# Leaf anatomy of the South African Danthonieae (Poaceae). V. Merxmuellera macowanii, M. davyi and M. aureocephala

R. P. ELLIS\*

# ABSTRACT

Transverse sections and abaxial epidermal scrapes, of herbarium and freshly fixed leaf blade material, of *Merx-muellera macowanii* (Stapf) Conert, *M. davyi* (C. E. Hubb.) Conert and *M. aureocephala* (J. G. Anders.) Conert, were examined using light microscopy. The leaf anatomy of these three species is very similar in all respects with the exception of certain *M. aureocephala* specimens. In addition, the anatomy indicates a relationship between these three species and *M. disticha* (Nees) Conert. This group of species differs anatomically from *M. stricta* (Schrad.) Nees, and related species such as *M. drakensbergensis* (Schweick.) Conert and *M. stereophylla* (J. G. Anders.) Conert, in the sequence of vascular bundles along the width of the leaf blade and associated characters. However, the *M. aureocephala* specimens, not having the *M. disticha* type of vascular bundle arrangement, anatomically resemble the *M. stricta* group of species, and *M. aureocephala* appears to be intermediate between these two species groups.

## RÉSUMÉ

# L'ANATOMIE DE LA FEUILLE DU DANTHONIEAE (POACEAE) SUD AFRICAIN. V. MERXMUELLERA MACOWANII, M. DAVYI ET M. AUREOCEPHALA

Des sections transversales et des grattages epidermaux abaxiaux, d'herbarium et de matériel de feuille fraichement fixée, de Merxmuellera macowanii (Stapf) Conert, M. davyi (C. E. Hubb) Conert et M. aureocephala (J. G. Anders.) Conert, ont été examinées en utilisant la microscopie lumineuse. L'anatomie de la feuille de ces trois espèces est três similaire dans tous les domaines à l'exception de certains specimens de M. aureocephala. De plus, l'anatomie indique une relation entre ces trois espèces et M. disticha (Nees) Conert. Ce groupe d'espèces diffère anatomiquement de M. stricta (Schrad.) Nees, et des espèces apparentées telles que M. drakensbergensis (Schweick.) Conert et M. stereophylla (J. G. Anders.) Conert, dans la succession des faisceaux vasculaires le long de la largeur de la feuille et des caractères associés. Cependant, les specimens de M. aureocephala, n'ayant pas le type d'arrangement de faisceaux vasculaires de M. disticha ressemblent anatomiquement au groupe d'espèces M. disticha et M. aureocephala apparait etre intermédiaire entre ces deux groupes d'espèces.

# INTRODUCTION

Merxmuellera macowanii (Stapf) Conert (= Danthonia macowanii Stapf), M. davyi (C. E. Hubb.) Conert (= D. davyi C. E. Hubb.), and M. aureocephala (J. G. Anders.) Conert (= D. aureocephala J. G. Anders.) (Conert, 1970) are all wiry, tufted, tussock-forming, perennial grasses. M. macowanii, in particular, forms large, lax tussocks up to 60 cm in diameter with leaves up to 100 cm long arching outwards from the tuft base. M. macowanii and M. davyi are summer-flowering, whereas M. aureocephala is a winter-flowing species.

These three species occur in mountain vegetation along the eastern escarpment of southern Africa. *M. davyi* is found at altitudes above 2 000 m on Mt Mlanje in Malawi, the Inyanga mountains of Zimbabwe and Mariepskop in the eastern Transvaal Drakensberg (Conert, 1975). *M. macowanii* occurs from the Transvaal Drakensberg southwards as far as the Witteberge, Stormberge and Amatole Mountains of the eastern Cape. It occurs between 1 500 and 3 000 m and is also found in the midlands of Natal. *M. aureocephala* appears to be localized and restricted to the high Drakensberg of Natal in the Cathedral and Cathkin Peak areas.

