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Leaf anatomy of the South African Danthonieae (Poaceae). VII. *Merxmuellera decora, M. lupulina* and *M. rufa*

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ABSTRACT

The leaf anatomy of *Merxmuellera decora* (Nees) Conert, *M. lupulina* (Thunb.) Conert and *M. rufa* (Nees) Conert is described and illustrated. The epidermal structure is shown to be uniform in all three taxa and to be unique in the genus. The leaf anatomy is very variable and three distinct types are evident. *M. lupulina* is consistent, but all three anatomical types are represented in the samples examined of both *M. decora* and *M. rufa*. The anatomical types show similarities with *Pentaschistis involuta* (Steud.) Adamson, *M. dura* (Stapf) Conert, *M. stricta* (Schrad.) Conert and *M. disticha* (Nees) Conert. *M. decora, M. lupulina* and *M. rufa*, together with *P. involuta*, therefore, appear to form a recognizable group intermediate between *Pentaschistis* and *Merxmuellera*.

INTRODUCTION

These three danthonoid grass species were not included in the genus *Merxmuellera* in the original description (Conert, 1970). Later, however, they were referred to *Merxmuellera* as *M. decora* (Nees) Conert (= *Danthonia zeyheriana* Steud.), *M. lupulina* (Thunb.) Conert [= *D. lupulina* (Thunb.) Beauv. ex Roem. & Schult.] and *M. rufa* (Nees) Conert [= *D. lanata* (Schrad.) Schrad. and *D. macrocephala* Stapf] (Conert, 1971).

Morphologically these species comprise a distinct group within *Merxmuellera* and can easily be distinguished from the 14 other species of this genus. They are all strong perennials with distinctly bulbous bases consisting of the old woolly leaf sheaths which are deeply sunken into the ground. In addition, the lower, and, sometimes, even the upper leaf sheaths, are covered with woolly hairs on the outer surface. This wooliness is not found in any other *Merxmuellera* species (Chippindall, 1955). All these species are obviously fire-adapted and commonly occur in firebreaks and are particularly conspicuous after burns. They occur on mountain slopes from the Cape Peninsula as far east as Knysna — being restricted to the extreme south of the African continent.

Although these species form a homogeneous morphological entity they are difficult to separate from one another satisfactorily. *M. rufa*, in particular, is a variable taxon where all specimens intermediate between *M. lupulina* and *M. decora* are accommodated. Size of spikelets and degree of branching of the inflorescence is particularly variable and a hybrid origin appears to be indicated.

Anatomy, to some extent, confirms these morphological indications and confirms the morphological relationships of *M. rufa* with either *M. decora* or *M. lupulina*. In addition, the leaf anatomy reveals that at least three separate taxa are referred to *M. decora* and that *M. lupulina* shows very close similarities with some *Pentaschistis* species, in particular *P. involuta* (Steud.) Adamson. Anatomically these species are, therefore, very variable with virtually every population differing in leaf anatomy, especially of the leaf as seen in transverse section. This makes specific descriptions of the leaf anatomy largely meaningless and, consequently, only abbreviated anatomical descriptions are given. The terminology adopted by Ellis (1976, 1979) will be used for the descriptions together with the following abbreviations:

vb/s—vascular bundle/s
1'vb/s—first 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 DECORA*

In the sample studied three distinct anatomical types can be distinguished.

Type 1 (Figs 1 & 2)

Leaf outline: permanently infolded with elliptical outline (Figs 1 & 2); channel width somewhat variable; leaf width markedly greater in centre of lamina (Fig. 1). *Ribs and furrows:* adaxial furrows deep and cleft like; present between all vbs; ribs rounded with vertical sides. Abaxial ribs and furrows well developed on either side of the median vb and adjacent one (Fig. 2) or two (Fig. 1) vbs. This character is diagnostic for this type of *M. decora*. *Median vascular bundle:* similar to lateral 1'vbs. *Vascular bundle arrangement and structure:* 9 or 11 vbs in section; 1 3'vb between successive 1'vbs; all bundles circular and without sclerified tissue in the phloem. *Vascular bundle sheaths:* obs cells round and without chloroplasts; sheath circular and entire except for abaxial interruption in 1'vbs; adaxial extensions consist of parenchyma cells intergrading into the sclerenchyma girder (Fig. 1). Ibs complete in 1'vbs but reduced in 3'vbs. *Sclerenchyma:* adaxial girders inversely anchor-shaped; abaxial girders trapezoidal. *Mesophyll:* small, tightly packed, isodiametric cells in X-shaped groups; no colourless cells. *Adaxial epidermis:* small bulliform cells at bases of all furrows. *Abaxial epidermis:* small bulliform cells at bases of furrows; costal epidermis cells large, regular; no macro-hairs, prickles or papillae.

