

Leaf anatomy of the South African Danthonieae (Poaceae).

I. The genus *Dregeochloa*

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ABSTRACT

The anatomical structure, of the leaf blade as seen in transverse section, and the abaxial epidermis, of *Dregeochloa pumila* and *D. calvinensis* is described and illustrated. A generic description is included and the relationships of the genus are briefly discussed.

RESUME

ANATOMIE DE LA FEUILLE DES DANTHONIEAE (POACEAE) SUD-AFRICAINES. I. LE GENRE DREGEOCHLOA

La structure anatomique du limbe foliaire vu en coupe transversale, ainsi que l'épiderme abaxial de *Dregeochloa pumila* et de *D. calvinensis* sont décrits et illustrés. On y joint une description du genre avec une brève discussion de ses relations.

INTRODUCTION

The genus *Dregeochloa* Conert was described to accommodate the species *Danthonia pumila* Nees and a newly described species *Dregeochloa calvinensis* Conert (Conert, 1966). These two species have certain distinct characteristics of spikelet morphology, leaf anatomy and especially the structure of the mature caryopsis, which indicates that this genus occupies a unique and somewhat isolated position in the Danthonieae. Plants of the genus were previously assigned to the genus *Danthonia* DC. (Chippindall, 1955), and certain authors (De Wet, 1954, 1956; Jacques-Felix, 1962) have suggested their inclusion in *Asthenatherum* Nevski. However, they can readily be distinguished from both genera by the development of the leaves, the insertion of the central awn and the structure of the caryopsis (Conert, 1966). In addition, these species exhibit characteristic leaf anatomy which tends to confirm their placement together in a separate genus, but throws little light on the phylogenetic position of this genus. 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 THE GENUS *DREGEOCHLOA*

Leaf in transverse section

Leaf outline: U-shaped or canaliculate with two halves of lamina curved upwards to varying degrees on either side of median vascular bundle; forming no angle. Leaves narrow (between 1,60 mm and 3,50 mm wide), proportionately very thick (between 0,30 mm and 0,70 mm). **Ribs and furrows:** adaxial furrows present between all vbs; equally sized, rounded, adaxial ribs present over all vbs irrespective of order. Abaxial ribs and furrows well developed; furrows equal to or deeper than adaxial furrows; ribs in form of flat-topped sclerenchyma caps with horizontal prickles at edges interlocking over cleft-like furrow. **Median vascular bundle:** present; midrib or keel not developed. **Vascular bundle arrangement:** 5 1'vbs in blade;

no 2'vbs present; all bundles located nearer abaxial surface. **Vascular bundle structure:** all bundles usually rounded in section although *D. pumila* exhibits a tendency for bundles to be vertically elongated and elliptical; phloem of 1'vbs adjoins inner, thickened sheath; no lysigenous cavity or protoxylem vessels developed; metaxylem vessels extremely narrow (diameter less than adaxial ibs cells), angular and only slightly thickened. **Vascular bundle sheaths:** round in shape in all 3'vbs and most 1'vbs, but in *D. pumila* 1'vb sheaths may be slightly elliptical. Obs always entire with no extensions; comprised of 11–15 cells around 3'vbs and 12–17 cells around 1'vbs; all cells similar in shape, thin-walled and conspicuous but not larger than mesophyll cells. **Sclerenchyma:** abaxial strands well developed in wide, straight, deep bands forming caps on flat abaxial ribs; no sclerenchyma between vbs; fibres thick-walled with lumen narrow; walls stain blue-green with safranin and fast green. **Margin:** sclerenchyma a well developed cap, somewhat pointed; crescent-shaped or fibres may extend abaxially. Sclerenchyma of margin never extends further than directly above and below ultimate vb. Margin without angular prickles. **Mesophyll:** indistinctly radiate; chlorenchyma of elongated, tabular cells relatively loosely and irregularly arranged; air spaces frequent. **Colourless cells:** entirely lacking except for bulliform cells. **Adaxial epidermis:** costal prickles with bases not larger than, and situated between, normal epidermal cells; frequent; hairs slender and elongated, those of *D. pumila* ($\pm 0,10$ mm) about twice the length of those of *D. calvinensis* ($\pm 0,05$ mm); no papillae. **Abaxial epidermis:** outer tangential wall of cells flattened or slightly arched; not papillose.

