

# Leaf anatomy of the South African Danthonieae (Poaceae).

## III. *Merxmuellera stricta*

R. P. ELLIS\*

### ABSTRACT

The anatomical structure, of the leaf blade as seen in transverse section, and of the abaxial epidermis, of *Merxmuellera stricta* (Schrad.) Conert is described and illustrated. In this variable species four distinct anatomical "forms" are recognized viz. the typical *M. stricta* form, the Cathedral Peak form, the Drakensberg form and the alpine form. The alpine and Cathedral Peak forms have recently been described as *M. guillarmodiae* Conert (1975). The degree of anatomical differentiation of these "forms" resembles the situation described in *M. disticha* (Nees) Conert (Ellis, 1980). Populations of both *M. stricta* and *M. disticha* from the Drakensberg mountains display extensive anatomical diversification which appears to be correlated with environmental factors. In addition, morphological differences are exhibited as well and the anatomical "forms" of *M. stricta* probably warrant taxonomic recognition.

### RÉSUMÉ

#### ANATOMIE FOLIAIRE DES DANTHONIEAE (POACEAE) D'AFRIQUE DU SUD. III. MERXMUELLERA STRICTA

La structure anatomique du limbe foliaire en coupe transversale et celle de l'épiderme abaxial de *Merxmuellera stricta* (Schrad.) Conert sont décrites et illustrées. Dans cette espèce variable on reconnaît quatre "formes" anatomiques distinctes, soit la forme *M. stricta* typique, la forme Cathedral Peak, la forme du Drakensberg et la forme alpine. Les formes alpine et Cathedral Peak ont récemment été décrites sous le nom de *M. guillarmodiae* Conert (1975). Le degré de différenciation anatomique de ces "formes" ressemble à la situation décrite chez *M. disticha* (Nees) Conert (Ellis, 1980). Dans les montagnes du Drakensberg des populations tant de *M. stricta* que de *M. disticha* montrent une large diversification anatomique qui est apparemment en corrélation avec des facteurs de milieu. En outre, des différences morphologiques sont également manifestes et il est probable que les "formes" anatomiques de *M. stricta* méritent d'être reconnues taxonomiquement.

### INTRODUCTION

*Merxmuellera stricta* (Schrad.) Conert (1970) [= *Danthonia stricta* (Nees) Schrad.] is widely distributed in the southern mountainous areas of South Africa. It occurs from Namaqualand in the north-west southwards to the south-western Cape, then eastwards to the north-eastern Cape mountains from where the distribution continues in a northerly direction along the Drakensberg mountains to Lesotho and the eastern Orange Free State. Together with *M. disticha* (Nees) Conert, *M. stricta* is an important constituent of the Karroid *Merxmuellera* Mountain Veld along all the higher mountains of the False Karoo and the Central Upper Karoo (Acocks, 1975). To the west of Beaufort West, *M. stricta* replaces *M. disticha* as the dominant grass of the Mountain Renosterbosveld (Acocks, 1975). *M. stricta* is also common in the fynbos communities of the south-western Cape.

*M. stricta* is a variable perennial, forming coarse, wiry tufts. Chippindall (1955) states that "There is considerable variation in the plants referred to *D. stricta*, and it is possible that they comprise more than one variety". In the north-west *M. stricta* may be confused with *M. dura* (Stapf) Conert, but *M. stricta* can be recognized by the glabrous condition of the lemma at the point of insertion of the central awn and is distinct anatomically (Ellis, in prep.). In the north-east, in the Drakensberg mountains, a situation exists, similar to that observed in *M. disticha* (Ellis, 1980), with three additional anatomical "forms" being present.

These anatomical "forms" appear to be correlated with morphological characters and habitat differences. Certain of the spikelet differences and other morphological characters must be of considerable magnitude

as Conert (1975) has independently described a new species, *M. guillarmodiae* Conert, from *M. stricta* collections from the alpine region of the Drakensberg.

Unfortunately, the specimens cited by Conert (1975) as belonging to *M. guillarmodiae* fall into two of the anatomical categories recognized in the present study, while the remaining two "forms" fall in *M. stricta* as currently constituted. If the precedent created by the description of *M. guillarmodiae* is to be followed, it implies that a further two species require description. Similarly, by the same token, two new species, presently referred to *M. disticha*, also warrant description (Ellis, 1980).

In the present context *M. stricta* is viewed in its widest sense, and for convenience *M. stricta* sens. lat. has merely been sub-divided into four "forms" for descriptive purposes: the typical form (*M. stricta*), the Cathedral Peak form (*M. guillarmodiae*), the Drakensberg form (*M. stricta*) and the alpine form (*M. guillarmodiae*). Each of these "forms" exhibits characteristic leaf anatomy and epidermal structure which will be described and discussed according to the terminology of Ellis (1976; 1979).

In the anatomical descriptions which follow, the following abbreviations will be used:

- vb/s—vascular bundle/s
- 1'vb/s—first order vascular bundle/s
- 2'vb/s—second order vascular bundle/s
- 3'vb/s—third order vascular bundle/s
- ibs—inner bundle sheath; mestome sheath
- obs—other bundle sheath; parenchyma sheath.