Type 2 (Fig.3)

Leaf outline: permanently infolded with elongated elliptical outline (Fig. 3); adaxial channel a

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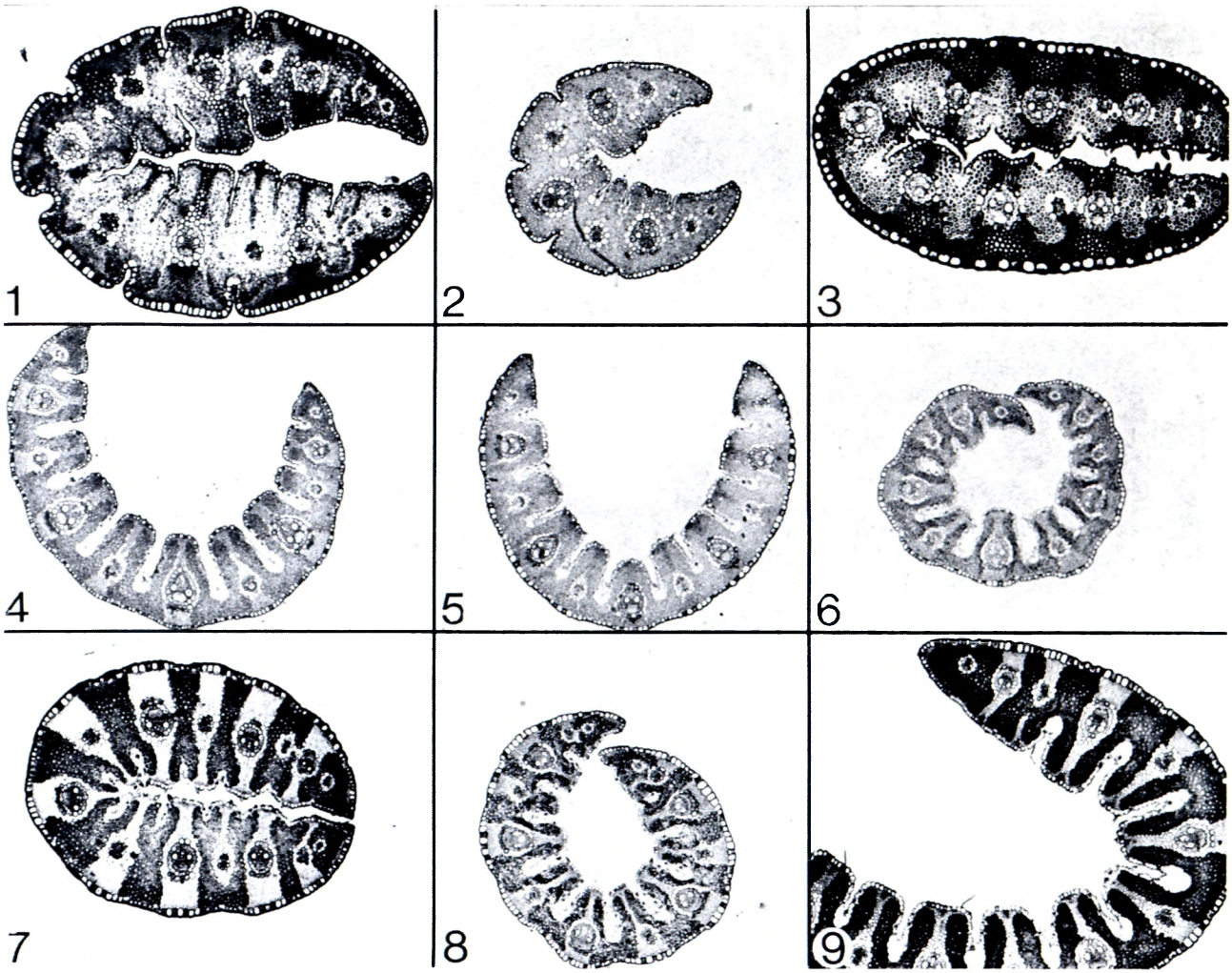


FIGS 1–9.—Leaf blade outline in transverse section. 1–3, *Merxmuellera decora.* All setaceous, permanently infolded leaves: 1, *Ellis* 2543, × 100; 2, *Ellis* 657, × 100; 3, *Ellis* 2553, × 160. 4–6, *Merxmuellera lupulina.* Inrolled leaves that can expand. All × 100: 4, *Ellis* 2254; 5, *Ellis* 2256; 6, *Taylor* 4513. 7–9, *Merxmuellera rufa.* Variable leaf outline. All × 100: 7, *Ellis* 2517; 8, *Kruger* 491; 9, *Ellis* 2483.