*M. macowanii* is frequently dominant along streambanks and in marshy areas of the montane and subalpine belts of the Drakensberg (Killick, 1963; Edwards, 1967) but is, nevertheless, a xeromorphic grass with sclerophyllous leaves. *M. davyi* and *M. aureocephala*, on the other hand, prefer more xeric habitats and occur on steep grassy slopes and in rocky situations in mountain grassveld (Anderson, 1962). These habitat preferences bear striking resemblances to the niches occupied by *M. drakensbergensis* (Schweick.) Conert and *M. stereophylla* (J. G. Anders.) Conert (Ellis, 1981). Furthermore, *M. macowanii* and *M. drakensbergensis*, both of which occupy mesic streambank and seepage habitats, display vegetative similarities in that the old leaf blades break off a short distance above the ligule, split along the mid-vein and then recurve outwards (Chippindall, 1955; Anderson, 1960). The above five species are considered to form a more or less closely related group within the genus (Anderson, 1962) and, therefore these ecological and morphological parallels are not unexpected.

The present study examined these relationships anatomically and indications are that two groups actually exist within these five species. *M. drakensbergensis* and *M. stereophylla*, therefore, display more anatomical similarities with each other than with either *M. macowanii* or *M. davyi*. It is significant that this anatomical sub-division separates species occupying similar niches and exhibiting similar old leaf blade behaviour. *M. aureocephala* specimens appear to be somewhat intermediate anatomically and possibly form a link between these two groups.

*M. macowanii, M. davyi* and *M. aureocephala* resemble one another anatomically, and, therefore, a combined description of their leaf blade anatomy will suffice. The terminology of Ellis (1976, 1979) will be used in the description with the following abbreviations:

vb/s	— vascular bundle/s
l'vb/s	— first order vascular bundle/s
2'vb/s	<ul> <li>second order vascular bundle/s</li> </ul>
3'vb/s	<ul> <li>— third order vascular bundle/s</li> </ul>
ibs	— inner bundle sheath; mestome sheath
obs	— outer bundle sheath; parenchyma sheath

<sup>\*</sup>Botanical Research Institute, Department of Agriculture and Fisheries, Private Bag X101, Pretoria, 0001.

## 494 LEAF ANATOMY OF THE SOUTH AFRICAN DANTHONIEAE (POACEAE). V. MERXMUELLERA MACOWANII, M. DAVYI AND M. AUREOCEPHALA

#### COMBINED ANATOMICAL DESCRIPTION OF MERXMUELLERA MACOWANII, M. DAVYI AND M. AUREOCEPHALA

# Leaf in transverse section

Leaf outline: infolded with reduced U- or V-shaped outline; opening to at least  $45^{\circ}$  possible (Fig. 2) except in certain *M. aureocephala* specimens which are permanently infolded with elliptical outlines (Figs 7 & 8). Adaxial channel deep and either cleft-like or variable depending on degree of infolding prevailing. Lamina always assymmetrical about the median vb; 1'vbs of opposite halves of lamina alternate and an extra 3'vb is usually present in one half e.g. four 3'vbs in the lower half and three in the upper half of Fig. 1. This assymmetry occurs in all specimens except typical *M. davyi* specimens (Figs 4 & 5). Leaf size: the total number of vbs in the leaf

section varies from 13–17 in *M. aureocephala*, 15–17 in *M. davyi* and 17–27 in *M. macowanii*. Leaf thickness varies between 0,35–0,45 mm in *M. aureocephala* and *M. davyi* but up to 0,55 mm in *M. macowanii*. *Ribs* and *furrows*: massive adaxial ribs with rounded to triangular apices associated with 1'vbs and small triangular ribs with 3'vbs. Medium depth adaxial furrows between all vbs; cleft-like depending on degree of infolding of leaf; Y-shaped as massive ribs almost meet laterally and then furrow diverges on either side of rib over 3'vb (Fig. 11); found in all specimens except certain *M. aureocephala* specimens where lateral 1'vbs are not interspaced by 3'vbs (Figs 7, 8 & 10). Abaxial surface smooth. *Median vascular bundle*: present, characteristically smaller than lateral 1'vbs. *Vascular bundle arrangement*: no 2'vbs present; 1'vbs and 3'vbs alter-



