

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

IV. *Merxmuellera drakensbergensis* and *M. stereophylla*

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ABSTRACT

The leaf blade anatomy of *Merxmuellera drakensbergensis* (Schweick.) Conert and *M. stereophylla* (J. G. Anders.) Conert is described and illustrated. These two closely related species have virtually identical leaf anatomy—both the leaf in section and the abaxial epidermis. The close anatomical resemblance between these two species raises doubts about their specific status. This is especially significant when compared with the considerable differences observed between the anatomical 'forms' recognized in *M. disticha* (Nees) Conert (Ellis, 1980) and *M. stricta* (Schröd.) Conert (Ellis, 1980a).

RÉSUMÉ

L'ANATOMIE DE LA FEUILLE DU *DANTHONIEAE* (POACEAE) SUD AFRICAINE. IV. *MERXMUELLERA DRAKENSBERGENSIS* ET *M. STEREOPHYLLA*

L'anatomie de la feuille de *Merxmuellera drakensbergensis* (Schweick.) Conert et *M. stereophylla* (J. G. Anders.) Conert est décrite et illustrée. Ces deux espèces étroitement apparentées ont une anatomie de la feuille virtuellement identique—tant la section de la feuille que l'épiderme abaxial. La ressemblance anatomique étroite entre ces deux espèces soulève des doutes au sujet de leur statut spécifique. Ceci est spécialement significatif quand on compare les différences considérables observées entre les "formes" anatomiques reconnues dans *M. disticha* (Nees) Conert (Ellis, 1980) et *M. stricta* (Schröd.) Conert (Ellis, 1980a).

INTRODUCTION

Merxmuellera drakensbergensis (Schweick.) Conert (1970) (= *Danthonia drakensbergensis* Schweick.) and *M. stereophylla* (J. G. Anders.) Conert (1970) (= *D. stereophylla* J. G. Anders.) are wiry-leaved perennials forming rigid, erect tussocks. The unbranched culms grow vertically and the leaves are rigid and taper to a pungent apex. In both species these leaves are setaceous and tightly involute or canaliculate.

These two species are conspicuous components of the alpine vegetation of the Drakensberg mountains to which they are restricted. *M. drakensbergensis* occurs in the Barkly East and Maclear Districts of the north-eastern Cape, along the Drakensberg mountains of Natal and Lesotho and at Mariepskop in the Drakensberg of the north-eastern Transvaal. *M. stereophylla* has a more limited distribution, being found only in the Drakensberg areas of Natal and Lesotho at altitudes above 2 000 m. Although the distribution of these two species overlaps in the Natal and Lesotho alpine areas, they can, nevertheless, be distinguished both ecologically and morphologically.

M. drakensbergensis occupies mesic situations in the streambank and mud patch communities (Killick, 1963; Edwards, 1967) of the alpine belt along the summit of the high Drakensberg. The habitat of *M. stereophylla*, on the other hand, is essentially xeric and this species is common in the alpine grassland of the basalt cliffs as a crevice and ledge plant. In the *Danthonia* Tussock Grassland (Edwards, 1967) *M. drakensbergensis* is dominant around sponges and mud patches, but on rocky areas *M. stereophylla* is the principal grass. Although these two closely related species (Anderson, 1960) have long been confused, they are distinct ecologically and in the field can readily be distinguished by their differing habitat requirements.**

Vegetatively, these species can also be easily recognized. *M. stereophylla* has rigid, erect, grey-green

leaves, whereas *M. drakensbergensis* has softer leaves which are olive-green in colour. *M. drakensbergensis* plants are up to 100 cm tall and *M. stereophylla* is a slightly smaller plant up to 80 cm high. A characteristic feature of *M. drakensbergensis*, which is not evident in *M. stereophylla*, concerns the behaviour of old leaf blades (Anderson, 1960). These normally break off above the ligule and the remaining portion of blade splits along the median nerve and the resultant halves recurve outwards in opposite directions. This useful field diagnostic character appears to be consistent and it is only in recently burnt plants that this character is not evident. However, as these species are badly injured by fire (Edwards, 1967) they are largely confined to fire-protected moist or rocky habitats. *M. macowanii* (Stapf) Conert also exhibits this vegetative characteristic and can, therefore, be confused with *M. drakensbergensis*. Both species are also streambank plants, but *M. macowanii* appears to be limited to the montane and sub-alpine belt below the summit of the Drakensberg.