narrow cleft; leaf width not markedly thicker in centre of lamina as in Type 1. *Ribs and furrows:* adaxial furrows shallow, cleft-like becoming reduced towards the margin; present between all vbs. Abaxial ribs and furrows absent in contrast to Type 1. *Median vascular bundle:* similar in size and shape to lateral 1'vbs. *Vascular bundle arrangement:* 9–11 vbs in section. Lateral 1'vbs not interspaced by 3'vbs as in Type 1. *Vascular bundle structure:* similar to Type 1. *Vascular bundle sheaths:* broad adaxial and abaxial interruptions present; no bundle sheath extensions present. *Sclerenchyma:* adaxial girders inversely anchor-shaped with short thick stems; abaxial sclerenchyma continuous sub-epidermal band of varying thickness, with large trapezoidal girders extending to, and interrupting the obs. *Mesophyll:* small, tightly packed, isodiametric cells in Y-shaped groups (not X-shaped as in Type 1); no colourless cells. *Adaxial epidermis:* very small bulliform cells at bases of all furrows. *Abaxial epidermis:* no bulliform cells; epidermal cells of regular size and shape with outer periclinal wall thickened and covered by continuous, thickened cuticle; no macrohairs, prickles or papillae.

Type 3

Virtually identical to *M. lupulina* and the relevant description will suffice.

ANATOMICAL DESCRIPTION OF *MERXMUELLERA LUPULINA*

The anatomy of the leaf as seen in transverse section is remarkably consistent in the sample studied. This is Type 3 of Table 1.

Leaf outline: not permanently infolded; loosely involutely inrolled (Figs 4–6); 11 vbs in section in all specimens except van Rensburg *199* which has 19. *Ribs and furrows:* medium, narrow to cleft-like adaxial furrows present between all vbs; ribs rounded but with vertical sides; all ribs similar in shape. No abaxial ribs or furrows developed. *Median vascular bundle:* indistinguishable structurally from the lateral 1'vbs. *Vascular bundle arrangement:* 1'vbs and 3'vbs alternate; 1'vbs centrally positioned but 3'vbs located slightly towards the abaxial side (Figs 4 & 5). *Vascular bundle structure:* 1'vbs and 3'vbs circular in outline;

narrow xylem vessels; no sclerosed phloem. *Vascular bundle sheaths:* obs round; adaxial and abaxial interruptions; no extensions. Obs cells colourless, thinwalled and rather small; not conspicuous. Ibs entire; walls heavily but uniformly thickened. *Sclerenchyma:* adaxial girders inversely anchor-shaped; stem long and thin; trapezoidal abaxial girders (Figs 4 & 5). All fibres of girders of cellulose as they only stain green with fast green and safranin. This is exceptional in the genus *Merxmuellera* where sclerenchyma is always lignified. *Mesophyll:* not radiate; homogeneous, regular, small cells tightly packed, no colourless cells. *Adaxial epidermis:* bulliform cells well developed; fan-shaped; situated at bases of furrows. Few hooks present. *Abaxial epidermis:* epidermal cells of regular size and shape with outer periclinal wall somewhat thickened and covered by a continuous cuticle; no epidermal appendages or bulliform cells.

ANATOMICAL DESCRIPTION OF *MERXMUELLERA RUFA*

Anatomy extremely variable and intergrades with both Types 1 and 2 of *M. decora* as well as *M. lupulina*. For convenience, these three types will be briefly described separately.

Type 1

Resembles Type 1 of *M. decora* closely in that abaxial grooves are developed. These grooves are cleft-like and tend to fade toward the margin. The only appreciable difference is that these specimens do not seem to have permanently infolded leaves but show a tendency to be able to open to a certain degree. In addition, the adaxial ribs are not as regular as in *M. decora* but ribs associated with 1'vbs tend to be massive and those overlying 3'vbs triangular.

Type 2 (Fig. 7)

Permanently infolded type without abaxial ribs and furrows. In all specimens 1'vbs alternate with 3'vbs (Fig. 7), whereas in the *M. decora* type which this resembles (Fig. 3), there are successive 1'vbs situated laterally. Obviously this type intergrades with the next type which has a more open leaf (Fig. 9).