FIGS 1–11.—Anatomy of the leaf blade in transverse section of Merxmuellera macowanii, M. davyi and M. aureocephala. 1–3, 6, M. macowanii, all × 100, considerable variation in leaf width evident. (1, Story 476; 2, Ellis 2394; 3, Ellis 3282; 6, Codd & De Winter 3239.) 4–5, M. davyi, × 100. (4, Davidson & Mogg 33315; 5, Van der Schijff 5832.) 7–9, M. aureocephala, all × 100, note sequence of vascular bundles. (7, Killick 3540; 8, Ellis 3179; 9, Edwards 843.) 10, M. aureocephala, × 400. (Ellis 3179.) 11, M. macowanii, × 400, phloem divided into two groups by intrusive fibres. (Ellis 3282.)

nate along width of lamina except near margin where two or more consecutive 1'vbs may be present; at least two 3'vbs occur between the median vb and these successive 1'vbs near the margin (Table 1) except in certain specimens of *M. aureocephala* (Figs 7 & 8) where only a single 3'vb may be present on either side of the median vb followed by four or five 1'vbs. All vbs located in centre of blade. Vascular bundle structure: vbs elliptical (Fig. 11) or round (Fig. 10) in outline; xylem and phloem distinguishable in 3'vbs: phloem of 1'vbs divided into two similar groups by intrusion of fibres (Figs 10 & 11). Protoxylem vessel and lysigenous cavity present; metaxylem vessels circular, of slightly greater diameter than obs cells. Vascular bundle sheaths: obs elliptical or horseshoeshaped with wide adaxial interruptions; interruption especially pronounced in some M. aureocephala specimens (Fig. 10) such that obs only present opposite xylem; these specimens without adaxial interruptions or extensions (Fig. 10). In all other specimens adaxial extensions present; of colourless cells gradually decreasing in size as walls increase in thickness until they merge into sclerenchyma strand (Fig. 11). Obs cells slightly larger in diameter than mesophyll cells; all similar in shape; rounded; without chloroplasts. Ibs entire with uniformly thickened walls (Fig. 11) or with inner tangential walls thickened (Fig. 10) in certain M. aureocephala specimens. Sclerenchyma: adaxial girders inversely anchorshaped with long, wide stem on all bundles. Abaxial sclerenchyma continuous sub-epidermal band of varying thickness, with large trapezoidal girders extending to, and interrupting, the obs. Fibres either heavily lignified (Fig. 10) or resemble collenchyma in section (Fig. 11). Marginal sclerenchyma cap small and pointed. Mesophyll: arrangement non-radiate; cells uniform, small, isodiametric and tightly packed. Restricted to Y-shaped groups on sides and bases of furrows. Arms of Y uneven due to difference in size of adaxial ribs associated with 1'vbs and 3'vbs (Fig. 11) except in certain *M. aureocephala* specimens (Fig. 10). Colourless cells: absent. Adaxial epidermis: restricted groups of 3-4 bulliform cells present at base of furrows; better developed in M. macowanii (Fig. 11) than M. aureocephala (Fig. 10) and M. davyi. In M. davyi prickles with straight, broad barbs and without bulbous bases common and well-developed (Figs 4 & 5); present in M. macowanii to a slightly lesser degree (Figs 1-3) but absent in certain M. aureocephala specimens where adaxial epidermis consists of papillate cells. Abaxial epidermis: no bulliform cells; outer periclinal wall thickened and covered by continuous, thickened cuticle. No macrohairs, prickles or papillae occur.

# Abaxial epidermis

Intercostal zone: undifferentiated; entire abaxial epidermis essentially costal in structure (Figs 14 & 16) due to hypodermal sclerenchyma development. Stomata: absent. Prickle hairs: not present. Microhairs: not developed on abaxial surface. Macrohairs: absent. Silica bodies: elliptical (Fig. 13) to tall and narrow (Fig. 15); outlines smooth. Closely associated with cork cell or pair of short cells. Width of silica bodies narrower than adjacent costal short and long cells (Fig. 13). Silica bodies sparsely developed or even absent (Fig. 17). Costal cells: silica cells and cork cells, either singly or in pairs, alternate with costal long cells throughout abaxial epidermis. Long cells elongated; at least  $3 \times$  longer than wide; sides parallel; anticlinal walls heavily thickened and slightSpecimens examined:

# M. macowanii

TRANSVAAL.—2530 (Lydenburg): Dullstroom (-AC), Codd & De Winter 3239; De Winter & Codd 183. 2730 (Vryheid): Wakkerstroom (-AD), Devenish 1152.

