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Leaf anatomy of the South African Danthonieae (Poaceae). VII. *Merxmuellera dura* and *M. rangei*

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ABSTRACT

The leaf anatomy of *Merxmuellera dura* (Stapf) Conert and *M. rangei* (Pilg.) Conert is described and illustrated. These two species both occur in the arid, north-western parts of the winter-rainfall region, but they display differing anatomical adaptations to these harsh climatic conditions. *M. dura* has an infolded leaf blade with both adaxial and abaxial furrows and appears to form a link between the *M. disticha* (Nees) Conert group of species and the genus *Dregeochloa* Conert. Anatomical evidence suggests that *M. rangei* occupies an isolated taxonomic position and the cylindrical leaf blades of this species are unique in the genus.

INTRODUCTION

Merxmuellera dura (Stapf) Conert and *M. rangei* (Pilg.) Conert are two additional danthonoid species that have recently been removed from the genus *Danthonia* DC. and referred to the genus *Merxmuellera* Conert (Conert, 1970). Both these species have long been known to science, *M. dura* having been described in 1899 and *M. rangei* in 1909. However, *M. rangei* is unaccountably not mentioned in the standard reference to the South African grasses (Chippindall, 1955) although neither the status of this taxon nor the validity of the name seem to be in doubt. Therefore *M. rangei* is recognized by Conert (1970) and the name has been accepted by the National Herbarium, Pretoria (PRE) (Gibbs Russell & Smook, 1980).

M. dura and *M. rangei* are the two southern African *Merxmuellera* species that extend furtherest northward into the arid, north-western parts of the winter rainfall region of the Cape Province and South West Africa/Namibia. *M. dura* is found mainly in the Mountain Renosterbosveld and Western Mountain Karoo veld types but also occurs in the Arid Karoo. *M. rangei* is found even further to the north in the Lüderitz-Süd District of South West Africa/Namibia. It has been collected in the Aus area as well as further south between Witputz and Lorelei.

M. rangei appears to be restricted to dry, sandy habitats such as the plains between granite koppies and in dry water-courses. *M. dura* also occurs in sandy riverbeds or other habitats with accumulated fine, loose sand but, in addition, it appears to favour warm, dry rocky localities. Consequently it is also found on steep, north-facing, rocky, sandstone slopes. In this respect *M. dura* occupies a very similar niche to *M. arundinacea* albeit in a more northerly direction and their distributional ranges do not appear to overlap.

M. dura and *M. rangei* can be readily distinguished on morphological criteria and this distinction is further accentuated by the leaf anatomy. 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

ANATOMICAL DESCRIPTION OF *MERXMUELLERA DURA*

Leaf in transverse section

Leaf outline: reduced U-shaped (Figs 1 & 2) or elliptical (Fig. 3); channel width somewhat variable as leaf possesses limited ability to open and close; channel very deep and leaf width at median vb narrower than lateral parts. *Ribs and furrows:* adaxial furrows shallow, cleft-like and present between all vbs; adaxial ribs rounded with vertical sides and all of similar size. Abaxial ribs and furrows present; ribs flat-topped and separated by cleft-like furrows (Figs 1–3); present opposite all vbs. *Median vascular bundle:* smallest 1'vb in section. *Vascular bundle arrangement:* 7–9 1'vbs in section; 1 3'vb between successive 1'vbs; all vbs situated equidistant from abaxial and adaxial epidermides. *Vascular bundle structure:* all bundles elliptical; phloem without sclerified tissue; 3'vbs exhibit more phloem than xylem tissue. *Vascular bundle sheaths:* obs of 1' and 3'vbs similar in composition and structure; obs elliptical to tall and narrow; adaxial interruption slight; abaxial interruption slight to wide in 1'vbs; extensions consist of parenchyma cells on either side of sclerenchyma girders. Obs cells rounded and decrease in size along extensions; lack chloroplasts; slightly larger than mesophyll cells. Ibs complete in 1'vbs but reduced and opposite phloem only in 3'vbs; consist of heavily thickened cells with small lumens. *Sclerenchyma:* adaxial girders inversely anchor-shaped with very long, narrow stems; abaxial girders trapezoidal, narrowing towards vbs; consist of heavily thickened fibres. No sclerenchyma between bundles. *Mesophyll:* small, tightly-packed isodiametric cells in tall, elongated, X-shaped groups especially in freshly fixed material (Figs 1 & 2). No colourless cells present. *Adaxial epidermis:* no bulliform cells except at the bases of the two furrows on either side of the median vb; few elongated prickles on adaxial ribs. *Abaxial epidermis:* no bulliform cells even at bases of furrows; cuticle thick; no macro-hairs, prickles or papillae.