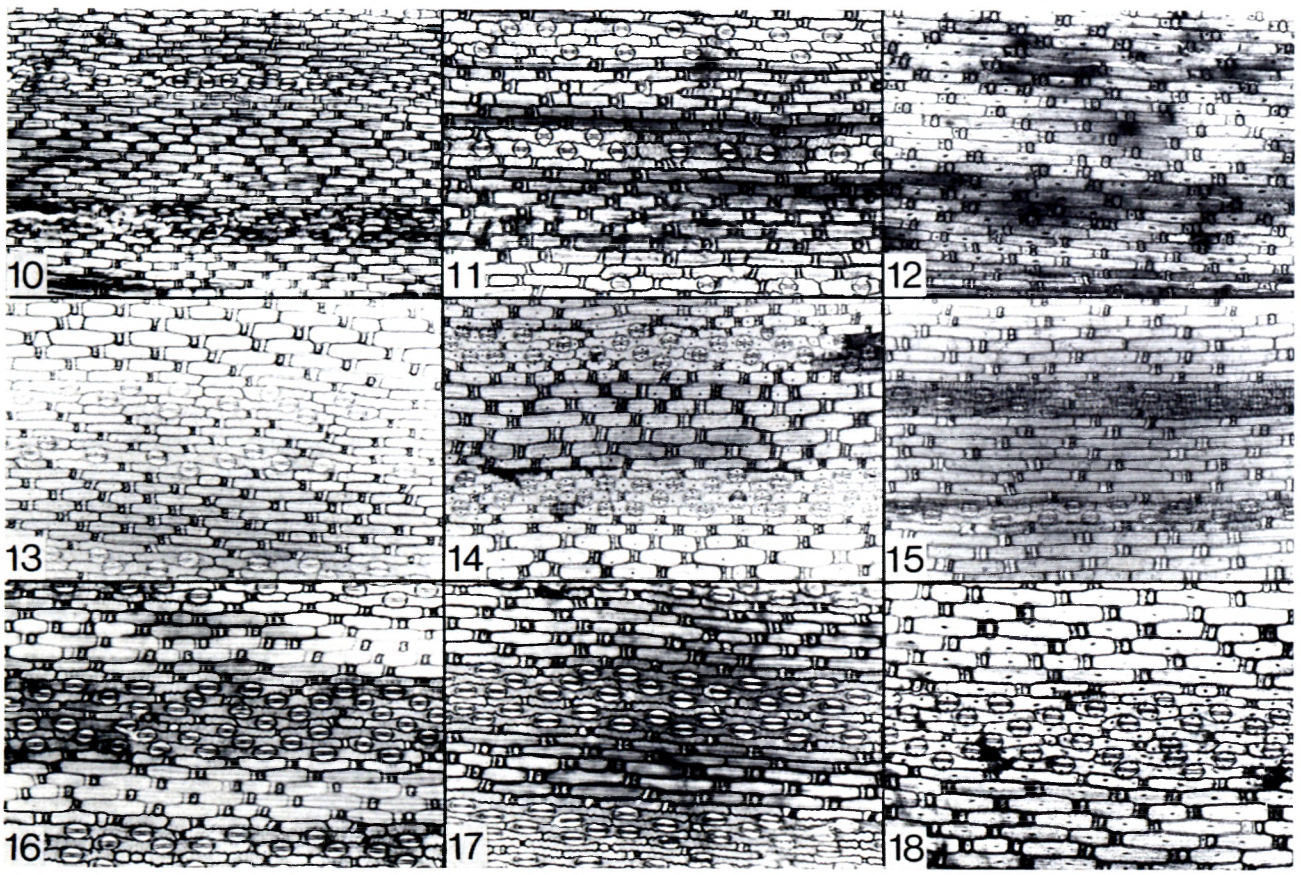
Type 3 (Figs 8 & 9)

All specimens conform to the description of *M. lupulina* very closely. The only deviation observed is in one specimen where the sclerenchyma is lignified (Fig. 9) and not of cellulose (Fig. 8). Due to staining, this difference is enhanced but structurally there is actually very little difference.

COMBINED DESCRIPTION OF EPIDERMAL HISTOLOGY OF *MERXMUELLERA DECORA, M. LUPULINA* AND *M. RUFA*

Abaxial epidermis

Intercostal zone: present in all specimens except Type 2 of *M. decora* (Fig. 12) where it is absent due



FIGS 10–18.—Abaxial epidermis as seen in surface view. 10–12, *Merxmuellera decora:* 10, *Ellis* 2543, × 160; 11, *Ellis* 2553, × 250; 12, *Ellis* 657, × 250. 13–15, *Merxmuellera lupulina.* All × 250: 13, *Ellis* 2254; 14, *Ellis* 2256; 15, *Taylor* 5477. 16–18, *Merxmuellera rufa.* All × 250: 16, *Ellis* 2483; 17, *Ellis* 2517; 18, *Ellis* 1190.