O.F.S.-2828 (Bethlehem): Golden Gate Highlands National Park (-DA), *Ellis 2394*.

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve (-CC), *Ellis 1455, 3282; Killick 1090.* 2929 (Underberg): Estcourt (-BB), *Acocks 10659.* 2930 (Pietermaritzburg): Pietermaritzburg (-AC), *Edwards 2673;* Greytown (-BA), *Ellis 3372.* 

CAPE.—3027 (Lady Grey): Barkly East (-DC), Joubert s.n. (Matatiele): Naudé's Nek (-CA), Story 476. 3126 (Queenstown): Buffelsfontein (-BC), Stretton 182.

## M. davyi

TRANSVAAL.—2430 (Pilgrim's Rest): Mariepskop (-DB), Van der Schijff 5832; Wedermann & Oberdieck 1908; God's Window (-DD), Davidson & Mogg 33315.

#### M. aureocephala

NATAL.—2829 (Harrismith): Cathedral Peak Forest Reserve (-CC), *Ellis 3179, Killick 3450, 1727;* Mweni Pass, *Edwards 843.* 2929 (Underberg): Cathkin Peak area (-AB), *Edwards 2453.* 

## DISCUSSION AND CONCLUSIONS

The leaf anatomy of *M. macowanii* and *M. davyi* is remarkably similar-both the leaf in transverse section (Figs 1-6) and the abaxial epidermis (Figs 12–15). From the limited number of *M. davyi* specimens available for examination in this study (none of which was collected and fixed in the field), the only difference detected was a tendency for M. davyi leaves to be narrower with fewer vascular bundles per section. This is not a distinct difference, however, and several specimens overlap in this characteristic (Table 1). M. macowanii and M. davyi are considered to be closely allied (Anderson, 1962) and their leaf anatomy supports this close relationship. However, this anatomical evidence casts some doubt on the specific status accorded these two taxa and a closer comparison of these two species is necessary.

In contrast to the leaf anatomy, *M. macowanii* and *M. davyi* seem well separated ecologically and occupy different habitats—mesic streambank and seepage areas (Killick, 1963; Edwards, 1967) as opposed to drier rocky situations (Anderson, 1962). In addition, these two species are almost entirely separated geographically with only a small area of possible sympatry in the eastern Transvaal at Mariepskop and God's Window (Fig. 18). *M. davyi* extends northwards into central Africa along the eastern mountains, whereas *M. macowanii* occurs southwards as far as the north-eastern Cape.

Spikelet differences also appear to adequately differentiate these two species and the degree of fusion and the awned nature of the lemma lobes appear to be distinctive. In this respect *M. macowanii* and *M. davyi* apparently differ considerably and *M. davyi* actually bears a stronger resemblance to *M. aureocephala* than to *M. macowanii* which has characteristic adnate, awnless lemma lobes (Anderson, 1962).

Theoretically these ecological and morphological differences appear to be diagnostic yet in practice their application seems to have been inconsistent. Thus the specimens collected at God's Window and Mariepskop (*Davidson & Mogg* 33315 and *Van der Schijff* 5832) were initially identified as *M. maco*-

496 LEAF ANATOMY OF THE SOUTH AFRICAN DANTHONIEAE (POACEAE). V. *MERXMUELLERA MACOWANII, M. DAVYI* AND *M. AUREOCEPHALA* 



FIGS 12–17.—The abaxial epidermis of Merxmuellera macowanii, M. davyi and M. aureocephala as seen in surface view. 12–13, M. macowanii. (12, De Winter & Codd 183, × 250, large number of single costal short cells without silica bodies; 13, Stretton 182, × 1 000, irregular short cell arrangement.) 14–15, M. davyi. (14, Davison & Mogg 33315, × 250, only single short cells occur; 15, Wedermann & Oberdieck 1908, × 1000.) 16–17, M. aureocephala. (16, Killick 3450, × 250; 17, Ellis 3179, × 640.)