### ANATOMICAL DESCRIPTION OF *MERXMUELLERA STRICTA* SENS. LAT.

#### *Leaf in transverse section*

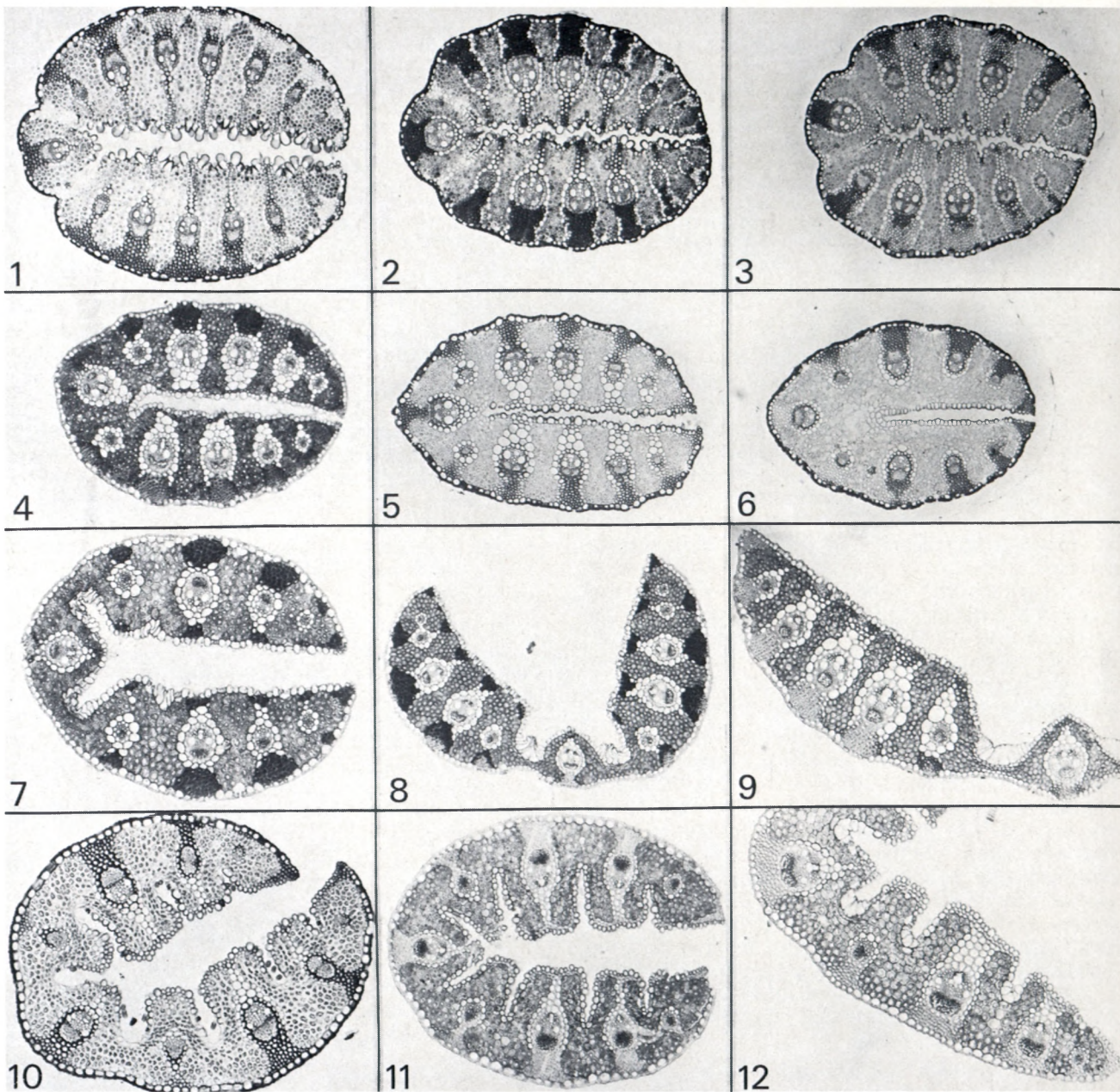
*Leaf outline*: infolded with an elliptical or U-shaped outline. Permanently infolded in typical and Cathedral Peak forms (Figs 1-6) but regular opening to 180°

\* Botanical Research Institute, Department of Agricultural Technical Services, Private Bag X101, Pretoria, 0001.



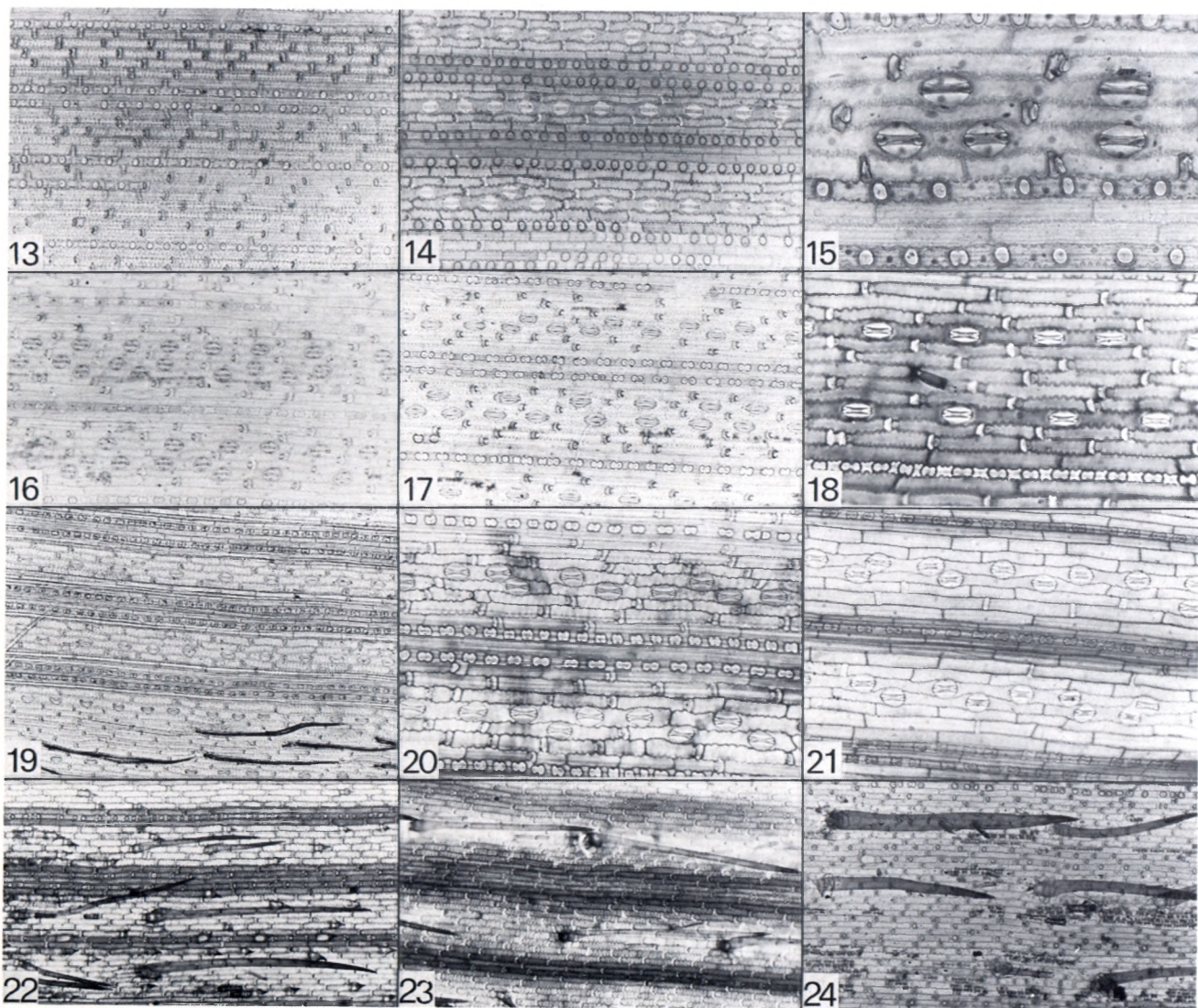
occurs in Drakensberg form (Fig. 9) and to 45° in the alpine form (Fig. 12). Lamina symmetrical about the median vb. 9–13 vbs present in leaf section (Table 1) with the alpine form always with 9 vbs (Figs 10–12) and typical *M. stricta* with 11 or 13 (Figs 1–3). Adaxial channel an extremely narrow and deep cleft in the typical and Cathedral Peak forms and is narrower than the lamina thickness in the Drakensberg and alpine forms when infolded. Leaves narrow (<1.1 mm wide) when folded. *Ribs and furrows*: adaxial furrows of variable depth but constant for each of the “forms” (Table 1); narrow, cleft-like. Similar ribs over all vbs when present; rounded or flat-topped with one vb per rib. Abaxial surface smooth except in typical *M. stricta* where grooves are present on either side of the median vb (Figs 1–3). *Median vascular bundle*: present; indistinguishable