to development of hypodermal sclerenchyma (Fig. 3); in Type 2 of *M. rufa* girders do not fuse (Fig. 7) and intercostal zones are present (Fig. 17); present in abaxial furrows in Types 1 of *M. decora* (Fig. 10) and *M. rufa* and between the vbs in *M. lupulina* and Types 3 of *M. decora* and *M. rufa*. *Stomata:* low dome-shaped; seldom high-dome-shaped as in Fig. 11; occur in every file of intercostal zones; usually separated by single interstomatal long cell (Figs 16 & 18); interstomatal long cells short to elongated with parallel side walls; slightly undulating; sometimes separated by single short cell. *Papillae:* absent. *Prickles:* none observed. *Micro-hairs:* uncommon; basal cell extremely long; equal to 3× the length of the stomata; distal cells not observed. *Macro-hairs:* absent. *Silica bodies:* uniform in shape; round to slightly vertically elliptical; throughout costal zones; always associated with a narrow cork cell. *Costal zone:* arrangement very uniform; silico-suberose couples always separated by single costal long cell; adjacent files alternate resulting in brickwork pattern. Costal long cells are distinctive in that they are wide and distinct with side walls usually bowed outwards due to the cells being somewhat inflated (Figs 13, 14, 16 & 18); this is not always the case and the side walls may be parallel (Figs 12 & 15). Costal zones are from 7–13 files of cells wide and composition and arrangement is consistent throughout.

Specimens examined:

M. decora

Type 1

CAPE.—3320 (Montagu): Barrydale (–DC), *Ellis 657.* 3321 (Ladismith): Garcias Pass, Riversdale (–CC), *Ellis 2543.*

Type 2

CAPE.—3322 (Oudtshoorn): Robinsons Pass, Outeniqua Mts. (–CC), *Ellis 2549, 2552, 2553.*

Type 3

CAPE.—3322 (Oudtshoorn): George (–CD), *Cook* s.n. Cradocksberg, *Fourcade 4086.*

M. lupulina

CAPE.—3318 (Cape Town): Jonkershoek, Stellenbosch (–DD), *Ellis 2254, 2255, 2256, Taylor 4513, 5477, Van Rensburg 199.*

M. rufa

Type 1

CAPE.—3418 (Simonstown): Cape Point (–AD), *Ellis 2324,* Red Hill, *Taylor 5243.*

Type 2

CAPE.—3318 (Cape Town): Red Hill (–DB), *Taylor 4130.* 3418 (Simonstown): Cape Hangklip (–BD), *Ellis 2517.* 3419 (Caledon): Lebanon (–AA), *Kruger 199.*

Type 3

CAPE.—3118 (van Rhynsdorp): Giftberg (–DC), *Esterhuysen 22128.* 3219 (Wuppertal): Sneeuberg, Clanwilliam (–AC), *Edwards 158;* Buffelberg Pass, Citrusdal (–CA), *Ellis 1190.* 3318 (Cape Town): Kirstenbosch (–CD), *Compton 12014.* 3319 (Worcester): Witzenberg Mts., Ceres (–AC), *Ellis 2483.* 3418 (Simonstown): Hottentots Holland Mts., Sugarloaf Peak (–BB), *Ellis 2298.* 3419 (Caledon): Lebanon (–AA), *Kruger 491.* 3420 (Bredasdorp): Bontebok Nat. Park, Swellendam (–BB), *Liebenberg 6593.*