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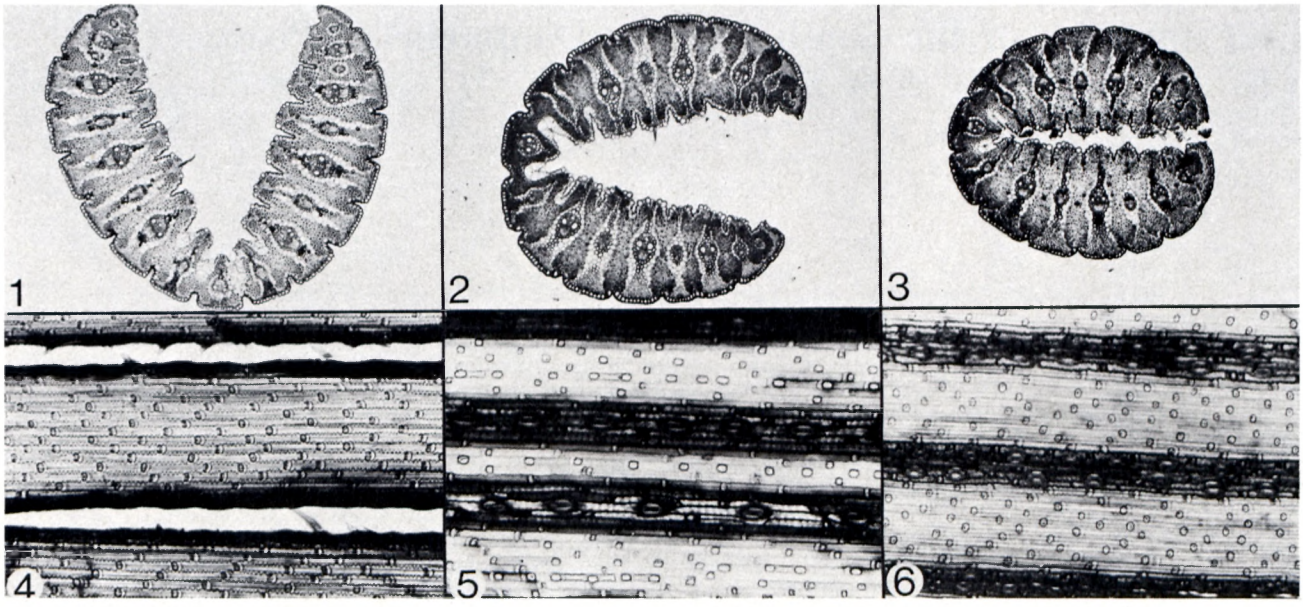


FIGS 1–6.—Leaf blade anatomy of *Merxmuellera dura*. 1–3, leaf blade outline in transverse section. All × 100. Note adaxial furrows. (1, *Ellis* 1719; 2, *Ellis* 2455; 3, *Ellis* 2465.) 4–6, abaxial epidermis in surface view. All × 250. (4, *Ellis* 2464; 5, *Ellis* 2455; 6, *Ellis* 2465.)