The relatively recent description and recognition of *M. drakensbergensis* and *M. stereophylla* is somewhat surprising in view of these distinct ecological and vegetative differences. *M. drakensbergensis* was only described in 1938 (Schweikerdt, 1938), prior to which it was referred to *M. macowanii*. *M. stereophylla* received recognition as recently as 1960 (Anderson, 1960), although Chippindall (1955) mentioned an undescribed species from the high Drakensberg and was undoubtedly referring to this species. A probable reason for these species remaining undescribed for so long is the relative inaccessibility of the area in which they occur, as well as the fact that

**According to Killick (1978) *M. drakensbergensis* is an ubiquitous species in the alpine belt of the Sani Pass area of the southern Drakensberg: it often occurs in flushes or along streambanks but is also found on rock outcrops and in Alpine Grassland, sometimes covering fairly large areas. *M. stereophylla*, on the other hand, appears to be restricted to dry outcrops at higher altitudes in this part of the Drakensberg. *M. drakensbergensis* is, therefore, not restricted to semi-aquatic communities in this area but displays a wider ecological tolerance. It, nevertheless, prefers deeper and moister soils than *M. stereophylla*.

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spikelet differences are slight and only a matter of degree. Thus the arrangement of the hairs on, and the length of, the lemmas (including lobes and awns) differ slightly (Anderson, 1960, 1962).

That these two species are very closely related (Anderson, 1960) is confirmed by the anatomy of their leaf blades which is almost identical. No consistent and measurable structural differences are evident and evidence from leaf anatomy, therefore, casts some doubt on the validity of granting these species specific status. This is especially significant when compared with the situation in *M. stricta* (Schrad.) Conert (Ellis, 1980a) and *M. disticha* (Nees) Conert (Ellis, 1980) where disjunct, relatively important anatomical differences were found to occur within each of these species. These anatomical differences were found to be consistently correlated with ecological and morphological differences and, therefore, these 'forms' of *M. stricta* and *M. disticha* appear to warrant similar taxonomic treatment to *M. drakensbergensis* and *M. stereophylla*. The granting of specific status to *M. drakensbergensis* and *M. stereophylla*, therefore, requires reassessment.

The only anatomical differences observed between these two species are slight differences in size and

