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Leaf anatomy of the South African Danthonieae (Poaceae). II. *Merxmuellera disticha*

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ABSTRACT

The anatomical structure, of the leaf blade as seen in transverse section, and of the abaxial epidermis, of *Merxmuellera disticha* (Nees) Conert is described and illustrated. Three distinct anatomical "forms" are recognized viz. typical *M. disticha*, the Drakensberg form and the alpine bog form. These three anatomical groups also appear to have differing environmental requirements and probably warrant taxonomic status.

RÉSUMÉ

ANATOMIE FOLIAIRE DES DANTHONIEAE (POACEAE) D'AFRIQUE DU SUD. II. MERXMUELLERA DISTICHA

La structure anatomique du limbe foliaire en coupe transversale et celle de l'epiderme abaxial de Merxmuellera disticha *(Nees) Conert sont décrites et illustrées. On reconnaît trois "formes" anatomiques distinctes, soit la forme* M. disticha *typique, la forme du Drakensberg et la forme du marécage alpin. Ces trois groupes anatomiques semblent également avoir des exigences de milieu différentes et il est probable qu'elles méritent un statut taxonomique.*

INTRODUCTION

Merxmuellera disticha (Nees) Conert (1970) (=*Danthonia disticha* Nees) is probably the best known and most distinctive southern African representative of this genus. It is a wiry, tussock grass and is economically relatively important (Acocks, 1971) as it may become dominant, and completely usurp the position of better grazing grasses in certain areas. It occurs over extensive areas along the south coast and eastern mountain ranges and is an important constituent of the following veld types: *Themeda—Festuca* Alpine Veld, Stormberg Plateau Sweetveld and Karroid *Merxmuellera* Mountain Veld (Acocks, 1975).

This species is easily recognized by the inflorescence, which is an oblong, uninterrupted, distichous spike. It is the only species of this genus which can have 2-flowered spikelets and both the upper and lower glumes 3-nerved (Chippindal, 1955). *M. disticha* is thus distinct morphologically and only the plants with 2-flowered spikelets may be confused with *Pentaschistis basutorum* Stapf (Chippindal, 1955).

It was, therefore, most unexpected to discover that three distinct anatomical "forms" are present in this species. In addition, from the sample examined in this study, it appears that each of these three "forms" has different habitat requirements. For convenience, *M. disticha* sens. lat. has been sub-divided into three "forms" in the following descriptions and discussions: typical *M. disticha*, the Drakensberg form and the alpine bog form. Each of these forms exhibits charcteristic leaf anatomy and epidermal structure.

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—outer bundle sheath; parenchyma sheath.

For definitions of terminology used see Ellis (1976, 1979).