Abaxial epidermis

Intercostal zone: in form of stomatal groove and only visible on a few specimens (Figs 5 & 6). Intercostal long cells elongated, with parallel side walls and vertical end walls; walls slightly thickened and either straight or slightly undulating; no bulliform cells present. *Stomata:* if visible low dome-shaped; one or two rows per intercostal zone; successive stomata separated by single very elongated interstomatal cell (Fig. 5). *Intercostal short cells:* usually absent. Solitary, square with smooth walls if present. *Papillae:* absent. *Prickles:* usually not present; if present with medium bases and long barbs (Fig. 4). Present along margins of costal zones; overly stomatal groove. *Micro-hairs:* none seen. *Macro-hairs:* absent. *Silica bodies:* In specimens without stomata the silica bodies are tall and narrow, elliptical or cresent-shaped (Fig. 4) with closely associated cork cell. If stomata are present the bodies are rounded (Fig. 6) to oblong (Fig. 5) in shape without associated cork cells. Similar silica bodies present throughout costal zones; same width as costal long cells. *Costal cells:* silica cells or silica-suberose couples alternate with costal long cells with crenate walls (Fig. 4); adjacent costal files also alternate in the position of the silica cells.

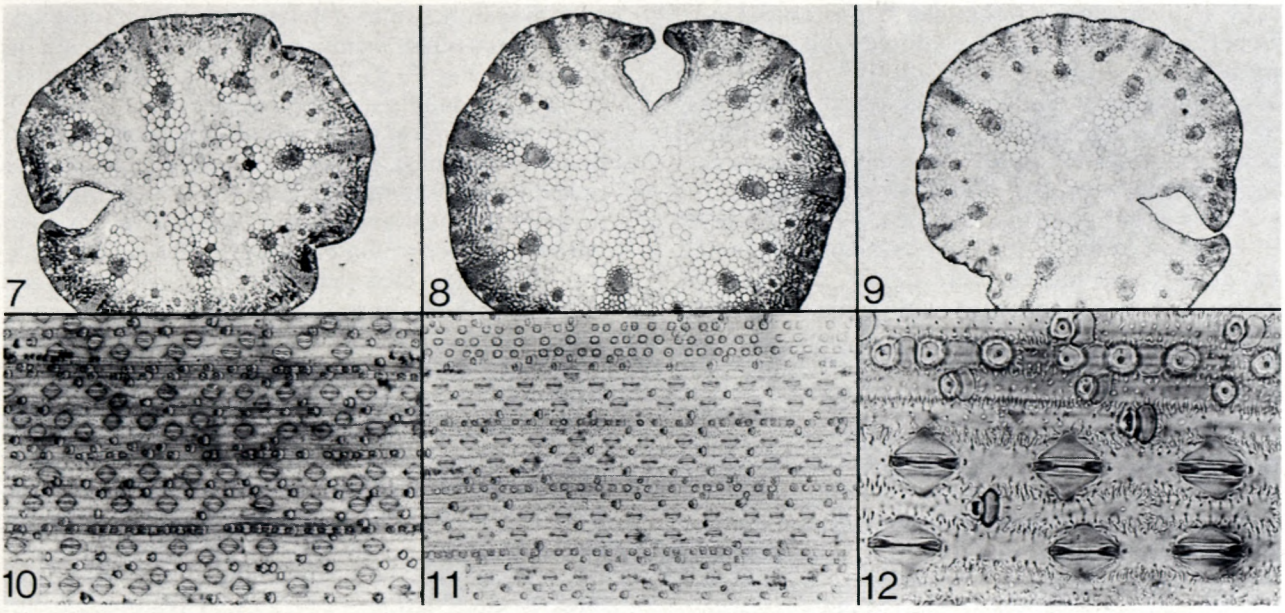
Specimens examined:

CAPE.—3119 (Calvinia): Nieuwoudtville (–AC), *Ellis 2455;* Hantam Mts (—BC), *Middlemost 2166;* Lokenburg (–CA), *Ellis 1719;* Perdefontein, Calvinia (–DD), *Acocks 17295.* 3220 (Sutherland): Middelpost (–AB), *Ellis 2464;* Sutherland (–BC), *Ellis 2465.*