structurally from lateral l'vbs. *Vascular bundle arrangement*: no 2'vbs; 3'vbs absent between lateral l'vbs. 3 or 4 l'vbs in each half of the lamina in typical form but decreasing to two in alpine form. All bundles located in centre of blade. *Vascular bundle structure*: vbs circular or elliptical in shape; xylem and phloem distinguishable in all vbs; phloem adjoins ms; often divided by intrusion of fibres in typical *M. stricta* (Figs 2 & 3) and the Cathedral Peak form (Fig. 5). Lysigenous cavities present. Metaxylem vessels thickened, circular and very narrow. *Vascular bundle sheaths*: obs circular or elliptical but normally horse-shoe shaped due to wide abaxial interruptions. Adaxial extensions present but cell composition differs in each of the “forms”. Obs cell shape variable from round to elliptical but all cells in a given leaf similar in shape. Obs cells conspicuous but not larger than the



FIGS 1–12.—Leaf blade outline of *Merxmuellera stricta* sens. lat. as viewed in transverse section. 1–3, typical *M. stricta* form, all  $\times 160$ . Note abaxial grooves on either side of median bundle only. (1, Ellis 2476; 2, Ellis 2445; 3, Ellis 2441.) 4–6, Cathedral Peak form, all  $\times 160$ . Adaxial groove, but no furrows present. (4, Ellis 3295; 5, Ellis 2372; 6, Trauseld 833.) 7–9, Drakensberg form. Very deep adaxial furrow on either side of median vascular bundle. Leaf not permanently infolded. (7, Ellis 3318,  $\times 250$ ; 8, Ellis 3322,  $\times 160$ ; 9, Ellis 3321,  $\times 250$ .) 10–12, alpine form, all  $\times 250$ . Furrows developed between all vascular bundles. (10, Ellis 3181; 11, Ellis 3317; 12, Ellis 3308.)





Figs 13–24.—Abaxial epidermis of *Merxmullera stricta* sens. lat. as seen in surface view. 13–15, typical *M. stricta* form. All with round silica bodies. (13, Roberts 2034,  $\times 250$ , note absence of intercostal zones; 14, Ellis 1156,  $\times 250$ , note stomatal files and intercostal zones; 15, Ellis 2317,  $\times 640$ .) 16–18, Cathedral Peak form. Silica bodies dumb-bell shaped. (16, Ellis 2372,  $\times 250$ ; 17, Galpin 10357,  $\times 250$ ; 18, Ellis 3289,  $\times 400$ .) 19–21, Drakensberg form. Dumb-bell shaped silica bodies. (19, Acocks 22069,  $\times 160$ ; 20, Ellis 1428,  $\times 400$ ; 21, Ellis 3290,  $\times 400$ .) 22–24, Alpine bog form. Silica bodies crescent-shaped, round or irregularly dumb-bell shaped. Macro-hairs, micro-hairs and prickles common. All  $\times 160$ . (22, Du Toit 2206; 23, Ellis 3181; 24, Ellis 1393.)

mesophyll cells; without chloroplasts (Fig. 26). Ibs complete; small cells with U-shaped thickenings; adaxial cells larger than lateral cells (Fig. 26). *Sclerenchyma*: Adaxial sclerenchyma variable from minute strands in the Cathedral Peak form (Figs 4–6) to well-developed, inversely anchor-shaped girders in typical *M. stricta* (Figs 1–3) or the alpine form (Figs 10–12) (Table 1). Abaxial girders well developed; either trapezoidal (Fig. 1 & 7) or narrower than the vb (Figs 2 & 5). In certain specimens of typical *M. stricta* individual girders fuse forming a continuous, abaxial, hypodermal band (Fig. 1). *Margin*: small, triangular, sclerenchyma caps developed. *Mesophyll*: not radiate; composed of regular, small, isodiametric, tightly packed cells (Fig. 26). Tall, narrow groups of chlorenchyma tissue between consecutive vbs separated by sclerenchyma girders. No colourless cells. *Adaxial epidermis*: bulliform cells poorly developed; basal cells of furrows may be slightly enlarged to form small, fan-shaped groups (Table 1). Epidermal cells inflated with outer wall slightly thickened. Macro-hairs and prickles absent; hooks occur irregularly.

Cells variously papillate; one papillus per cell. Adaxial papillae best developed in typical *M. stricta* (Fig. 1). *Abaxial epidermis*: no bulliform cells developed. Hooks, prickles, macro-hairs and papillae lacking. Outer tangential wall flattened with smooth, continuous cuticle.