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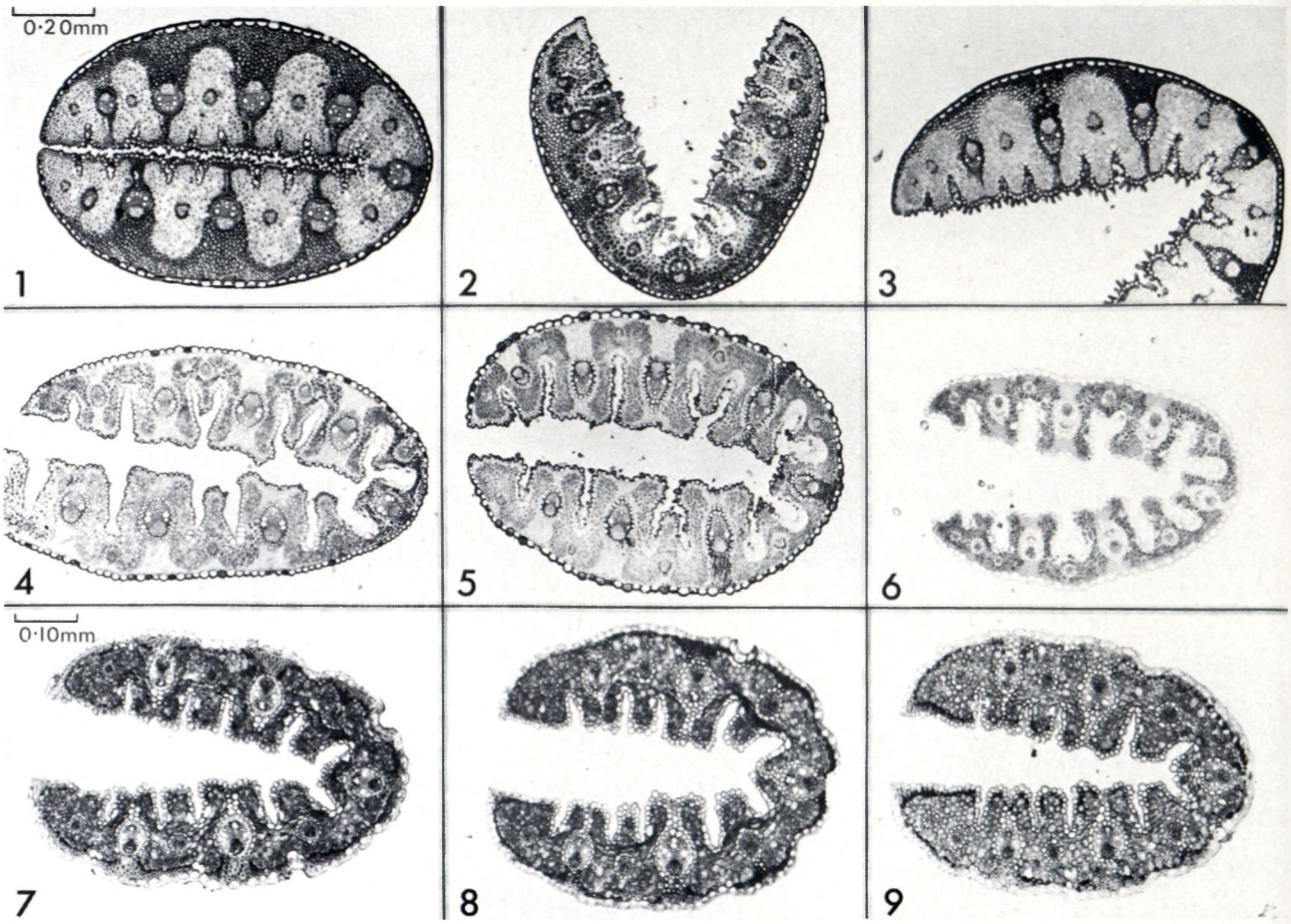
ANATOMICAL DESCRIPTION OF *MERXMUELLERA DISTICHA* SENS. LAT.

Leaf in transverse section

Leaf outline: infolded with an elliptical or U-shaped outline. Symmetry about the median bundle not perfect with the 1'vbs of opposite halves of the lamina alternating. This tendency particularly marked in the Drakensberg form (Fig. 4). Leaves narrow (<1,1 mm wide) when folded. Adaxial channel normally a deep, narrow cleft. *Ribs and furrows:* adaxial furrows narrow, cleft-like and located between all vbs except the penultimate 3'vb which lies at the base of a furrow. Adaxial ribs flat-topped and angular; 1'vb ribs larger than those overlying 3'vbs. Abaxial surface without ribs or furrows. *Median vascular bundle:* present; indistinguishable structurally from other 1'vbs. *Vascular bundle arrangement:* no 2'vbs present; one 3'vb between consecutive 1'vbs; 1'vbs decrease in size towards margin. *Vascular bundle structure:* vbs circular or elliptical in shape; phloem adjoins ibs; lysigenous cavity and protoxylem vessels present; metaxylem vessels circular, extremely narrow with thickening of the walls. *Vascular bundle sheaths:* obs of 3'vbs circular or with slight abaxial interruptions in the Drakensberg form (Fig. 5); no sheath extensions. Cells rounded or elliptical, inconspicuous and much smaller than the mesophyll cells; thin walled; chloroplasts few or absent. Ibs indistinct, complete and with uniformly thickened walls. Obs of 1'vbs elliptical or horse-shoe shaped with wide adaxial and abaxial interruptions; no extensions. Sheath cells inconspicuous; smaller than both the mesophyll and the ibs cells; rounded or, more often, elliptical; thin-walled or may resemble ibs cells with u-shaped wall thickenings in typical *M. disticha* only (Fig. 1). Few or no chloroplasts present. Ibs complete; inner radial and tangential walls thickened; often adaxial ibs cells larger than lateral cells. *Sclerenchyma:* small, shallow adaxial strands associated with 3'vbs. Inversely anchor- or T-shaped adaxial girders associated with 1'vbs; width and length of girder stem variable (Table 1); girder interrupts obs. Abaxial girders not associated with 3'vbs except in Drakensberg form (Figs 4 & 5). 1'vb girders usually trapezoidal narrowing toward the bundle; fibres interrupt the obs. Continuous abaxial hypodermal sclerenchyma well