Abaxial epidermis

Intercostal zones: cleft-like, intercostal, abaxial furrows make study and illustration of cells of this zone difficult. **Intercostal long cells:** length slightly greater than width; parallel-sided; moderate undulations of anticlinal walls. **Stomata:** appear low-dome shaped; 1–2 rows on each vertical wall of cleft-like furrow. **Papillae:** absent. **Prickle-hairs:** interlocking prickles present overlying stomatal furrow; single row of prickles on edge of costal zones. **Micro-hairs:** none observed. **Macro-hairs:** absent. **Silica-bodies:** present throughout costal zone; silica cells alternate with costal short cells.

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ANATOMICAL DESCRIPTIONS OF THE SPECIES

1. *Dregeochloa pumila* (Nees) Conert*Leaf in transverse section*

Leaf outline: U-shaped leaves with base and sides about equal in length or more commonly less inrolled with wide, broad base to U. Width from 3,00 mm to 3,45 mm and thickness from 0,63 mm to 0,70 mm in freshly fixed leaves. Dried herbarium specimens narrower (2,00 mm wide) and thinner (0,30 mm thick). **Ribs and furrows:** adaxial furrows very shallow relative to leaf thickness; furrows narrow and cleft-like in sections from dried herbarium material but with broad bases with relatively steep sides in freshly fixed material. Abaxial ribs taller than adaxial ribs; interlocking prickles well-developed and common. **Vascular bundle arrangement:** 1' vbs separated by single 3'vb except on either side of median vascular bundle where there are two 3'vbs. **Vascular bundle structure:** 3'vb diameter almost same as 1'vbs. **Vascular bundle sheaths:** obs cells rounded or with radial walls straight and tangential walls inflated; translucent, without chloroplasts or with few chloroplasts similar to those of mesophyll. Ibs not distinct around 3'vbs; probably absent; present around 1'vbs; entire, composed of small thickened cells; thickening may be on inner tangential and radial walls or equally on all walls when lumen may become more or less excluded. Adaxial cells of ibs larger than lateral cells; relatively thin walled. **Adaxial sclerenchyma:** small strands developed; shallow sub-epidermal strip or deeper groups of fibres. Strands similar in size over all vbs. **Mesophyll:** indistinctly radiate with chlorenchyma surrounding each individual bundle divided by abaxial furrows and large adaxial bulliform cells. Adaxial chlorenchyma groups narrow and composed of palisade-like cells between adjacent bulliform cell groups. **Adaxial epidermis:** bulliform cells resemble fan-shaped groups with exceptionally large central cell with straight sides occupying more than $\frac{1}{2}$ the leaf thickness. Costal epidermal cells unthickened or with thin cuticle. **Abaxial epidermis:** bulliform cells small, in fan-shaped groups situated at base of furrows; largest bulliform cell not larger than obs cells. Costal epidermal cells with outer wall slightly thickened. Located on sides of adaxial ribs are horizontally projecting prickles with bases not larger than, and situated between normal epidermal cells; barbs thick and relatively very long (0,10 mm), interlocking over furrows.

Abaxial epidermis

Prickles: short, hook-like base; barb long ($\pm 0,10$ mm); barb developed from apex of base; barbs lie at right-angles across abaxial furrows. **Silica bodies:** Round, circular to oblong in shape; sometimes shortly dumb-bell shaped with a wide middle portion (Fig. 8).

Specimens examined

S.W.A.—2615 (Luderitz): 1,6 km south of Luderitz lagoon (-CA), Giess & van Vuuren 653. 2715 (Bogenfels): Pomona (-AB), Dinter 4018.

CAPE.—2816 (Oranjemund): 2 km west of Beauvallon on road to Alexander Bay (-DA), Ellis 2173, 2174: 9 km west of Beauvallon, Tölken 5278.