#### *Abaxial epidermis in surface view*

*Intercostal zones*: differentiated except in typical *M. stricta* specimens with continuous hypodermal sclerenchyma layer (Figs 1 & 13). Long cells medium to elongated with parallel, slight to moderately undulating, side walls. Silico-suberose couples between successive long cells. No bulliform cells. *Stomata*: absent in alpine form (Figs 22–24) and in those typical *M. stricta* specimens with hypodermal sclerenchyma layer (Fig. 13). Low dome-shaped, 1–2 files of stomata in centre of each intercostal zone; files adjacent to one another. One interstomatal cell between successive stomata. *Intercostal short cells*: silico-suberose couples; cork cell tall and narrow to crescentic; occur between most intercostal long cells. *Papillae*:



TABLE 1.—The differences in leaf anatomy and spikelet morphology between the different forms of *Merxmuellera stricta*

Character	Typical <i>M. stricta</i> form	Cathedral Peak form	Drakensberg form	Alpine form
1. Outline of lamina	1. Permanently infolded	1. Permanently infolded	1. Infolded but regularly opens to 180°	1. Infolded but opening to 45° possible
2. Number of vbs in leaf section	2. 13 (sometimes 11)	2. 11 (sometimes 9)	2. 9 vbs	2. 9 vbs
3. Adaxial furrows	3a. Slight to medium > ½ leaf thickness 3b. Present between all vbs	3a. Absent 3b. No furrows present	3a. Deep > ½ leaf thickness 3b. A single furrow on either side of median vb only	3a. Medium ½ leaf thickness 3b. Present between all vbs
4. Abaxial furrows	4. Single furrow on either side of median vb	4. Slight undulations associated with all vbs	4. Absent except when leaf open	4. Absent
5. Phloem	5. Usually divided into two groups by intrusive fibres	5. Sometimes exhibits sclerosed phloem	5. No intrusive fibres	5. No sclerosed phloem
6. Adaxial extensions of outer bundle sheath	6a. Parenchymatous grading gradually into fibres 6b. Long, narrow extensions of more than 5 cells	6a. Thin-walled colourless parenchyma 6b. Medium extensions of 4 or less cells	6a. Thickened parenchyma abruptly becoming sclerenchyma 6b. Short, wide extensions of 3 or 4 cells deep	6a. Thick-walled parenchyma decreasing in size to epidermis 6b. Long, wide or narrow extensions of more than 5 cells deep
7. Adaxial sclerenchyma	7. Inversely anchor-shaped with long, thin stem	7. Minute strand only; sometimes absent	7. Small strands narrowing towards base of extension	7. Inversely anchor-shaped girder with narrow or wide stem
8. Bulliform cells	8. Poorly developed only at base of furrow on either side of median vb	8. Absent	8. Well-developed fan shaped groups at base of furrow on either side of median vb	8. Poor to well developed fan shaped groups in the bases of all furrows
9. Epidermal hairs	9. Micro-hairs only; rare	9. Micro-hairs only	9. Micro-hairs but sometimes macro-hairs occur	9. Micro-hairs, macro-hairs and prickles common
10. Silica body shape	10. Rounded or elliptical	10. Dumb-bell shaped	10. Dumb-bell shaped but round in a few specimens	10. Rounded to elliptical but enfolded by crescentic cork cell
11. Lower glume length	11. (11–) 15,2 mm (–22)	11. (9–) 10,7 mm (–12)	11. (14–) 17,8 mm (–22)	11. (10–) 12,2 mm (–14)
12. Length of lower lemma awn	12. (9–) 12,5 mm (–16)	12. (8–) 9,8 mm (–11)	12. (8–) 12,0 mm (–14)	12. (5,0–) 5,5 mm (–6,5)
13. Hairs on back of lemma at point of insertion of awn	13. Glabrous; occasionally very sparse, scattered hairs present	13. Densely hairy; hairs 2–3,2 mm long	13. Always glabrous	13. Sparsely hairy; hairs up to 2 mm long

absent. *Prickle-hairs*: only present on alpine form (Fig. 22) (Table 1). Barbs short. *Micro-hairs*: present but very rare in typical *M. stricta* and then only in specimens with intercostal zones; common in other three "forms". Bicellular, elongated (especially in alpine form); basal cell slightly longer than distal cell; tapering distal cell thin-walled (Fig. 18). *Macro-hairs*: absent except on all specimens of alpine form; occur in groove on either side of median vb in one specimen of Drakensberg form (Fig. 19). Unicellular, inflexible; 2–3 specialized epidermal cells associated with base of hair; base somewhat swollen in relation to hair thickness. *Silica bodies*: differ in different "forms" (Table 1). Costal bodies rounded or elliptical in typical *M. stricta* (Figs 14 & 15) and in certain specimens of Drakensberg form; dumb-bell shaped in Drakensberg and Cathedral Peak form (Figs 18, 20, 21); small rounded to elliptical and associated with crescentic cork cell in alpine form (Figs 22 & 24). Granules present. Width same as adjacent costal long cells except in alpine form. *Costal cells*: silica cells alternate with costal short cells except in alpine form where silico-suberose couples alternate with costal short cells; files with silica cells alternate with files of costal long cells in all forms except alpine form.

Specimens examined.

Typical *M. stricta* form

CAPE.—3119 (Calvinia): Van Rhyns Pass (–AC), *Ellis* 1139, 1140; Kobe Mts (–CA), *Ellis* 2445, 2447\*. 3126 (Queenstown): Bushmanhoek Pass (–AD), *Ellis* 2577\*; Hangklip Mt (–DD),

*Roberts* 2034\*. 3218 (Clanwilliam): Pakhuis Pass (–BB), *Ellis* 1705\*. 3219 (Wuppertal): Pakhuis Pass (–AA), *Ellis* 1151, 1156; Buffelberg Pass (–CA), *Ellis* 1189. 3225 (Somerset East): Grootfontein valley (–CB), *Van der Walt* 184\*. 3318 (Cape Town): Jonkershoek, Stellenbosch (–DD), *Ellis* 2241, 2242, 2258. 3319 (Worcester): Gydoberg (–AD), *Ellis* 2476\*; Karooport, Ceres (–BC), *Hafström & Acocks* 100\*. Franschoek Pass (–CD), *Ellis* 687, 688. 3320 (Montagu): 23 km from Barrydale on road to Montagu (–DC), *Ellis* 643. 3322 (Oudtshoorn): Swartberg (–AC), *Ellis* 2579\*; Robinsons Pass (–CC), *Ellis* 2583\*. 3323 (Willowmore): Uniondale (–CA), *Ellis* 1641\*. 3325 (Port Elizabeth): Gamtoos Valley (–CC), *Acocks* 16112. 3326 (Grahamstown): Peddie (–BC), *Fairall* 240. 3418 (Simons-town): Red Hill (–AB), *Ellis* 2317, 2318. 3419 (Caledon): Kleinmond (–AC), *Ellis* 2514, *Van Heerden* 75. 3420 (Bredasdorp): Bredasdorp (–AA), *Ellis* 1265\*.