*wanii* and have only recently been assigned to *M. davyi* (Conert, 1975)—notwithstanding the fact that a key was published in 1962 specifically to facilitate the identification of *M. davyi*, *M. macowanii* and other closely related species (Anderson, 1962). In addition, the specimen *Codd & De Winter* 3239 has similarly proved difficult to identify satisfactorily. In 1947 it was named *M. macowanii*, changed to *M. davyi* in 1975 but again placed in *M. macowanii* during the present study. Anatomical indications are that this specimen is better placed in *M. macowanii* (Fig. 6).

Therefore, although anatomical evidence appears to be in conflict with morphological and ecological indications, closer analysis shows that *M. macowanii* and *M. davyi* are, in fact, not consistently separable and are probably very closely related. In the light of the above evidence, a reassessment of their specific status, therefore, appears justified.

An additional consideration, which must be borne in mind when assessing the taxonomic status to be accorded these two taxa, is the almost identical situation observed in *M. drakensbergensis* and *M. stereophylla* (Ellis, 1981). These two species are also inseparable on anatomical grounds and a gradation in leaf size and vascular bundle number was also noted. Several other parallels exist between these two pairs of species. *M. drakensbergensis* and *M. macowanii* both occupy mesic, damp habitats and both display characteristic behaviour of the old leaf blades. *M. stereophylla* and *M. davyi* occur in drier, rocky situations and tend to have narrower leaves.

*M. macowanii* and *M. davyi* have purposely been considered separately from *M. drakensbergensis* and



FIG. 18.—Distribution of Merxmuellera macowanii (△), M. davyi (♦) and M. aureocephala (▼) in southern Africa. Shaded symbols represent localities of specimens studied anatomically. Compiled from specimens at the National Herbarium, Pretoria (PRE).

*M. stereophylla*, even although they share so many common characteristics. This is because a distinct anatomical attribute consistently separates these two species pairs-the arrangement of the different orders of vascular bundles along the width of the lamina. In M. macowanii and M. davyi at least two alternating pairs of first and third order bundles, commencing with the median bundle, are present before consecutive lateral first order bundles are encountered (Table 1). In M. drakensbergensis and M. stereophylla, on the other hand, only a single third order bundle is present between the median bundle and successive lateral first order bundles. The alternating sequence of first and third order bundles is correlated with several other anatomical characters such as form of the adaxial furrows and shape of the mesophyll cell groups.

It is possible that position along the length of the leaf blade may affect this arrangement of the first and third order vascular bundles. However, it has been shown that, towards the apex of the lamina, the lateral veins disappear one by one, commencing with the marginal pair, until the median bundle remains to form the pungent tip (Burbidge, 1946). It is unlikely, therefore, that the bundle sequence, as noted here, will be affected by the position of the sections examined as all material was taken from the central third of the leaf blade between ligule and apex (Ellis, 1976) and, in addition, the relevant bundle sequence is not marginal but adjacent to the median bundle or midrib (Table 1).

Up to this point M. aureocephala has been excluded from this discussion because, in respect of this anatomical difference, it does not conform with either of the vascular bundle sequences described above but exhibits mixed and intermediate conditions. Fig. 7 illustrates the condition typical of M. drakensbergensis and M. stereophylla where a single third order bundle is followed by successive first order bundles. Fig. 9, on the other hand, shows the alternating pattern of first and third order bundles characteristic of M. macowanii and M. davyi. M. aureocephala, therefore, exhibits both types of bundle arrangement that consistently separate M. macowanii and M. davyi from M. drakensbergensis and *M. stereophylla*. In addition, similar differences are found in different leaves of the same plant and even in single leaves. Thus leaf samples were taken from duplicate specimens of Killick 3450 and one showed the *M. drakensbergensis/M. stereophylla* type of bundle sequence (Fig. 7) whereas the other showed the *M. macowanii/M. davyi* type (Table 1). An exceptional case is illustrated in Fig. 8 where each of these two types of vascular bundle arrangement occur within a single leaf-one type in each half of the lamina.