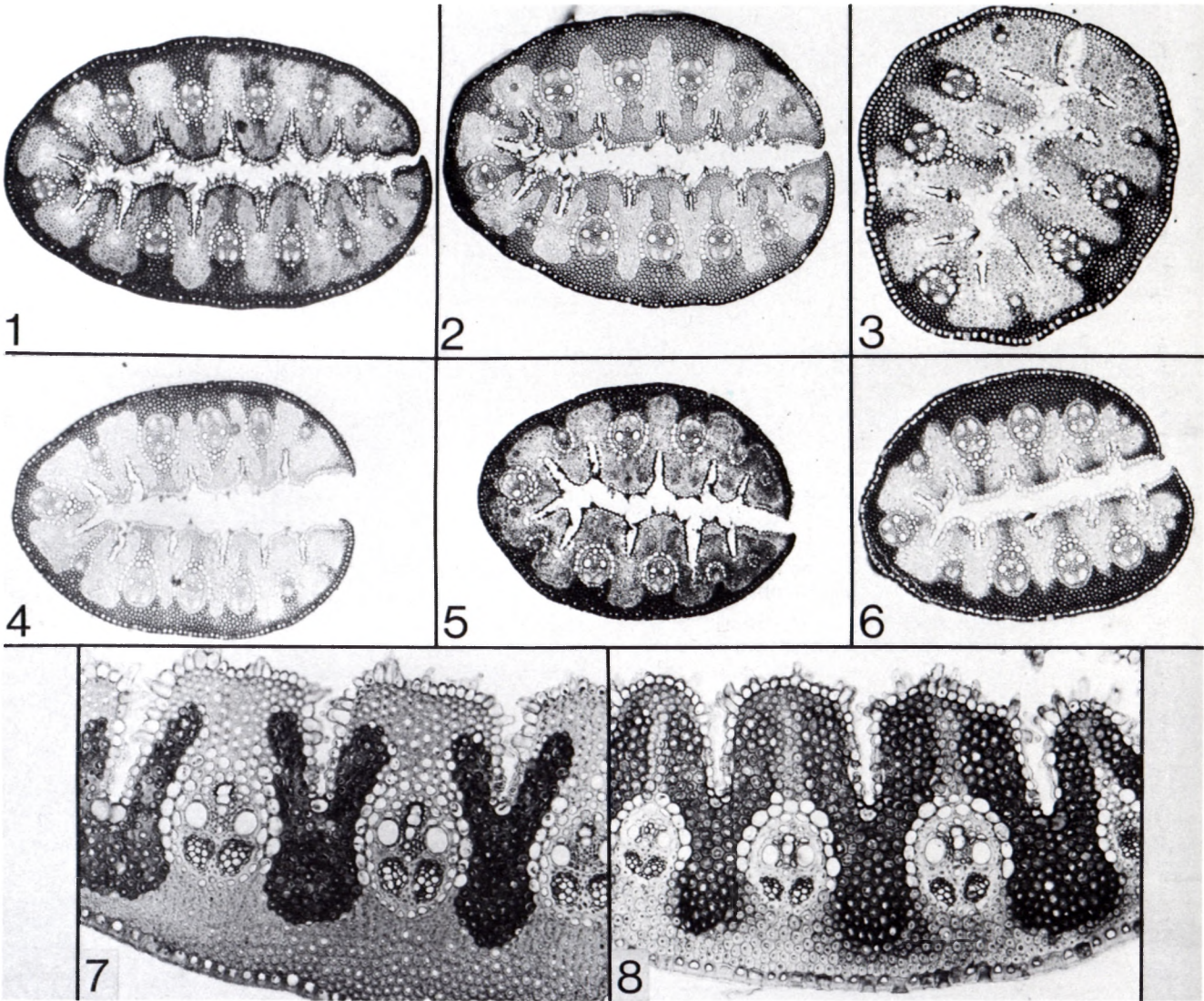
hence a combined description will suffice for both. Leaf anatomy and epidermal structure will be described following the terminology of Ellis (1976, 1979) and the following abbreviations will be used in the description:

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

COMBINED ANATOMICAL DESCRIPTION OF
MERXMUELLERA DRAKENSBERGENSIS AND
M. STEREOPHYLLA

Leaf in transverse section

Leaf outline: permanently and tightly infolded with elliptical outline. Laminae slightly assymetrical about the median vb such that adaxial furrows of one half of lamina align with adaxial ribs on other half of lamina. As a result margins overlap slightly. Adaxial channel always a deep, narrow cleft with a slight opening where margins overlap. *Leaf size:* setaceous; leaves narrow (0,56 mm–3,60 mm wide)



FIGS 1–8.—Leaf blade outline of *Merxmuellera drakensbergensis* and *M. stereophylla* in transverse section. 1–3, *M. drakensbergensis*, all $\times 160$. (1, Du Toit 669; 2, Liebenberg 5707; 3, Du Toit 2313.) 4–6, *M. stereophylla*, all $\times 160$. (4, Jacot Guillarmod 3733; 5, Roberts 3152; 6, Edwards 2284.) 7, *M. drakensbergensis*, $\times 400$. (Ellis 3191.) 8, *M. stereophylla*, $\times 400$. (Ellis 3139.)