ANATOMICAL DESCRIPTION OF *MERXMUELLERA RANGEI*

Leaf in transverse section

Outline of lamina: circular or rounded in section; solid cylinder with adaxial surface reduced to small groove (Figs 7—9). *Ribs and furrows:* absent on both surfaces; irregularities as in Fig. 7 probably due to inadequate rehydration of herbarium material. Tendency for slight abaxial undulations to be present opposite 1'vbs. *Median vascular bundle:* no keel or midrib developed. *Vascular bundle arrangement:* 7 1'vbs in leaf section; 1 3'vb between consecutive larger bundles and 1 2'vb between consecutive 1'vbs. 1'vbs centrally located in blade and 2' and 3'vbs abaxially situated (Fig. 8). *Vascular bundle description:* all vbs somewhat angular and elliptical in outline; xylem and phloem distinguishable. Protoxylem and metaxylem vessels of 1'vbs extremely narrow with diameters even less than those of the ibs cells. *Vascular bundle sheaths:* obs of 2' and 3'vbs circular to elliptical in shape; entire; no extensions. 1'vbs obs elliptical but with both adaxial and abaxial extensions. Adaxial extensions wide and merge gradually with the thin-walled colourless parenchyma cells of the interior of the leaf; more than 5 cells long. Abaxial extensions narrow and grade rapidly into conspicuous sclerenchyma strand. Obs cells with straight radial walls; cells large, inflated, conspicuous and considerably larger than the mesophyll cells; walls thicker than mesophyll cell walls; no chloroplasts. Ibs entire, comprised of very small cells irregularly thickened. *Sclerenchyma strands:* no adaxial sclerenchyma present; abaxial strands associated with 2' and 3'vbs; well-developed; as deep or deeper than wide as seen in transverse section; relatively narrow but deep girders associated with 1'vbs; narrower than the vbs; fibres thick-walled. *Mesophyll:* chlorenchyma irregularly arranged but somewhat pallisade-like in abaxial chlorenchyma; restricted to zone adjacent abaxial epidermis. Adaxial half of leaf consisting entirely of colourless cells; these are inflated, large, thin-walled parenchyma cells, regular in size; form pith-like tissue with uniform appearance (Figs 7–9). *Epidermal cells:* bulliform cells not present on either surface; no macro-hairs, papillae, hooks or prickles.



FIGS 7–12.—Leaf blade anatomy of *Merxmuellera rangei*. 7—9, transverse sections of the leaf blade. All × 100. Note cylindrical form with adaxial surface reduced to groove. (7, *Merxmüller & Giess* 28264; 8, *Schlieben* 11599; *De Winter & Giess* 6323.) 10–12, preparations of the abaxial epidermis. Note numerous stomata and narrow costal zones. (10, *De Winter & Giess* 6323, × 250; 11, *Merxmüller & Giess* 28264, × 250; 12, *Merxmüller & Giess* 28264, × 1000.)

Abaxial epidermis

Intercostal long cells: elongated, side walls parallel, end walls vertical, anticlinal walls heavily thickened and visibly pitted (Fig. 12); moderately to deeply sinuous; undulations U-shaped. Shape and size constant throughout all intercostal zones (Figs 10 & 11). No bulliform cells present. *Stomata:* triangular in shape with apices of subsidiary cells often evaginated (Fig. 12). Usually two, but sometimes three, rows of stomata per intercostal zone. Stomatal files separated by single file of long cells only (Fig. 12) or files with stomata adjoining (Fig. 10). Stomata present throughout intercostal zones. One interstomatal long cell between successive stomata (Fig 12); relatively short and much shorter than intercostal long cells. Stomata conspicuous and very numerous. *Intercostal short cells:* paired, silico-suberose couples with crescentic cork cell enfolding silica cell (Fig. 12); occur between most long cells. *Papillae:* absent. *Prickle hairs:* none seen. *Micro-hairs:* appear to be totally lacking. *Macro-hairs:* absent. *Silica bodies:* consistently round in shape; fitting into concavity of cork cell in intercostal zones; single silica cells or cork-silica cell pairs in costal zones (Fig. 12). Granules present. Costal cell arrangement variable.