The presence of all these intermediates in *M. aureocephala* casts some doubt on the importance attached to this difference in bundle arrangement in the present study. *M. aureocephala*, therefore, appears to hold the key to the understanding of relationships within this group of closely related species. Unfortunately, however, the taxonomic status of *M. aureoce*-

 TABLE 1.—The arrangement of first (1') and third (3') order vascular bundles along the leaf blade from the median vascular bundle (midrib) to the margin

Specimens examined	Midrib Vascular bundle sequence												
Merxmuellera davyi Wedermann & Oberdieck 1908 Van der Schijff 5832 Davidson & Mogg 33315	1' 1' 1'	3' 3' 3'	1' 1' 1'	3' 3' 3'	1' 1' 1'	3' 1' 3'	3' 3' 1'	1'	3'				
Merxmuellera macowanii Killick 1090 Killick 1090 (another leaf) Devenish 1152 Stretton 182 Ellis 1455 Story 476 Acocks 10659 Codd & De Winter 3239 De Winter & Codd 183 Joubert s.n. Edwards 2673 Ellis 2394 Ellis 3282	1' 1' 1' 1' 1' 1' 1' 1' 1'	3'''''''''''''''''''''''''''''''''''''	1' 1' 1' 1' 1' 1' 1' 1' 1'	3' 3' 3' 3' 3' 3' 3' 3' 3' 3' 3'	1 ' 1 ' 1 ' 1 ' 1 ' 1 ' 1 ' 1 ' 1 ' 1 '	1' 3' 3' (3') (3') 3' 3' 3' 3' 3' 3' 3' 3' 3'	3' 1' 1' 1' 1' 1' 1' 1' 1' 1' 1'	3' 3' 1' 1' (3') (3') (3') (3') 3' 3'	3' 3' 3' 1' 1' 1' 1' 1' 1'	3' (3') (1') (1') 1' 1' 1' 3'	3' 3' 3' 1' 1'	3' 3' 3'	(3')
Merxmuellera aureocephala Edwards 843 Killick 3450 Ellis 3179 Edwards 2453 Killick 3450 (another leaf)	1' 1' 1' 1'	3' 3' 3' 3'	1' 1' 1' 1' 1'	3' 3' (3') (3') 1'	1' 1' 1' 1' 1'	3' 1' 1' 1' 1'	1' 1' 1' 3' 3'	1' 1' 1' (3')	3' 3' 3'	(3′)			

*phala* itself appears somewhat tenuous. To date this species is only known from six collections, all from a restricted area, of less than 20 km in diameter, in the subalpine belt of the Cathedral and Cathkin Peak areas of the Drakensberg (Fig. 18). Morphologically it is very similar to *M*. *davyi* except that the spikelets are larger in all parts, and the glumes are lanceolate instead of narrowly lanceolate (Anderson, 1962). Its winter-flowering habit, in fact, is the single diagnostic character separating M. aureocephala from its four close relatives. However, the specimens assigned to *M. aureocephala* may actually represent examples of late or early flowering in the other Merxmuellera species, e.g. Edwards 2284 has been determined by Conert 1973 as being M. aureocephala, but it is now considered as being *M. stereophylla*. Winter visits to these inhospitable mountains, to study fertile field populations, seem essential to a better understanding of the taxonomic status of all the summer-rainfall area Merxmuellera species.

Until these field studies have been undertaken, the true significance of the different vascular bundle arrangement sequences cannot be assessed. However, assuming that these patterns are a phylogenetically important difference, the available evidence indicates that *M. aureocephala* occupies a basic systematic position in this group from which each of the two distinct types have been derived. This implies a close relationship for these five species as postulated by Anderson (1962) as well as an origin in the Drakensberg mountains and not in the temperate, winterrainfall areas of the Cape.

If the distribution of these two types of bundle arrangement is examined in all the summer-rainfall Merxmuellera species, however, a different origin seems likely. M. disticha (Nees) Conert, including each of its anatomical forms, exhibits the alternating sequence of first and third order vascular bundles (Ellis, 1980). M. disticha, therefore, shares this character with M. macowanii, M. davyi and some M. aureocephala specimens (Table 2). All the four M. stricta (Schrad.) Conert anatomical forms (including M. guillarmodiae Conert), on the other hand, have similar bundle arrangement to M. drakensbergensis and M. stereophylla as well as other M. aureocephala specimens (Ellis, 1980a) (Table 2). Thus, within this group of 12 summer-rainfall Merxmuellera taxa (Table 3), M. aureocephala remains the only taxon intermediate for this anatomical character.