DISCUSSION AND CONCLUSIONS

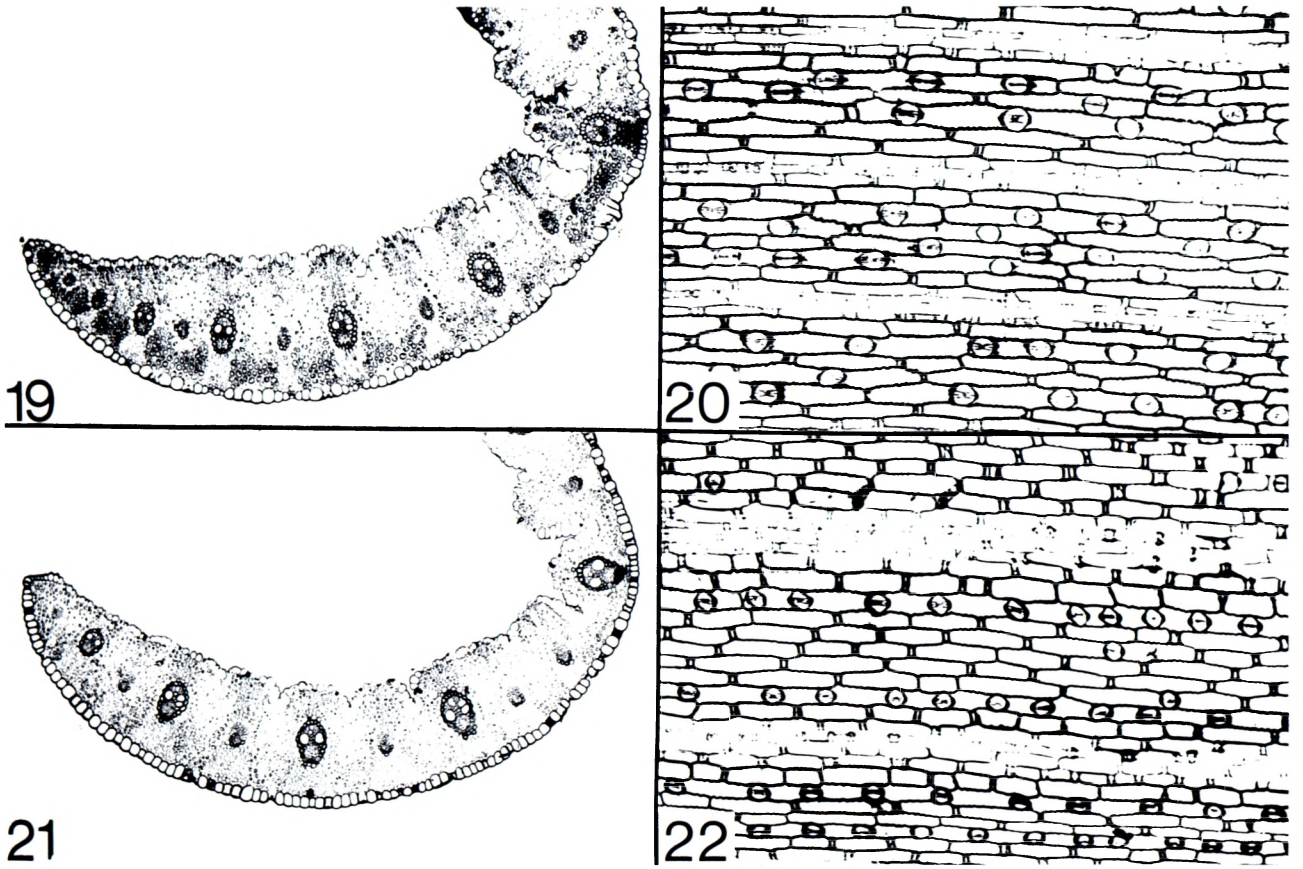
Epidermal structure, particularly of the costal zones, is remarkably consistent throughout the three species studied. All specimens have rounded to elliptical silica bodies which are closely associated with a tall and narrow cork cell. These silico-suberose couples are separated by characteristic costal long cells which have the side walls outwardly bowed. Adjacent files alternate in their arrangement resulting in a brickwork pattern (Figs 10–18). This type of epidermal configuration is unique in the South African danthonoid grasses and differs from all other *Merxmuellera* species. This inflated nature of the costal long cells coupled with the silicose-suberose pairs has also been described in the Drakensberg and Alpine bog farms of *M. disticha* (Nees) Conert (Ellis, 1980). This resemblance is not close, however, and no significance is placed on it. The epidermis of *M. dura* (Ellis, 1982) bears the strongest resemblance with this type.

Morphologically these three species form a distinct group within the genus *Merxmuellera* — their woolly leaf sheaths and expanded bases sunken into the ground being unique in the genus. This close relationship is confirmed by the anatomy, particularly of the epidermis, but this also emphasizes the isolated position within the genus that these species occupy. Epidermal structure, and the cross-sectional anatomy of the majority of the specimens examined, in fact indicates nothing to suggest a close relationship with *Merxmuellera* at all.

The *M. lupulina* type of anatomy (Figs 4–6) is characterized by the leaf not being permanently infolded but involute as well as very little lignin being present in the girders. This structural type occurs in 62% of the 26 specimens examined in this study — all the *M. lupulina* specimens and 2 *M. decora* and 8 *M. rufa* specimens (Type 3 of Fig. 23). Consequently all these specimens bear little resemblance to any *Merxmuellera* species based on leaf anatomy as well as epidermal histology.

This observation is made more significant by the fact that these Type 3 specimens of Fig. 23 show close anatomical resemblances to *Pentaschistis involuta* (Steud.) Adamson and some *P. viscidula* (Nees) Stapf specimens. This is particularly so in the case of the leaf in transverse section (Figs 19 & 21). The epidermis superficially resembles the condition in the *M. lupulina, M. decora & M. rufa* group in that the long cells are inflated and the silica bodies are associated with cork cells. However, closer examination shows that these inflated long cells are actually intercostal cells and not costal cells — the costal zones, although very reduced, being entirely different (Figs 20 & 22). All intermediates do occur between the two extremes, however, and the anatomical indications are, therefore, that the *M. lupulina* type of anatomy has more in common with *P. involuta* than with any of the other *Merxmuellera* species.