but tend to be thinner in *M. stereophylla* (0.56 mm–1.13 mm wide) than in *M. drakensbergensis*. This tendency reflected in number of vbs in leaf section. 11–15 vbs present with 11 vbs always in *M. stereophylla* (Figs 4–6) and *M. drakensbergensis* usually with 13 or 15 vbs (Figs 1 & 2) but sometimes only 11 vbs present (Fig. 3). *Ribs and furrows*: medium to deep cleft-like adaxial furrows between all vbs; rounded (Fig. 8) or slightly flat-topped (Fig. 7) ribs over all vbs; one vb per rib. Abaxial surface smooth or with very slight undulations associated with vbs (Fig. 3). *Median vascular bundle*: present but indistinguishable structurally from 1'vbs. *Vascular bundle arrangement*: no 2'vbs; 3'vbs absent between consecutive lateral 1'vbs. All bundles centrally located between upper and lower epidermides. *Vascular bundle structure*: vbs circular or elliptical in shape. Xylem and phloem distinguishable in all vbs; phloem adjoins ibs; phloem divided vertically into two equal groups by intrusion of fibres (Figs 7 & 8). Metaxylem vessel diameter narrow being only slightly greater than the diameter of the obs cells; slightly thickened. *Vascular bundle sheaths*: obs of all vbs horse-shoe shaped with wide abaxial interruptions. Adaxial interruptions usually fairly narrow (Fig. 8) but may be wide (Fig. 7) especially in *M. drakensbergensis*. No bundle sheath extensions present. Obs cells round or elliptical, sometimes with straight radial walls (Fig. 8); all obs cells similar in shape but small, being only slightly larger than the mesophyll cells in cross-sectional area; cell walls slightly but distinctly thickened; without chloroplasts. Inner sheath complete around all vbs; ibs cells similar in size to the obs cells but with considerably thicker walls, especially inner tangential wall (Fig. 8). *Sclerenchyma*: adaxial girders inversely anchor-shaped with narrow (Fig. 8) or sturdy (Fig. 7) stem; fibres interrupt obs. Abaxial sclerenchyma in form of continuous subepidermal band (especially well developed adjacent lateral 1'vbs) of varying thickness with large trapezoidal girders extending to, and interrupting, the obs; girders comprised of thick-walled fibres usually lignified although fibres near margin may be of cellulose (Fig. 1). *Leaf margin*: very small, pointed, poorly developed cap. *Mesophyll*: non-radiate; chlorenchyma of regular, small, isodiametric cells; tightly packed with air spaces not visible; in

Y-shaped groups occupying sides and bases of adaxial furrows (Figs 7 & 8). No colourless cells present. *Adaxial epidermis*: poorly developed bulliform cells at bases of furrows. Macro-hairs absent. Pointed prickles with broad, but not bulbous bases; present throughout costal zones. Outer walls of epidermal cells arched and somewhat inflated and appear to be papillate. These may, however, represent sections, through varying planes, of the prickles. *Abaxial epidermis*: bulliform cells absent. Outer cell walls markedly thickened with a continuous, thick cuticle. No macro-hairs, prickles or papillae.