SPECIES	VASCULAR BUNDLE ARRANGEMENT
M.disticha	1° 3° 1° 3° 1° 3°(1° 3°)(1° 3°)
M.davyi	1° 3° 1° 3°(1° 3°) <u>1° 1</u> ° 3°
M.macowanii	1° 3° 1° 3° 1° 3°(1° 3°)(1° 3°)(1°3°) <b>11°</b> 3°
	1° 3° 1° 3° 1° 3° <b>1° 1°</b> 3°
M.aureocephala	1° 3° 1° 3° <u>1° 1° 1</u> ° 3°
	1° 3° <u>të të 1° 1° (19</u> 3°
M.drakensbergensis	1º 3º <u>1º 1º (19/19)</u> 3º
M.stereophylla	1° 3° <u>1° 1° (19</u> 3°
M.guillarmodiae	1° 3° 🎦 3°
M.stricta	1° 3° <u>1° 1° (19)(19)</u> 3°

TABLE 2.—The arrangement of first (1') and third (3') order vascular bundles along the leaf blade from median vascular bundle to margin in the summer-rainfall *Merxmuellera* species

Table 3 diagramatically illustrates each of these twelve Merxmuellera taxa arranged according to vascular bundle sequence and grouped into the various habitats occupied by these various taxa. It is immediately evident from Table 3, that in each of the niches occupied by Merxmuellera spp. a taxon displaying each of the bundle sequence types occurs. A representative of each type of bundle arrangement occurs in the cave sandstone, basaltic soils, alpine bogs, alpine xeric sites and mesic sites. In addition, morphological and anatomical similarities often exist between these pairs of taxa inhabiting similar niches e.g. the old leaf blade behaviour in M. macowanii and M. drakensbergensis and the mesophyll and epidermal structure in the alpine bog forms of M. stricta and M. disticha. Once again, M. aureocephala is the exception.

Typical M. stricta and M. disticha forms are both widespread in the Cape and extend to lower altitudes in the Drakensberg. Throughout this wide distributional range both species are very uniform in both morphology and anatomy. It is only at higher altitudes, above the cave sandstone, that anatomical and morphological diversification is prevalent. An alternative hypothesis is, therefore, that M. stricta and M. disticha have independently colonized the wide variety of microhabitats present at higher altitudes in the Drakensberg by evolving locally adapted ecotypes for each of the various niches. This adaptive radiation, in response to identical environmental conditions, has resulted in very similar phenotypic expressions by the ecotypic forms of each species. As M. stricta and M. disticha occur sympatrically throughout most of their ranges it must be assumed that they originally possessed distinct but diverse genotypes which somehow were capable of responding in similar ways to the different environmental conditions encountered in the Drakensberg. This appears to explain the unique morphological and anatomical convergence observed in all the habitats occupied. The bundle sequence may, therefore, reflect a basic genetic different between M. stricta and M. disticha ancestral forms that has been retained in all the ecotypic forms.

This hypothesis does not explain the position of M. aureocephala. If the origin of all these taxa is to be sought in putative ancestors of M. stricta and M. disticha then the only explanation for M. aureocephala lies in a hybrid origin. Once again population and cytogenetical studies seem necessary to elucidate this question.

From these antomical studies on the summer-rainfall Merxmuellera species (Ellis, 1980; 1980a; 1981) it is nevertheless clear that, at this stage, at least 12 entities can be recognized. A further two, presently placed in *Pentaschistis*, also merit consideration (Ellis, 1980a). All these taxa are undoubtedly interrelated and the most practical systematic treatment, at this stage, appears to be the upholding of only two basic species (M. stricta and M. disticha) with numerous infraspecific taxa, possibly of subspecific rank, included in each. M. guillarmodiae, M. macowanii, M. davyi, M. drakensbergensis and M. stereophylla should be reduced to subspecific rank, whereas, the anatomical forms of M. stricta and M. disticha justify taxonomic recognition with subspecific status as well. *M. aureocephala* is the one entity on which the present studies have shed very little light and a taxonomic recommendation at this stage would be unwise.