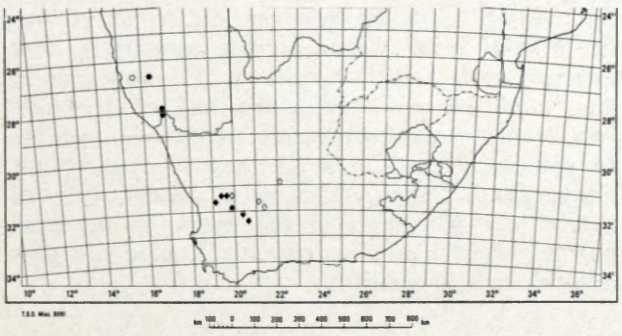


FIG. 13.—Distribution of *Merxmuellera dura* (◇) and *M. rangei* (○) compiled from specimens in the National Herbarium, Pretoria (PRE). Shaded symbols represent localities of specimens examined anatomically.

Specimens examined:

S.W.A.—2616 (Aus); (–CB), *Schlieben 11599*, 2716 (Witputz): Lüderitz-Süd (–DD), *Merxmüller & Geiss 28264*. 2816 (Oranjemund): Lorelei (–BB), *De Winter & Geiss 6323*.

DISCUSSION AND CONCLUSIONS

Although *M. dura* and *M. rangei* both occur in the drier areas of the nothern parts of the winter-rainfall region (Fig. 13) they differ considerably in both anatomy and morphology. They are obviously not closely related and this study of the leaf anatomy accentuates the considerable differences that exist between these two species.

The leaf anatomy of *M. dura* conforms closely with that of most of the *Merxmuellera* species described previously (Ellis, 1980; 1980a; 1981; 1981a; 1982). Such attributes as vascular bundle and sheath structure, mesophyll composition and arrangement and epidermal structure are typical of the genus and are shared by *M. dura* and these other species. In the sequence of arrangement of the different orders of vascular bundle along the width of the blade *M. dura* resembles the '*M. disticha* type' with alternating first and third order bundles (Ellis, 1980; 1981a). This type of bundle arrangement has been described in *M. disticha* (Nees) Conert, *M. davyi* (C.E. Hubb.) Conert and *M. macowanii* (Stapf) Conert (Ellis, 1981a) and possibly also *M. arundinacea* (Berg.) Conert (Ellis, 1982). Anatomical indications are, therefore, that *M. dura* is a typical representative of the genus belonging to the *M. disticha* group of species.

This anatomical resemblance with the *M. disticha* group of species is most unexpected as morphologi-

cally *M. dura* closely resembles *M. stricta* (Schrad.) Conert and may easily be confused with one of the forms of this species (Chippindall, 1955). There is an overlap in panicle size and in the length of the awns of the lobes and the arrangement of the marginal hairs is not always clear. The only character that satisfactorily separates these two species is the glabrous or hairy condition of the lemma at the point of insertion of the central awn (Chippindall, 1955). *M. dura* is also usually more robust, with coarser, more rigid leaf blades and with a longer panicle. These two species are not easy to separate using morphological criteria and they appear to be closely related.

Anatomically *M. dura* and *M. stricta* can easily be distinguished. The most obvious difference being the presence of abaxial furrows between all the bundles in *M. dura* — a character it alone possesses amongst all the *Merxmuellera* species. This development of abaxial stomatal grooves is of interest because it is a feature present in two other danthonoid genera from these drier areas. This condition has already been described in *Dregeochloa* Conert (Ellis, 1977) and it also occurs in both species of *Asthenatherum* Nevski (Conert, 1962) and must be of adaptive significance in this hot, arid climate. The presence of abaxial stomatal grooves, is in marked contrast to the total absence of abaxial stomata in most *Merxmuellera* species from the mountainous areas to the east where rainfall is not a limiting factor. These abaxial furrows also possibly indicate a phylogenetic link between *M. dura* and *Dregeochloa,* although they differ in mesophyll structure and bulliform cell type and their generic separation is undoubtedly justified.