FIGS 1–9.—Leaf blade outline of *Merxmuellera disticha* sens lat. in transverse section. 1–3, typical *M. disticha* form. All × 160. (1, *Ellis* 2572; 2, *Ellis* 2564; 3, *Ellis* 669.) 4–6, Drakensberg form. All × 160. (4, *Du Toit* 675; 5, *Ellis* 1404; 6, *Ellis* 3152.) 7–9, Alpine bog form. All × 250. (7, *Ellis* 3315; 8, *Ellis* 3306; 9, *Ellis* 3316.)

developed in typical *M. stricta* (Fig. 1) but only a shallow interrupted hypodermal layer present in the alpine bog form (Figs 7–9) (Table 1). Fibres with both lignified and cellulose cell walls present in individual sections. *Margin:* relatively small, pointed, sclerenchyme cap developed. *Mesophyll:* not radiate; cells isodiametric, regular and tightly packed. Mesophyll tissue not continuous between all vbs; U-shaped chlorenchyma groups occupy sides and bases of furrows between consecutive l'vbs. No colourless cells. *Adaxial epidermis:* bulliform cells poorly developed; basal cells of furrows may be slightly enlarged to form small, fan-shaped bulliform cell groups. Epidermal cells inflated with the outer wall slightly thickened. No macro-hairs, hooks or prickles developed. Cells variously papillate; one papillus per cell. *Abaxial epidermis:* no bulliform cells present. Cuticle and epidermal cell thickening differs in the three forms. Hooks, prickles and papillae absent; macro-hair bases present in alpine bog form (Figs 7 & 8).