Abaxial epidermis in surface view

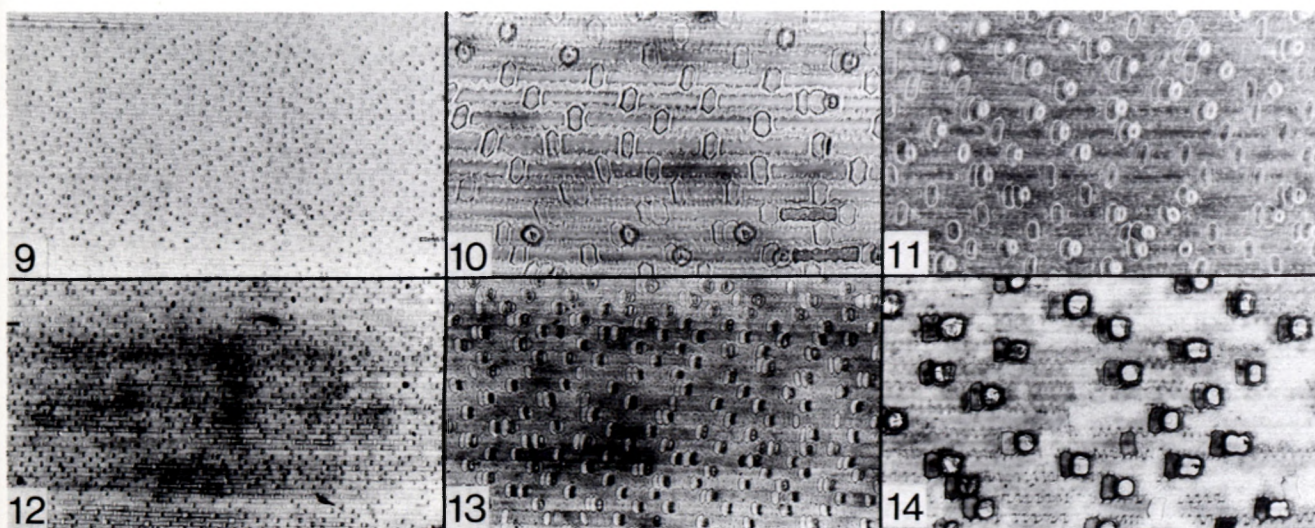
Intercostal zone: undifferentiated and entire abaxial epidermis similar in structure (Fig. 9 & 12) and essentially a costal zone due to development of continuous sub-epidermal fibrous layer. *Stomata*: absent from abaxial surface. *Prickle-hairs*: hooks and prickles not present. *Micro-hairs*: not seen on any of the specimens examined. *Macro-hairs*: absent. *Silica bodies*: equidimensional in surface view; either cuboid (Fig. 14), round (Fig. 10) or somewhat elliptical (Fig. 11); usually fitting into concavity in closely associated cork cell. Granules present; cracks sometimes present (Fig. 14). Width of silica bodies slightly narrower than costal long cells and cork cells. Similar silica bodies present throughout abaxial epidermis. *Costal cells*: silica cells and cork cells alternate with single costal long cells throughout abaxial epidermis; all files of similar cell arrangement. Silica may be relatively sparse (Fig. 10) with many silico-suberose couples actually consisting of a pair of cells (a cork and a silica cell) or even only a single cork or silica cell. Costal long cells elongated horizontally; at least 3 × longer than wide; sides parallel; anticlinal walls heavily thickened and usually pitted (Fig. 10 & 13); undulations moderate to deep but difficult to distinguish clearly due to excessive cuticle thickening.

Specimens examined:

M. drakensbergensis

O.F.S.—2828 (Bethlehem): Witsieshoek-Mont-aux-Sources area (–DB), Ellis 3137, 3138, 3154, 3155, 3156.

NATAL.—2828 (Bethlehem): Sentinel (–DB), Du Toit 669. 2829 (Harrismith): Cathedral Peak Forest Reserve (–CC), Ellis 1398,



FIGS 9–14.—Abaxial epidermis of *Merxmüllera drakensbergensis* and *M. stereophylla*. 9–11, *M. drakensbergensis*. (9, Killick & Marais 2183, × 160; 10, Ellis 1398, × 640, note number of cork cells associated with silica bodies; 11, Staples 242, × 160, phase contrast.) 12–14, *M. stereophylla*. (12, Ellis 3139, × 160; 13, Ellis 3139, × 400; 14, Killick & Vahrmeijer 4019, × 640.)

3189, 3190, 3191, 3304. 2929 (Underberg): Sani Pass (—CB), *Du Toit* 2313.