The supposed close relationship between *M. stricta* and *M. dura* is not confirmed by the anatomical evidence which appears to indicate a common origin with the *M. disticha* group of species. This inference is based primarily on the alternating sequence of first and third order bundles which is assumed to be a basic difference between two major groups within *Merxmuellera* (Ellis, 1981a). This assumption is based on evidence from the twelve summer rainfall *Merxmuellera* taxa and it is concluded that it is phylogenetically a significant difference. The situation in *M. dura,* however, seriously questions this deduction as, anatomically, *M. dura* and *M. stricta* also share many similarities apart from this difference in the arrangement of the different orders of vascular bundle. Epidermal structure of *M. dura* is similar to that of the specimens of the typical *M. stricta* type possessing abaxial stomata (Ellis, 1980a). The development of abaxial furrows is all that is required to result in almost identical epidermides. In addition, the typical form of *M. stricta* often has a single abaxial furrow on either side of the median vascular bundle (Ellis, 1980a) and is the only other species of this genus with this development. These apparent contradictions are impossible to explain at present and await further study particularly of the cytogenetics of *M. dura, M. stricta* and *M. disticha.*

The leaf anatomy of *M. rangei* is clearly distinct and differs drastically from that of all the other representatives of the genus. The presence of adaxial parenchyma and the consequent development of the solid, cylindrical leaf form is unique in this genus (Figs 7–9). The possession of three orders of vascular bundle and the parenchyma sheath cell size is also atypical for the genus. The leaf anatomy, therefore, indicates that *M. rangei* occupies an isolated position within the genus and possibly suggests that it warrants generic status as has been accorded *Dregeochloa pumila* (Nees) Conert which was previously classified in the genus *Danthonia* together with *M. rangei.* In common with *D. pumila, M. rangei* has adaxial colourless cell development (bulliform cells in the case of *D. pumila)* and mesophyll tissue that is not composed of tightly-packed, angular, isodiametric chlorenchyma cells. In all other respects these two species differ considerably and certainly do not seem to belong to the same genus. The leaf blade anatomy of *M. rangei* is obviously highly specialized and the taxonomic status that should be accorded the unique terete leaf form is uncertain.

The abaxial epidermal structure of *M. rangei* is worthy of comment. The exceptionally large number of unprotected stomata and the narrow costal zones (Figs 10–12) are difficult to explain in a grass where all other modifications tend to suggest a reduction in water loss. The cuticle of *M. rangei* appears to be thick as indicated by the pitted outer epidermal cell walls (Fig. 12) and perhaps this reduces water loss through these cells and it can only be assumed that the stomata themselves only open on limited occasions. The other danthonoid grasses from similar habitats all have well-protected stomata at the bases of deep furrows often densely overlaid by interlocking prickles. *M. stricta* is the only other *Merxmuellera* species possessing abaxial stomata (Ellis, 1980a) and the epidermis of these two species is remarkably similar in all respects except that *M. stricta* sometimes has micro-hairs — a feature not observed on *M. rangei.* This similarity in epidermal structure can possibly be interpreted as evidence that *M. rangei* is best placed in *Merxmuellera* and that the exceptional anatomical adaptations of the leaf in section are only of specific taxonomic importance.

UITTREKSEL

Die blaaranatomie van Merxmuellera dura *(Stapf) Conert en* M. rangei *(Pilg.) Conert word beskryf en geïllustreer. Hierdie twee spesies kom albei in die droë, noord-westelike dele van die winterreënval-streek voor maar die anatomiese aanpassings wat vertoon word verskil aansienlik.* M. dura *het 'n toegevoude blaar met beide adaksiale en abaksiale groewe en verteenwoordig dalk 'n binding tussen die* M. disticha *(Nees) Conert spesiesgroep en die genus* Dregeochloa *Conert. Anatomiese aanduidings dui daarop dat* M. rangei *'n geïsoleerde taxonomiese posisie beklee en die silindriese blare van hierdie gras is uniek in die genus.*

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