Cathedral Peak form (*M. guillarmodiae*)

O.F.S.—2828 (Bethlehem): Golden Gate National Park, Brandwag Peak (–DA), *Ellis* 2371, 2372.

NATAL.—2829 (Harrismith): Royal Natal National Park (–CB), *Galpin* 10357; Cathedral Peak Forest Reserve (–CC), *Killick* 1110†, 1576†, *Ellis* 3289, 3295, 3297. 2929 (Underberg): Giants Castle Game Reserve (–AB), *Trauseld* 833; Nyiginye (–BA), *Du Toit* 2516; Highmoor Forest Reserve (–BC), *Du Toit* 2500.

Drakensberg form (*M. stricta*)

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve (–CC), *Ellis* 1428, 3290, 3299. 2929 (Underberg): Giants Castle Game Reserve, Bannermans Pass (–AD), *Ellis* 3318, 3321; Loteni Game Reserve (–DA), *Ellis* 3322.

\*Specimens with continuous abaxial hypodermal sclerenchyma layer and without stomata.

† Specimens cited by Conert (1975) as being *M. guillarmodiae*.



LESOTHO.—2929 (Underberg): Sehlabathebe National Park (-CC), *Du Toit* 2631, 2642.

CAPE.—3028 (Matatiele): Quachas Nek (-BA), *Ellis* 243\*; Ramatselisonek (-BB), *Acocks* 22069. 3226 (Fort Beaufort): Great Winterberg (-AD), *Story* 4522.\*

#### Alpine form (*M. guillarmodiae*)

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve, summit above Windy Gap (-CC), *Ellis* 1393, 3181, 3182, 3308. 2929 (Underberg): Giants Castle Game Reserve, summit of Bannermans Pass (-AD), *Ellis* 3317; top of Sani Pass (-CA), *Du Toit* 2206, 2242, 2286.

LESOTHO.—2828 (Bethlehem): Butha Buthe (-CC), *Roberts* 5844, *Lubke* 305; Tsehlanyane valley (-CD), *Jacot-Guillarmod* 3727†, 3734†.

CAPE.—3027 (Lady Grey): Doodmans Kranz, Barkly East (-DC), *Galpin* 6906†. 3028 (Matatiele): Quachas Nek, Temrock Peak (-BA), *Liebenberg* 5729.

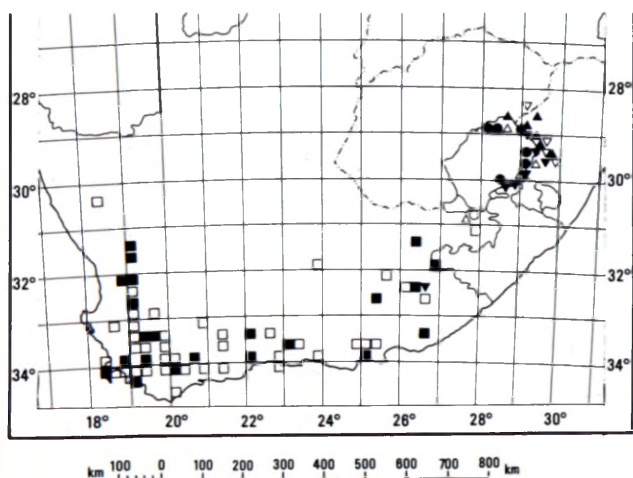


FIG. 33.—Distribution of *Merxmullera stricta* in South Africa. □—typical *M. stricta*; △—Cathedral Peak form; ▽—Drakensberg form; ○—Alpine form. Shaded symbols represent localities of specimens studied anatomically. Compiled from specimens at the National Herbarium, Pretoria (PRE).

#### DISCUSSION AND CONCLUSIONS

All the specimens examined in this study have the lateral first order vascular bundles located adjacent to one another and lack the single third order bundle interspaced between them which is characteristic of *M. disticha* (Ellis, 1980). *M. dura*, considered to be closely allied to *M. stricta* (Chippindall, 1955; De Wet, 1960), does not share this characteristic and has, therefore, been excluded from the present considerations.

Anatomically the leaf structure of the typical *M. stricta* form is remarkably constant throughout its wide distributional area (Fig. 33). The only anatomical difference worthy of mention is the development of a continuous abaxial hypodermal sclerenchyma layer (Fig. 1) with the resultant exclusion of the intercostal zones and stomata (Fig. 13). This structure was present in 40% of the specimens examined in this study, and occurs in plants from widely scattered localities, throughout the range of this form, and does not appear to be correlated with any obvious environmental factor. Morphologically there is a definite tendency for these specimens to have shorter glumes [(11–) 12,1 mm (-15)] than the remainder of the typical *M. stricta* specimens [(15–) 17,5 mm (-22)]. These two characters, therefore, appear to be con-

stantly linked and, on the basis of glume length, these shorter spikelets tend to resemble the Cathedral Peak form of *M. guillarmodiae* (Table 1). However, the *M. stricta* form has distinctly longer awns—averaging 11,1 mm as against 9,8 mm for the Cathedral Peak form. This form, however, does not have a continuous hypodermal sclerenchyma layer (Fig. 4) and has numerous stomatal files (Figs 16–18).

The anatomy of the Cathedral Peak form is unmistakable, due to the shape of the adaxial groove which lacks ribs and furrows, (Figs 4–6) and due to the occurrence of dumb-bell shaped silica bodies (Figs 16–18). This type of anatomical structure appears to be strongly correlated with *M. guillarmodiae* spikelet characters, such as the presence of hairs on the back of the lemma up to the point of insertion of the central awn (Conert, 1975). However, as Conert (1975) points out the hair arrangement of the cited Cathedral Peak form specimens (*Killick* 1100, 1576) resembles that of *M. guillarmodiae*, but the hairs themselves, are longer. The typical *M. guillarmodiae* (alpine form) specimens examined have hairs up to 2,0 mm in length with the lemmas being sparsely hairy but the Cathedral Peak form specimens are densely hairy on the back of the lemmas with the hairs being from 2,0–3,2 mm long.