HABITAT	VASCULAR BUNDLE SEQUENCE						
	1° 3° 1° 1° etc.	1°3°1°3°etc,					
WIDESPREAD S.WN.E. Cape; O.F.S. Sandstone	M.stricta - x 160 typical form	M. disticha - X 160 typical form					
DRAKENSBERG Subalpine belt Basalt	M. stricta - drakensberg form M. stricta - drakensberg form M. stricta - drakensberg form M. stricta - drakensberg form	M. disticha – x 160 drakensberg form					
DRAKENSBERG Alpine belt; summit Bogs + sponges	M. guillarmodiae - alpine bog form	M. disticha - <sup>X250</sup> alpine bog form					
DRAKENSBERG Alpine, Tvl.northwards Xeric, rocky sites	M. stereophylla	M. davyi					
DRAKENSBERG Alpine, E.Cape-Tvl. Mesic, streambanks	M. drakensbergensis	M. macowaniji					
DRAKENSBERG Subalpine belt Winter flowering	M. aure	x 100					

TABLE 3.—Diagrammatic representations of the leaf anatomy of the summer-rainfall Merxmuellera taxa according to habitat and vascular bundle arrangement

## ACKNOWLEDGEMENTS

Miss R. Manders is thanked for excellent technical assistance as are Dr B. de Winter and Miss L. Smook for identifying the voucher specimens. The Department of Forestry, the National Parks Board and the Natal Parks Board kindly gave permission to collect material on their property.

## UITTREKSEL

Dwarssnitte en abaksiale epidermale skrapings, van herbarium, asook vars gefikseerde blaarmateriaal, van Merxmuellera macowanii (Stapf) Conert, M. davyi (C. E. Hubb.) Conert en M. aureocephala (J. G. Anders.) Conert is met behulp van 'n ligmikroskoop ondersoek. Die blaaranatomie van hierdie drie spesies is in alle opsigte dieselfde, met die uitsondering van sekere M. aureocephala eksemplare. Verder toon die anatomie 'n verwantskap tussen hierdie drie spesies en M. disticha (Nees) Conert. Hierdie spesiesgroep verskil anatomies van M. stricta (Schrad.) Conert, en verwante soorte soos M. drakensbergensis (Schweick.) Conert en M. stereophylla (J. G. Anders.) Conert, in die volgorde van die vaatbondels langs die blaarwydte en geassosiëerde kenmerke. Die M. aureocephala eksemplare wat nie die M. disticha tipe vaatbondelvolgorde toon nie, lyk anatomies na die M. stricta groep van spesies, en M. aureocephala is dus intermediêr tussen hierdie twee spesiegroepe.

## REFERENCES

- ANDERSON, J. G., 1960. Notes and new records of African plants: Gramineae. *Bothalia* 7: 419-420.
- ANDERSON, J. G., 1962. Notes and new records of African plants: Gramineae. *Bothalia* 8: 170–172.
- BURBIDGE, N. T., 1946. Morphology and anatomy of the western Australian species of *Triodia* R. Br. II. Internal anatomy. *Trans. R. Soc. S. Aust.* 70: 221–234.
- CHIPPINDALL, L. K. A., 1955. In D. Meredith, The grasses and pastures of South Africa. Johannesburg: CNA.
- CONERT, H. J., 1970. Merxmuellera, eine neue Gattung der Gramineen. Senckenberg. Biol. 51: 129-133.
- CONERT, H. J., 1975. Merxmuellera guillarmodae Conert n.sp. Senckenberg. Biol. 56: 145-152.
- EDWARDS, D., 1967. A plant ecology survey of the Tugela River Basin, Natal. Mem. bot. Surv. S. Afr. 36: 1-285.
- 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.
- ELLIS, R. P., 1980a. Leaf anatomy of the South African Danthonieae (Poaceae). III. *Merxmuellera stricta. Bothalia* 13: 191–198.
- ELLIS, R. P., 1981. Leaf anatomy of the South African Danthonieae (Poaceae). IV. Merxmuellera drakensbergensis and M. stereophylla. Bothalia 13: 487-491.
- KILLICK, D. J. B., 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Mem. bot. Surv. S. Afr. 34: 1-178.