Abaxial epidermis

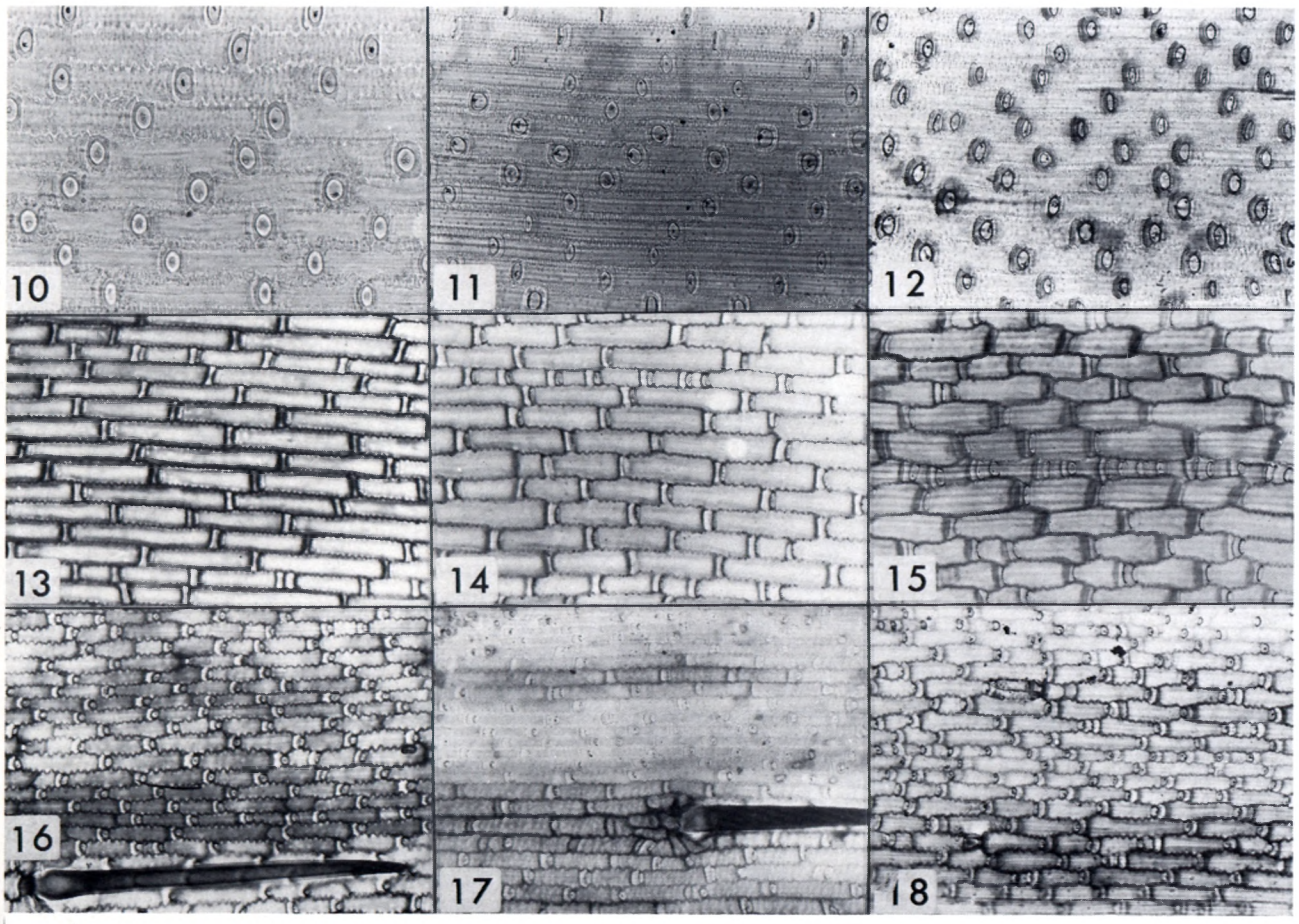
Intercostal zones: not differentiated. *Stomata:* absent throughout abaxial epidermis. *Papillae:* absent except in some specimens of the Drakensberg form where long cells are inflated and tend towards obliqu e papillae (Fig. 15). *Prickles:* absent. *Hooks:* none observed. *Micro-hairs:* absent except in the alpine bog form where bicellar hairs with short basal, and elongated, tapering distal, cells occur (Fig. 16). *Macro-hairs:* absent except on all specimens of alpine bog form (Figs 16 & 17). Uni-cellular; 2–3 specialized epidermal cells associated with hair base; base swollen in relation to hair thickness; short >1,25 mm long. *Silica bodies:* variable (Table 1); rounded in typical *M. disticha* (Figs 10–12) to tall and narrow in the Drakensberg form (Figs 13–15). Present throughout abaxial epidermis; granules present; width approximately the same as that of adjacent costal long cells especially in typical and Drakensberg forms. *Costal cells:* silico-suberose couples alternate with single costal long cell throughout abaxial epidermis; cork cells crescentic and enfolding the silica body except for tall and narrow cork cells associated with tall and narrow silica bodies in the Drakensberg form; costal long cells rectangular with straight to slightly inflated walls; slightly undulated.

Specimens examined:

Typical M. disticha

O.F.S.—2828 (Bethlehem): Golden Gate National Park, Brandwag Peak (–DA), *Ellis 2391*.