All morphological indications are, therefore, that this Cathedral Peak form is closely linked to the typical *M. guillarmodiae* or alpine form. However, one specimen, *Trauseld* 833, does not exhibit any of these *M. guillarmodiae* spikelet characteristics. Although the adaxial groove and silica bodies conform, it differs anatomically from the remainder of the Cathedral Peak form sample in that it lacks adaxial bundle sheath extensions and thus the mesophyll distribution is continuous adaxially and not restricted to separate tall and narrow groups (Fig. 6). This specimen was collected at Giants Castle and, although this area was revisited, no plants with Cathedral Peak form anatomy or morphology were located. The Drakensberg form, which *Trauseld* 833 resembles morphologically, is common in this area, but all specimens collected had the distinctive Drakensberg form anatomy. Specimens, conforming anatomically and morphologically with the Cathedral Peak form, do occur at Highmoor to the south of Giants Castle, e.g. *Du Toit* 2500.

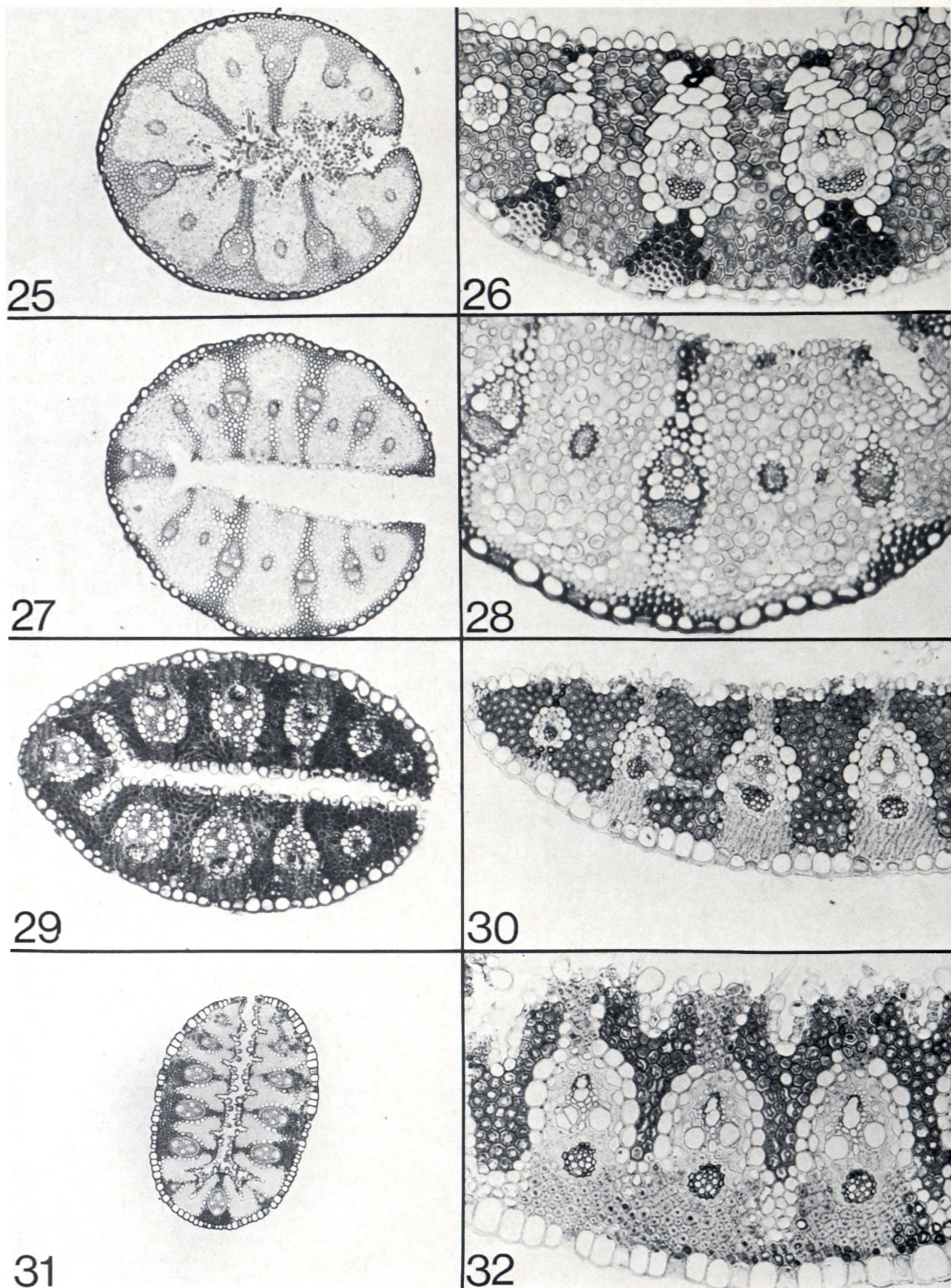
Further collections from the southern Drakensberg are required to help clarify the relationships of this Cathedral Peak form. It has been grouped under *M. guillarmodiae* (Conert, 1975) together with the alpine form, which it closely resembles morphologically. Anatomically, however, it has most in common with the Drakensberg form. Both these latter “forms” have similar sclerenchyma girders and bundle sheath extensions but, most significantly, both have dumb-bell shaped silica bodies.

The Drakensberg form, on the other hand, although resembling the Cathedral Peak form anatomically, differs significantly morphologically. The back of the lemmas are glabrous along the centre, as in typical *M. stricta*, and the lower glumes are much longer (Table 1). Anatomically the most important difference is the two deep adaxial furrows on either side of the median vascular bundle (Fig. 7) and the laminae are capable of opening to 180° (Fig. 9) especially during conditions of low irradiance. This ability is undoubtedly functionally significant and was possibly partly responsible for the relative success of this Drakensberg form in the north-eastern mountains.

\* Specimens with round or elliptical silica bodies.

† Specimens cited by Conert (1975) as being *M. guillarmodiae*.