LESOTHO.—2828 (Bethlehem): Maluti Mts (—CC), *Staples* 242. 2929 (Underberg): Pone Valley (—AC), *Coetzee* 824; Mokhotlong, *Liebenberg* 5707; Sani Pass summit (—CA), *Du Toit* 2209.

CAPE.—3028 (Matatiele): Naudes Nek (—CA), *Werdermann* & *Oberdieck* 1139.

M. stereophylla

O.F.S.—2828 (Bethlehem): Golden Gate National Park (—DA), *Roberts* 3152; Witsieshoek-Mont-aux-Sources area (—DB), *Ellis* 3139.

NATAL.—2828 (Bethlehem): Mont-aux-Sources (—DD), *Schelpé* 1390. 2829 (Harrismith): Cathedral Peak Forest Reserve (—CC), *Ellis* 1397, 1408, 3180, 3186, 3298, 3307, *Killick* 1317. 2929 (Underberg): Giants Castle Game Reserve (—AB), *Killick* & *Vahrmeijer* 4019, *Edwards* 2284.

LESOTHO.—2828 (Bethlehem): Letseng-la-Terai (—CA), *Loxton* & *Ellis* 997. 2829 (Harrismith): Cleft Peak area (—CC), *Killick* & *Marais* 2183. 2929 (Underberg): Sani Pass summit (—CA), *Du Toit* 2208; Tschlanyane Valley (—CD), *Jacot Guillarmod* 3733.

DISCUSSION AND CONCLUSIONS

From the above anatomical description of the leaf blades of *M. drakensbergensis* and *M. stereophylla*, and from the accompanying photomicrographs (Figs 1–14), it is clearly evident that the structure of these two species is remarkably similar—both the leaf sections and the epidermis. The only difference detected in this study is a small variation in the cross-sectional area and width of the leaf sections. The magnifications of Figs. 1–6 are identical and a comparison of *M. drakensbergensis* leaf blades (Figs 1–3) with those of *M. stereophylla* (Figs 4–6) reveals that the leaves of *M. drakensbergensis* have a tendency to be larger. This difference is not consistent as numerous intermediates occur. Nevertheless this size difference is correlated with the number of vascular bundles present in the leaf blade. *M. stereophylla* has 11 vascular bundles, whereas *M. drakensbergensis* has 13 or 15. However, even this distinction is not consistent e.g. Fig. 4 which is intermediate with 12 vascular bundles and Fig. 3, *M. drakensbergensis*, with only 10 vascular bundles.

These slight quantitative differences are, nevertheless, characteristic and consistent for the majority of the specimens examined in this study. However, in this representative and extensive sample there were several specimens which proved difficult to identify satisfactorily using Anderson's (1962) key. For example, both *Ellis* 1397 and *Loxton* & *Ellis* 997 were initially determined as being *M. stricta* but, on checking, were identified as *M. drakensbergensis* and finally placed in *M. stereophylla*, mainly because they do not exhibit the outward recurving of the old leaf blades. In these specimens the arrangement of the hairs on the lemmas is apparently atypical. *Edwards* 2284 is another specimen which has caused problems with identification. Anderson and Conert both determined this specimen as being *M. aureocephala* (J. G. Anders.) Conert, but in this study it has been classified as being *M. stereophylla*.

In these morphologically atypical specimens the number of vascular bundles in the leaf section, and the corresponding width of the leaf blade, appear to be of no assistance in identification. Thus, *Ellis* 1397, collected in saturated, spongy ground is probably ecologically best placed in *M. drakensbergensis*, although it would be a very small, atypical specimen. It has only 11 vascular bundles in the leaf section, which is characteristic of *M. stereophylla*. The

ecological, morphological and anatomical indications are, therefore, in conflict.