CAPE.—3124 (Hanover): Lootsberg (–DC), *Theron 486*. 3126 (Queenstown): Jamestown (–BB), *Ellis 2603*. 3225 (Somerset East): Groot Riet Vlei (–AD), *Acocks 11961*. 3226 (Fort Beaufort): 40 km from Tarkastad on Adelaide road (–AD), *Ellis 2572*. 3325 (Port Elizabeth): Addo Elephant National Park (–BC), *Liebenberg 6656*, 7713; King Neptune Beach (–DC), *Ellis 2564*. 3420 (Bredasdorp): between Swellendam and Riviersonderend (–AA), *Ellis 1263*; Potberg (–AD), *Ellis 669*; Cape Agulhas (–CC), *Loxton 246*.



FIGS 10–18.—Abaxial epidermis of *Merxmuellera disticha* sens. lat. All × 400. 10–12, *M. disticha* form. (10, *Liebenberg* 7713; 11, *Ellis* 1263; 12, *Ellis* 669.) 13–15, Drakensberg form. (13, *Ellis* 3157; 14, *Ellis* 3152; 15, *Ellis* 1404.) 16–18, Alpine bog form. (16, *Ellis* 3183; 17, *Ellis* 3192; 18, *Ellis* 3313.)

TABLE 1.—The anatomical differences between the different forms of *Merxmuellera disticha* as seen in transverse sections of the leaf blade and on epidermal preparations in surface view

Character	Typical Form	Drakensberg Form	Alpine bog Form
1. Number of 1'vbs in leaf section	1. 7 (sometimes 5)	1. 7 (sometimes 5)	1. 5 vbs
2. Outline of lamina	2. Permanently infolded but opening of 45° possible	2. Infolded but regular opening of 180° occurs	2. Permanently infolded
3. Depth of adaxial furrows	3a. Medium $< \frac{1}{2}$ leaf thickness	3a. Deep $> \frac{1}{2}$ leaf thickness	3a. Medium $< \frac{1}{2}$ leaf thickness
	3b. All furrows of equal depth	3b. Furrows on either side of midribs deeper than rest	3b. All furrows of equal depth
4. Vertical position of vascular bundles in blade	4. All bundles centrally located	4. 1'vbs centrally and 3'vbs abaxially positioned	4. All bundles centrally located
5. Adaxial sclerenchyma girders —inversely T-shaped	5. T with long, narrow stem (1–3 seriate)	5. T with short, sturdy stem (> 3 seriate)	5. T with variable stem
6. Abaxial sclerenchyma	6. Continuous hypodermal layer with girders to 1'vbs only	6. Well developed tall or trapezoidal girders associated with both 3' and 1'vbs. Hypodermal layer sometimes developed	6. Thin hypodermal layer with trapezoidal girders associated with 1'vbs only
7. Bulliform cells	7. Poorly developed at base of furrows	7. Well developed on two furrows on either side of the median bundle	7. Absent
8. Adaxial papillae	8. Long, broad, hair-like distally thickened papillae on most epidermal cells	8. Outer walls of epidermal cells inflated with a few elongated, thickened papillae present	8. Outer walls of all epidermal cells inflated
9. Abaxial epidermal cells	9. Outer tangential wall flattened with smooth, continuous cuticle	9. Outer wall inflated and projecting; not conspicuously thickened	9. Outer walls irregular but with a markedly thickened cuticle
10. Abaxial micro-hairs	10. Absent	10. Absent	10. Present
11. Macro-hairs	11. Absent	11. Absent	11. Present
12. Silica bodies	12. Rounded or circular to elliptical in shape. Equidimensional to vertically elongated	12. Tall and narrow with smooth outlines to crescentic or kidney shaped. Vertically elongated	12. Crescent or kidney shaped to cuboid or rounded. Equidimensional
13. Cork cells	13. Crescentic, enfolding silica body	13. Tall and narrow adjacent to silica body	13. Crescentic, enfolding silica body

Drakensberg form

O.F.S.—2828 (Bethlehem): Golden Gate National Park, Brandwag Peak (–DA), *Du Toit 675*. Wodehouse Peak, *Ellis 2382*; Witsieshoek—Mont-aux-Sources area (–DB), *Ellis 3133, 3152, 3157*.