FIGS 25-32.—A comparison between the leaf anatomy of the setaceous-leaved, summer rainfall *Pentaschistis* species with the anatomy of the leaves of the *Merxmuellera stricta* group. 25, *Pentaschistis basutorum*, Ellis 2368,  $\times 160$ . Note arrangement of large and small vascular bundles. 26, *Merxmuellera guillarmodiae*, Ellis 3289,  $\times 400$ . Detail of mesophyll and bundle sheath structure typical of the *M. stricta* group. 27-28, *Pentaschistis fibrosa*. (27, Du Toit 646,  $\times 160$ , note vascular bundle arrangement; 28, Du Toit 2301,  $\times 400$ , outer bundle sheath cells thin-walled and inconspicuous.) 29-30, *Pentaschistis tysonii*. (29, Ellis 3302,  $\times 250$ , third order bundles absent; 30, Ellis 3319,  $\times 400$ , bundle sheath cells distinct.) 31-32, *Pentaschistis* sp. (31, Ellis 1409,  $\times 100$ , no third order bundles between lateral first order bundles; 32, Ellis 3292,  $\times 400$ .)



This anatomical difference, although distinct and consistent, may, however, not be as significant as it initially appears. It can be simply explained by opposite developmental trends in respect of only a single character—a single adaxial furrow on either side of the median vascular bundle. The epidermis also closely resembles that of the Cathedral Peak form as both have dumb-bell shaped silica bodies (Figs 16–21).

The anatomical indications are, therefore, that the Drakensberg form resembles the Cathedral Peak form more closely than either of the other two forms. These similarities are not corroborated by spikelet structure, however, and in this respect the Drakensberg form displays typical *M. stricta* structure.

Some Drakensberg form specimens from the eastern Cape (Ellis 243; Story 4522), however, anatomically demonstrate this relationship with typical *M. stricta*. These specimens have round silica bodies, with characteristic *M. stricta* type epidermal structure but in section the anatomy is typical of the Drakensberg form. This observation, therefore, provides an important clue as to the affinities of this form and provides an anatomical link to support the morphological evidence. A degree of morphological and anatomical gradation appears to occur between these two forms in the areas of sympatry in the north-eastern Cape and once again further collecting is required to help confirm affinities between the Drakensberg, Cathedral Peak and typical *M. stricta* forms.

The anatomy of the alpine form specimens compares very favourably with that of the type specimen of *M. guillarmodiae* (Jacot-Guillarmod 3734). This form appears to be distinct, both anatomically and morphologically, from *M. stricta* (Conert, 1975) although the Cathedral Peak form is intermediate in most spikelet characters (Table 1). In addition it has specialized habitat requirements, being restricted to the higher alpine zone of the Drakensberg, often associated with boggy conditions. It is, therefore, not spatially associated with any of the other forms.

This alpine form of *M. guillarmodiae* exhibits striking resemblances, in habitat preferences, growth form and anatomy, with the alpine bog form described in *M. disticha* (Ellis, 1980). Anatomical similarities are rib and furrow distribution and form, mesophyll configuration and epidermal structure. The only difference is in the pattern of arrangement of the various orders of vascular bundle along the width of the lamina. This arrangement differs in the two "forms" but corresponds with the patterns found in either typical *M. stricta* or typical *M. disticha*. This difference is correlated with differences in inflorescence characters—a contracted panicle in *M. stricta* and a distichous spike in *M. disticha*—and appears to indicate the relationships of the alpine "forms". This seems to be an excellent example of convergent evolution in response to similar environmental conditions.

The most obvious morphological differences between the specimens of the four "forms" of *M. stricta*, recognized and examined in this study, are briefly summarized in Table 1. Typical *M. stricta* and the Drakensberg form have significantly longer lower glumes than do the alpine and Cathedral Peak forms. The longer glumes are associated with longer awns on the lower lemma except in the Cathedral Peak form which is intermediate between the alpine form and the other two. The Cathedral Peak and typical *M. stricta* forms are glabrous on the back of

the lower lemma along the central vein up to the base of the central awn, although, occasionally, a few scattered hairs may be present in *M. stricta* type specimens. In both the alpine and Cathedral Peak forms the back of the lemma is hairy—sparsely hairy with hairs up to 2 mm long in typical *M. guillarmodiae* (the alpine form) but densely hairy with longer hairs (2.0–3.2 mm long) in the Cathedral Peak form.

Morphological characters, therefore, indicate two groups in *M. stricta* sens. lat.—the typical *M. stricta* and Drakensberg forms sharing certain characters whereas, the same characters differ considerably in the alpine and Cathedral Peak forms. This grouping is not confirmed by anatomical evidence which indicates close relationships between the Cathedral Peak and Drakensberg forms with typical *M. stricta* and the alpine forms being distinct. However, a few specimens with anomalous anatomy tend to break down the rigid anatomical divisions and, thereby, add substance to the morphological grouping.

The acceptance of the morphological groupings as reflecting affinities, implies that silica body structure is of no significance in this instance. This would normally be considered unlikely as silica bodies are usually of considerable value taxonomically (Metcalf, 1960). Typical *M. stricta* specimens have classic rounded or elliptical festucoid-type silica bodies whereas, both the Drakensberg and Cathedral Peak forms have panicoid-type, dumb-bell shaped bodies (Clifford & Watson, 1977). All other indications are that typical *M. stricta* and the Drakensberg form are closely related except for silica body shape. In fact, these two "forms" of the same species possess silica bodies supposedly characteristic of different tribal groupings (Prat, 1932; 1936). De Wet (1954, 1956, 1960) notes the mixed character of the epidermis in *M. stricta* but actually refers to the association of micro-hairs (a panicoid character) with the festucoid elliptical silica bodies. Two panicoid epidermal characters may, therefore, occur in *M. stricta* sens. lat. but this is not supported by other anatomical evidence.

The recent description of *M. guillarmodiae* (Conert, 1975) as a separate species initially appears justified on the anatomical evidence presented in this paper. However, certain *M. guillarmodiae* specimens, included here in the Cathedral Peak form, differ dramatically from the type of *M. guillarmodiae* (the alpine form) and, applying the same criteria appear to merit specific status in their own right. The Drakensberg form would then also warrant specific status. This implies that a further two species require description, as is the case in *M. disticha* where an almost identical anatomical situation exists (Ellis, 1980). However, especially in *M. stricta*, these anatomical differences do not correlate very well with morphological differences.

This anatomical diversification within *Merxmuellera* populations in this restricted area of high altitudes and of climatic extremes also appears to be reflected by the description of *M. stereophylla*. (J. G. Anders.) Conert (Anderson, 1962) from *M. drakensbergensis* (Schweick.) Conert. The recognition of *M. stereophylla* was based on morphological and ecological grounds but, in this case, the anatomical differences are minimal in comparison with the differences between the anatomical "forms" of *M. stricta* and *M. disticha*.

