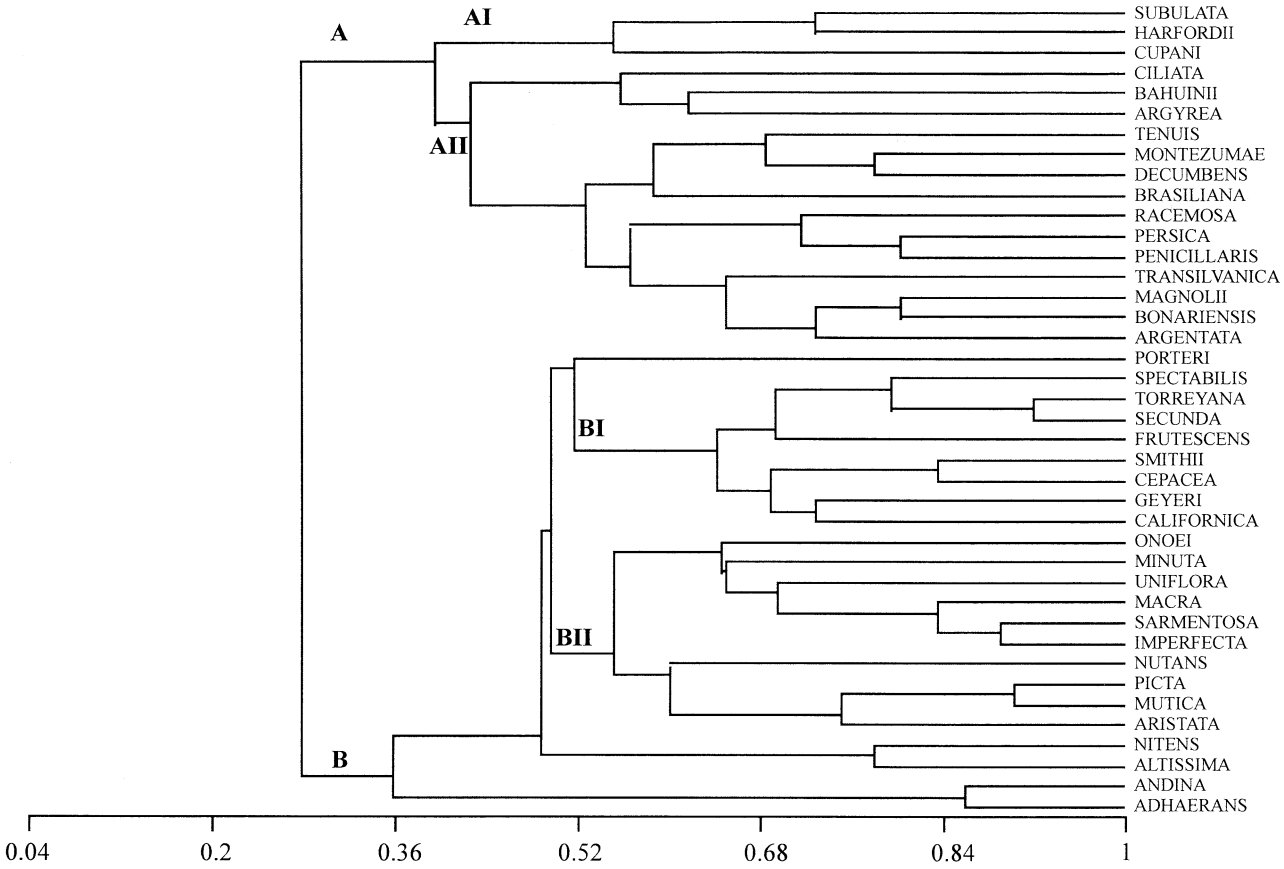


Figure 26. Dendrogram represents the UPGMA clustering of the *Melica* species.

We agree with Thomasson (1986) that lemma epidermal features have a limited taxonomic usefulness at the species level, because their features are relatively uniform for many species surveyed. However, phenetic analyses show two main clusters, A and B, grouped on the basis of presence or absence of macro-hairs and give some support to the classification of Papp (1928). Others associated characters found are: straight macro-hairs in subcluster AI; and geniculate macro-hairs in subcluster AII. On the other hand, cluster B split into subcluster BI on the basis of infrequent distribution of prickles in the intercostal zone and frequent distribution in the costal zone; and subcluster BII is grouped on the basis of absence of prickles in the intercostal zone and infrequent distribution of prickles in the costal zone.

CONCLUSIONS

1 *Melica* genus is split in the cluster on the basis of only one diagnostic character, the presence or absence of macro-hairs. Characters associated with this split were presence of straight or geniculate macro-hairs, distribution and frequency of prickles in both the costal zone and intercostal zone.

2 Species considered to be in the genus *Bromelica* by several authors are placed in the phenogram in both clusters A and B. Results from this phenogram (Fig. 26) show that *Melica* is not a coherent taxonomic grouping, and appears to have discontinuities; a simple segregation of the *Bromelica* genus from the *Melica* genus is rejected, and the *Melica* genus must be fragmented or divided into two groups, neither of which correspond to *Bromelica*.

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