NATAL.—2829 (Harrismith): Cathedral Peak, Organ Pipes Pass (–CC), *Ellis 1404, 3185, 3303, 3305*. 2929 (Underberg): Giants Castle Game Reserve (–AD), *McAllister 112*; Bannermans Pass, *Ellis 3312*.

LESOTHO.—2929 (Underberg): Mokhotlong (–AC), *Coetzee 834*.

Alpine bog form

NATAL.—2829 (Harrismith): Cathedral Peak, Organ Pipes Pass summit (–CC), *Ellis 3183, 3184, 3192, 3306, 3309*. 2929 (Underberg): Giants Castle, summit of Bannermans Pass (–AD), *Ellis 3313, 3315, 3316*; top of Sani Pass (–CB), *Du Toit 699*.

LESOTHO.—2929 (Underberg): above Sani Pass (–CA), *Du Toit 2207*.

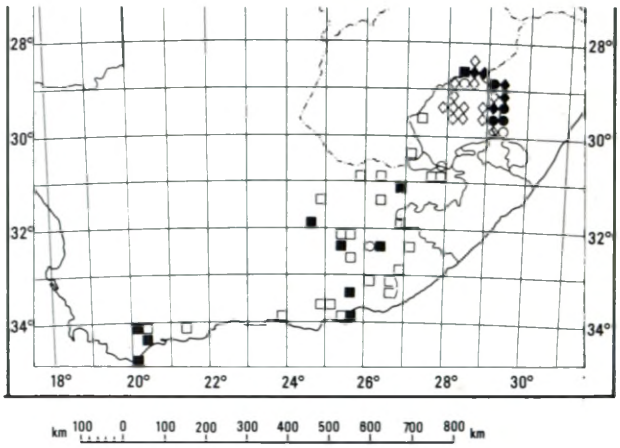


FIG. 19.—Distribution of *Merxmuellera disticha* in South Africa. □—typical *M. disticha* form; ◊—Drakensberg form; ○—Alpine bog form. Shaded symbols represent localities of specimens studied anatomically. Compiled from specimens at the National Herbarium, Pretoria (PRE).

DISCUSSION AND CONCLUSIONS

From the foregoing anatomical description of *M. disticha* sens. lat., and from the accompanying photomicrographs (Figs 1–18), it is evident that numerous anatomical differences exist between the three different forms of *M. disticha* recognized in this study (Table 1). These differences are of considerable magnitude and are much more obvious than are the anatomical differences among some of the other closely related *Merxmuellera* species e.g. *M. macowanii* (Stapf) Conert, *M. davyi* (C. E. Hubb.) Conert and *M. aureocephala* (J. G. Anders.) Conert or *M. drakensbergensis* (Schweick.) Conert and *M. stereophylla* (J. G. Anders.) Conert. In addition, the anatomical differences between *M. drakensbergensis* and *M. stereophylla*, for example, are merely a matter of degree and there is a tendency for the characters to grade from one species into the other. The differences among the three *M. disticha* forms, on the other hand, are distinctly disjunct with the characters being structurally different e.g. adaxial ribs, sclerenchyma girders, silica bodies etc. Furthermore, a number of correlated characters, from both the leaf blade in section and the epidermis, characterize each of the three forms. These diagnostic characters constantly occur in combination and with the detection of any single diagnostic character the remainder can safely be inferred. This evidence, based solely on leaf anatomical criteria suggests, therefore, that each of the forms of *M. disticha*, recognized in this study, warrants taxonomic status, possibly sub-specific rank.