In addition, two of the four setaceous-leaved *Pentaschistis* species from this same area, display remarkable anatomical similarities with *M. stricta*



sens. lat. (Figs 25–32). *P. basutorum* Stapf (Fig. 25) and *P. fibrosa* Stapf (Figs 27 & 28) have typical *Pentastichis* anatomy with thin-walled outer bundle sheath cells and somewhat diffuse mesophyll. The bundle sheath extensions and sclerenchyma associated with the third order bundles differ considerably from *M. stricta* sens. lat. (Fig. 26). *P. tysonii* Stapf (Figs 29 & 30) and *Pentastichis* sp (Figs 31 & 32), on the other hand, display typical *Merxmuellera* type anatomy, and, on anatomical grounds only, appear to have more in common with *Merxmuellera* and especially the *M. stricta* group than they do with *Pentastichis*.

The following *Pentastichis* specimens were examined:

*P. basutorum*

O.F.S.—2828 (Bethlehem): Golden Gate National Park (–DA), *Ellis* 2367, 2368, 2369, 2370, 2373; *Liebenberg* 7454.

*P. fibrosa*

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve (–CC), *Ellis* 3300; Sentinel (–DB), *Du Toit* 646. 2929 (Underberg): Highmoor Forest Reserve (–BC), *Ellis* 3169; Sani Pass (–CB), *Du Toit* 2301.

*P. tysonii*

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve (–CC), *Ellis* 3296, 3302; *Killick* 2280. 2929 (Underberg): Giants Castle Game Reserve, Bannermans Pass (–AD), *Ellis* 3314, 3319.

*Pentastichis* sp.

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve (–CC), *Ellis* 1409, 3291, 3292. 2929 (Underberg): Giants Castle Game Reserve, Bannermans Pass (–AD), *Ellis* 3320.

For the above reasons the description of numerous new *Merxmuellera* species from this summer rainfall area is to be cautioned against for the time being. The indications are that this temperate region of high altitudes has only relatively recently been colonized by these typically winter rainfall grasses from the south. Adaptive radiation appears to be actively continuing and the taxonomic picture is not at all clear. Further studies, especially those of a bio-systematic and autecological nature, are needed, within *Merxmuellera* and closely related genera in the Danthonieae, before reliable taxonomic conclusions can be reached. At present, the assigning of specific rank to any of these anatomical “forms” cannot be fully justified. However, for practical purposes, each of these anatomical “forms”, described in both *M. stricta* and *M. disticha* (Ellis, 1980), deserve taxonomic recognition but infraspecific groupings are recommended until the status of this genus in this area is better understood.

In arriving at a final conclusion, it must be remembered, that, in both *M. stricta* and *M. disticha*, the anatomical differences between the “forms” are of considerable magnitude, disjunct and are correlated with other anatomical, morphological and ecological characteristics. In many instances these differences are, therefore, greater than are those between other *Merxmuellera* species and even between some of the genera of the Danthonieae.

#### ACKNOWLEDGEMENTS

The author is grateful to the following organizations for permission to collect material on their property: the Department of Forestry, the National Parks Board and the Natal Parks, Game and Fish Preservation Board. The capable technical assistance of Miss R. Manders and Miss L. Breytenbach is gratefully acknowledged as is the advice and assistance given by Miss L. Smook on the identification and morphology of the specimens studied.

#### UITTREKSEL

*Die anatomiese struktuur, van die blaar in dwarsnee en die abaksiale epidermis, van Merxmuellera stricta (Schrad.) Conert word beskryf en geïllustreer. Vier afsonderlike anatomiese “vorme” word erken: die tipiese M. stricta vorm, die Cathedral Peak vorm, die Drakensberg vorm en die alpiene vorm. Die alpiene en Cathedral Peak vorme is onlangs beskryf as M. guillarmodiae Conert (1975). Die mate van anatomiese differensiasie van al hierdie “vorme” toon 'n ooreenkoms met die toestand wat in M. disticha beskryf is (Ellis, 1980). Populasies van, beide M. stricta en M. disticha, van die Drakensberge, vertoon anatomiese diversifikasie op groot skaal wat ook gekorreleer is met omgewingsfaktore. Boonop is morfologiese verskille ook sigbaar en hierdie anatomiese “vorme” van M. stricta verdien vermoedelik om taksonomiese erkenning te verkry.*

#### REFERENCES

- ACOCKS, J. P. H., 1975. Veld types of South Africa, 2nd ed. *Mem. bot. Surv. S. Afr.* 40: 1–127.
- ANDERSON, J. G., 1962. Notes on African plants: Gramineae. *Bothalia* 7: 419–420.
- CHIPPINDALL, L. K. A., 1955. In D. Meredith, *The grasses and pastures of South Africa*. Johannesburg: CNA.
- CLIFFORD, H. T. & WATSON, L., 1977. *Identifying grasses*. St. Lucia: Univ. of Queensland Press.
- CONERT, H. J., 1970. *Merxmuellera*, eine neue Gattung der Gramineen. *Senckenberg. Biol.* 51: 129–133.
- CONERT, H. J., 1975. *Merxmuellera guillarmodiae* Conert n.sp. *Senckenberg Biol.* 56: 145–152.
- DE WET, J. M. J., 1954. The genus *Danthonia* in grass phylogeny. *Am. J. Bot.* 41: 204–211.
- DE WET, J. M. J., 1956. Leaf anatomy and phylogeny in the tribe Danthonieae. *Am. J. Bot.* 43: 175–182.
- DE WET, J. M. J., 1960. Leaf anatomy and morphology in the South African species of *Danthonia*. *Bothalia* 7: 303–310.
- ELLIS, R. P., 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. *Bothalia* 12: 65–109.
- ELLIS, R. P., 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. *Bothalia* 12: 641–672.
- ELLIS, R. P., 1980. Leaf anatomy of the South African Danthonieae (Poaceae). II. *Merxmuellera disticha*. *Bothalia* 13: 185–189.
- METCALFE, C. R., 1960. *Anatomy of the monocotyledons. I. Gramineae*. Oxford: Clarendon Press.
- PRAT, H., 1932. L'Épiderme des Graminées. Étude anatomique et systématique: *Annls Sci. nat. (Bot.) ser. 10* 14: 117–324.
- PRAT, H., 1936. La systématique des Graminées. *Annls Sci. nat. (Bot.) ser. 10* 18: 165–258.