This anatomical resemblance is confirmed by the morphology and ecology of these two *Pentaschistis* species. The plant bases are somewhat swollen with persistent leaf sheaths which are sometimes woolly



FIGS 19–22.—Leaf anatomy of *Pentaschistis involuta* and *P. viscidula* for comparative purposes. 19–20, *Pentaschistis involuta, Ellis* 2542: 19, transverse section, × 100; 20, abaxial epidermis, × 160. 21–22, *Pentaschistis viscidula, Ellis* 2554: 21, transverse section, × 100; 22, abaxial epidermis, × 160.

but, nevertheless, usually hairy. *P. involuta* and *P. viscidula* both respond positively to burning and regenerate readily after fire, as do the group of *Merxmuellera* species under discussion. Anatomically *P. involuta* resembles *P. aristidoides* (Thunb.) Stapf more closely than any other *Pentaschistis* species. The similarity is mainly in the leaf anatomy and not the epidermis. It is interesting to note that *P. aristidoides* is the only other *Pentaschistis* with the lowest leaf sheaths woolly or silkily hairy at the base and with swollen bases (Chippindall, 1955).

The anatomy, therefore, suggests that all the *M. lupulina*-like specimens bear a strong link to *P. aristidoides* and that *P. involuta* cannot be satisfactorily separated from *M. lupulina*. This group of species appears to form a link between *Pentaschistis* and *Merxmuellera* and it will be interesting to see whether detailed spikelet comparisons and cytological studies confirm the anatomical indications.

The following *Pentaschistis* specimens bear a strong resemblance to *M. lupulina:*

P. involuta

CAPE.—3418 (Simonstown): Hottentots Holland Mts.; Sir Lowry's Pass (–BB), *Ellis 2284, 2285, 2290, 2291;* Kogelberg (–BD), *Boucher 1194.* 3321 (Ladismith): Garcias Pass, Langeberg (–CC), *Ellis 2542.*

P. viscidula

CAPE.—3320 (Montagu): Tradouws Pass, Barrydale (–DC), *Ellis 658.* 3322 (Oudtshoorn): Robinsons Pass, Outeniqua Mts. (–CC), *Ellis 2554.*

In the *M. decora* sample studied, the two specimens with *M. lupulina*-like anatomy (*Cook* s.n. & *Fourcade* 4086), have actually been examined by Conert and determined as being *M. decora.* The other specimens used in this study, although closely resembling the above two specimens in morphology, and accordingly identified as *M. decora* by the National Herbarium, differ radically in anatomy. Similarly, all the material of *M. rufa* determined by Conert has the *M. lupulina* type of anatomy (Fig. 8). Consequently it is just possible that no specimens which deviate anatomically from the *M. lupulina* type have been thoroughly studied taxonomically. This includes all the specimens listed under Types 1 & 2 for both *M. decora* and *M. rufa* under specimens examined. This may explain why morphological studies have not suggested the same patterns of variation as has this study of the anatomy.

The remaining specimens of both *M. decora* and *M. rufa* (with anatomical Types 1 and 2), which do not exhibit a close anatomical resemblance with *M. lupulina,* appear to confirm the relationship of this group of species with the genus *Merxmuellera.* Type 1, consequently, resembles *M. dura* (Stapf) Conert rather closely in transverse section. Both have alternating first and third order vascular bundles and distinct abaxial furrows (Ellis, 1982). The epidermis of *M. dura* also has distinct silico-suberose couples but lacks the inflated costal long cells. The Type 2 *M. decora* and *M. rufa* specimens either resemble the *M. disticha* (Nees) Conert, or the *M. stricta*