In certain spikelet characters, differences are also exhibited among these three forms of *M. disticha*. From the sample examined, it appears that, in both the Drakensberg and alpine bog forms, only 2-flowered spikelets are found. In typical *M. disticha*, all specimens had three or more florets. In typical *M. disticha* and in the Drakensberg form the length of the upper and lower glumes is greater than 12 mm whereas, in the alpine bog form they are 11 mm or less in length. In both typical *M. disticha* and the Drakensberg form the lower glume was always distinctly 3-nerved, whereas in the alpine bog sample only a single prominent nerve was present with two poorly developed lateral nerves sometimes being evident. From the small sample examined, it would appear, that a detailed study of the spikelet morphology of *M. disticha* sens. lat. should confirm the anatomical groupings and assist in reaching a taxonomic decision

The three forms of *M. disticha* show distinct vegetative differences as well, and can be readily recognised in the field. The alpine bog form has very narrow, short, setaceous leaves between 100–200 mm long and forms fine, delicate, compact but low tussocks. The younger green leaves are normally more or less straight and erect and the older, dry leaves curl, thus forming an irregularly matted "cushion" out of which the needle-like green leaves project. Typical *M. disticha* plants have a similar structure, except on a much larger scale with the leaves being from 300–500 mm long. The setaceous leaves are thicker and much more rigid and fibrous, with a very high tensile strength. The old, dry leaves of the tussock form a dense curly mass. The Drakensberg form, on the other hand, has leaves which are often not setaceous, but are open and up to 3,5 mm wide. This is especially conspicuous under conditions of reduced radiation such as on misty, cloudy days. In this state, the Drakensberg form is unmistakeable and it is regrettable that in the preparation of herbarium vouchers the leaves become infolded and setaceous and the herbarium specimens resemble typical *M. disticha*. However, the green leaves are softer, more flexible and more easily torn and the old leaf blades are exceptionally curly.

Differences in habitat requirements between the three forms became evident while collecting material in the field for the anatomical investigation. Thus, the alpine bog and Drakensberg forms occur in the Drakensberg mountains but only in basaltic soils above the cave sandstone layers. On the summit of this escarpment they often occur in close proximity to one another. The alpine bog form is restricted to saturated, humic soils in shallow bogs or seepage areas and is often found in water about 100 mm deep. The Drakensberg form may be found on raised mounds in the selfsame seepage areas but obviously requires better drainage conditions. It is also more widespread being found down to altitudes of about 2 000 m, whereas the bog form is restricted to the summit at over 3 500 m.

Typical *M. disticha* has a wide distribution in the Cape Province (Fig. 19) being found at low altitudes along the southern coast and then throughout the eastern and north-eastern Cape mountains. Inexplicably it appears to be absent from the Transkei and Natal, but is found in Lesotho and the sandstone mountains of the eastern Orange Free State. Thus at Golden Gate typical *M. disticha* occurs on the slopes of Brandwag Peak (*Ellis* 2931), but higher up the same mountain, on the basalt cap known as Wode-

house Peak, the Drakensberg form is found in black, peaty soils (*Ellis* 2382; *Du Toit* 675).

The type of intraspecific variation described here, has also been observed in *M. stricta* (Schrad.) Conert in similar habitats in the same mountains (Ellis, in prep.). Possibly the other closely related *Merxmuellera* species of the summer rainfall areas also represent the outcome of similar diversification and speciation e.g. *M. drakensbergensis* and *M. stereophylla* or *M. macowanii* and *M. aureocephala*. Within this genus, therefore, there appears to have been considerable adaptive radiation associated with altering environmental conditions. This applies particularly to altitude effects along this mountain range. These factors must be borne in mind when final taxonomic decisions are taken.

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UITTREKSEL

Die anatomiese struktuur van die blaar in dwarsnee en die abaksiale epidermis van Merxmuellera disticha *word beskryf en geïllustreer. Drie afsonderlike anatomiese "vorme" word erken: tipiese* M. disticha, *die Drakensberg vorm en die alpienevlei vorm. Dit blyk ook dat hierdie drie anatomiese groepe ook verskillende omgewingsbenodigdhede het en waarskynlik taksonomiese status verdien.*

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