Ellis 1397 and 1408 are specimens collected near or at the summit of the Drakensberg escarpment at Cathedral Peak. The *Merxmuellera* populations at this particular locality were characterized by being extremely variable morphologically. Anatomical studies of the *M. stricta* and *M. disticha* (*Ellis*, 1980, 1980a) specimens from this locality revealed that the various specimens actually belonged to different 'forms' with distinct anatomical, morphological and ecological characteristics and that it was mere coincidence that they were found growing in such close proximity. The *M. drakensbergensis* and *M. stereophylla* specimens from these populations, on the other hand, show no correlation between morphological, anatomical and ecological characteristics and *Ellis* 1397 and 1408 in fact represent true intermediates.

This observation, together with the close resemblance of the leaf anatomy of these two species, indicates that *M. stereophylla* and *M. drakensbergensis* are very closely related, more so, in fact, than the anatomical forms of *M. stricta* and *M. disticha*. The specific status of *M. stereophylla* and *M. drakensbergensis* is, therefore, questioned and indications are that these two taxa warrant similar taxonomic treatment to the anatomical forms of *M. stricta* and *M. disticha*.

Both *M. drakensbergensis* and *M. stereophylla* exhibit the same type of arrangement of vascular bundles along the width of the lamina, there being no third order vascular bundles between the lateral first order bundles. This is essentially similar to the position described in *M. stricta* (*Ellis*, 1980a) and indicates the relationship of *M. stricta* to *M. stereophylla* and *M. drakensbergensis*. In addition, the anatomical evidence indicates that *M. stereophylla* and *M. drakensbergensis* exhibit a similar degree of divergence from the typical *M. stricta* anatomical form as do the other three anatomical forms of *M. stricta* (*Ellis*, 1980a). This implies that consideration should be given to the granting of equivalent taxonomic status to *M. drakensbergensis*, *M. stereophylla*, typical *M. stricta* and to the three other forms of *M. stricta*. The evidence gained in the present study indicates that subspecific rank is probably justified for each of the above entities of the *M. stricta* group.

M. drakensbergensis and *M. stereophylla* are thought to be related to three other species of *Merxmuellera*, all of which also occur in the Drakensberg mountains. These are *M. macowanii* (*Stapf*) *Conert*, *M. davyi* (C. E. Hubb.) *Conert* and *M. aureocephala* (J. G. Anders.) *Conert* and together these five species form a more or less distinct and closely related group within the genus (Anderson, 1962). This is not confirmed by anatomy, however, which indicates a relationship between *M. disticha* and *M. macowanii* and *M. davyi*. This is based on the alternating arrangement of lateral first order bundles with third order vascular bundles common to the latter three species (and probably to *M. aureocephala*) (*Ellis*, in press). A similar relationship exists between *M. disticha* and *M. macowanii* and *M. davyi* to that demonstrated between *M. stricta* and *M. drakensbergensis* and *M. stereophylla*. Indications are, once again, that similar patterns of adaptive radiation have occurred in the Drakensberg area from parental stock of both *M. stricta* and *M. disticha*. Thus, in both groups, cave sandstone and

basalt, alpine bog, and streambank 'forms' appear to have evolved in response to the environmental conditions presently prevailing in the Drakensberg mountains. This unique situation will undoubtedly reward further population and cytogenetical studies.

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UITTREKSEL

Die anatomiese struktuur, van die blaar in dwars-snee en die abaksiale epidermis, van Merxmuellera drakensbergensis (Schweick.) Conert en M. stereophylla (J. G. Anders.) Conert word beskryf en geïllustreer. Hierdie twee naverwante spesies is feitlik onuitkenbaar op anatomiese kenmerke alhoewel hulle 'n sekere mate van ekologiese en morfologiese skeiding toon. Die sterk anatomiese ooreenkoms tussen hierdie twee spesies bevraagteken hulle spesifieke status veral wanneer vergelykings getref word met die aansienlike anatomiese verskille wat in M. stricta

(Schrader.) Conert (Ellis, 1980a) en M. disticha (Nees) Conert (Ellis, 1980) waargeneem is.

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