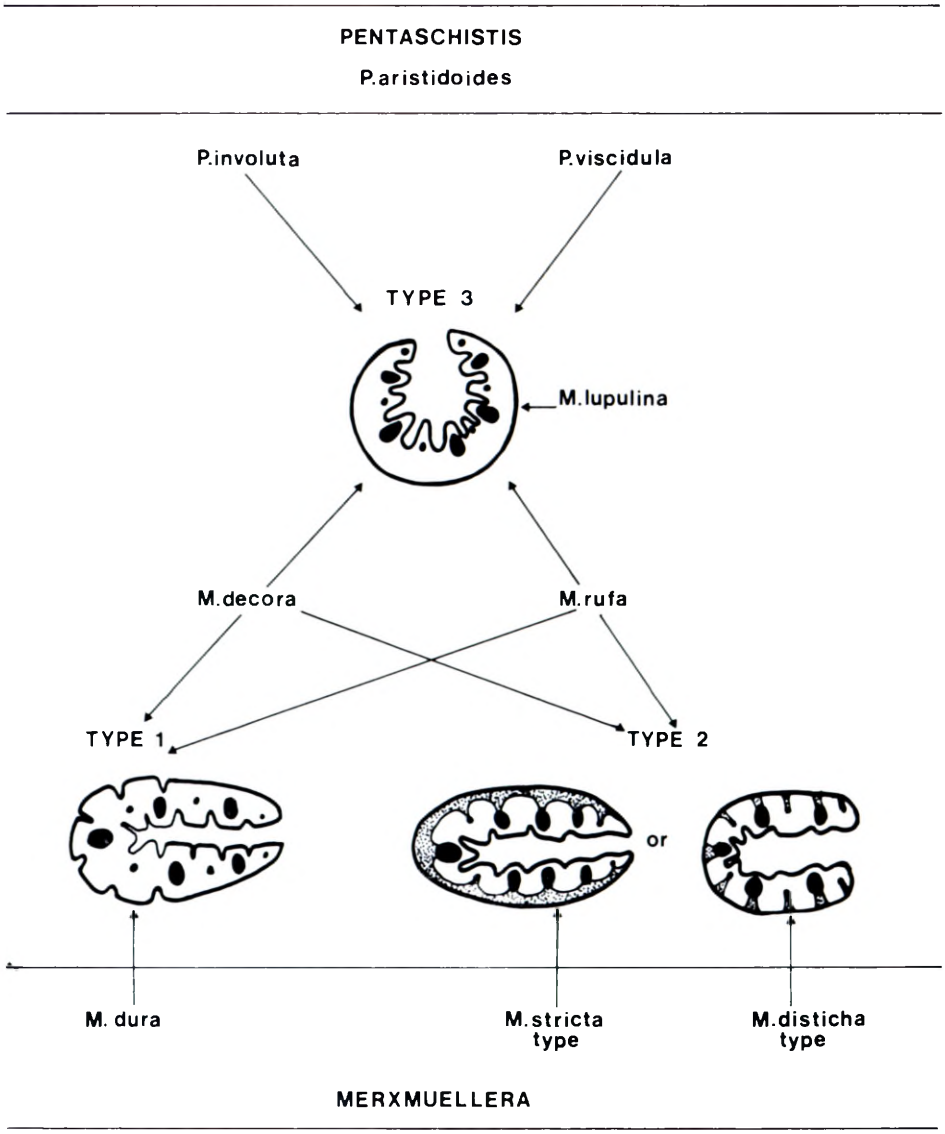


FIG. 23.—Schematic representation of relationships of *Merxmuellera decora, M. lupulina* and *M. rufa* to each other and to the genera *Pentaschistis* and *Merxmuellera*.

(Schrad.) Conert groups (Ellis, 1981). The alternating bundles of different orders of the *M. rufa* specimens of this type resemble the condition in the *M. disticha* group of species whereas the successive lateral first order bundle sequence in the *M. decora* specimens resemble the *M. stricta* type. It is, therefore, possible that these specimens indicate a hybrid origin with *M. stricta* and *M. disticha* (in which group *M. dura* is included).

M. decora, M. lupulina & M. rufa, together with *Pentaschistis involuta*, therefore, appear to form a distinct morphological and anatomical entity intermediate between the genera *Merxmuellera & Pentaschistis*. The taxonomic implications of these anatomical observations appear to be critical to a better understanding of these two danthonoid genera. Either they should all be placed in a new genus intermediate between *Merxmuellera* and *Pentaschistis* and accepted as such or the concept of the genus *Merxmuellera* must be altered. This questions the recognition of the genus *Merxmuellera* and raises the possibility of a reacceptance of the genus *Danthonia*. Careful morphological analyses are urgently required to resolve this question. Finally, this study has revealed that neither *M. decora* or *M. rufa* are homogeneous entities as presently constituted and it appears that a more satisfactory arrangement would be the grouping of all Type 1 specimens in one of these taxa and all Type 2 specimens in the other.

ACKNOWLEDGEMENTS

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UITTREKSEL

Die blaaranatomie van Merxmuellera decora *(Nees) Conert,* M. lupulina *(Thunb.) Conert en* M. rufa *(Nees) Conert word beskryf en geïllustreer. Dit is bewys dat die epidermisstruktuur in al drie spesies eenders is en dat dié struktuur uniek in die genus is. Die blaaranatomie varieer baie en drie verskillende soorte is duidelik. Die anatomie van* M. lupulina *is deurgaans konsekwent maar al drie anatomiese soorte is teenwoordig in die ondersoekte monsters van beide* M. decora *en* M. rufa. *Die anatomiese soorte*

toon ooreenkomste met Pentaschistis involuta *(Steud.) Adamson,* M. dura *(Stapf) Conert,* M. stricta *(Schrad.) Conert en* M. disticha *(Nees) Conert. Dit blyk dus dat,* M. decora, M. lupulina *en* M. rufa, *tesame met* P. involuta, *'n duidelik erkenbare groep vorm wat intermediêr tussen* Pentaschistis *en* Merxmuellera *ressorteer.*

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