Discussion

D. pumila is a short (3–10 cm tall), tufted perennial, often forming small, dense, flat cushions up to 15 cm in diameter. It grows in crevices or in loose sand amongst shale-like, schist rocks in a region of extremely low winter rainfall ($\pm 50,0$ mm), but where heavy sea mists occur frequently. It appears to be

restricted to the coastal belt, less than 15 km from the sea, from just south of the Orange River mouth to the Luderitz area in South West Africa (Fig. 13).

This region undoubtedly is a harsh habitat with extremes of temperature, insolation and precipitation. The proximity to the sea has a moderating effect on seasonal temperature range and frequent mists probably offset the lack of rainfall somewhat, but an extremely large diurnal temperature range is to be anticipated on the dark rocks which this plant prefers. However, xerophytic adaptations are not well reflected in the anatomy of the leaf of *D. pumila*. The leaf is not permanently infolded and the usual copious sclerenchyma and thickened cuticle, often correlated with dry localities, is lacking (Figs. 1 and 2). The stomata are, however, restricted to abaxial furrows which are further protected by numerous interlocking prickles. This arrangement must limit excessive water loss to a certain degree. In addition the leaves are very short with a leathery, succulent texture and the plant forms a low, dense cushion. These growth characteristics are commonly found in xerophytes but are exceptional in the Poaceae.

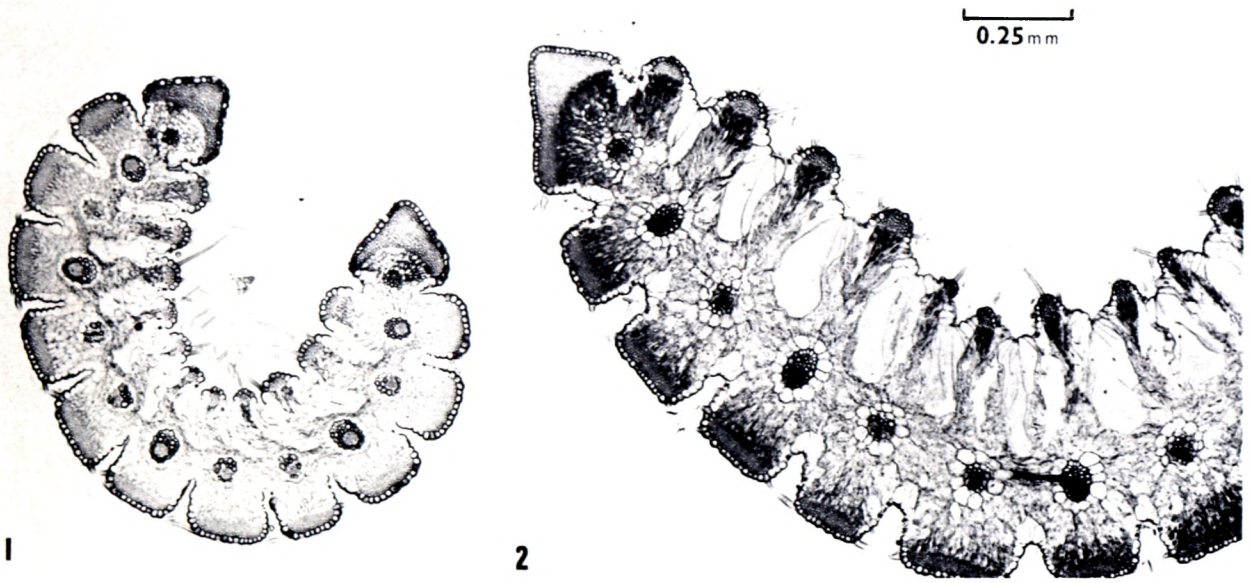
No other members of the Danthonieae are found in the same habitat as *D. pumila* although *Asthenatherum glaucum* (Nees) Nevski and *Merxmüllera rangei* (Pilg) Conert are found in the adjoining sandy areas but they extend further into Namaqualand, the Namib Desert and even the Kalahari in the case of *A. glaucum*. Anatomically these species are easily separated.

Sections taken from herbarium specimens have a somewhat more xerophytic appearance. The adaxial and abaxial furrows are more narrow and cleft-like and the bulliform cells appear reduced in size. In fact, these specimens superficially resemble *D. calvinensis* sections (of which only herbarium material was studied) more closely than fully turgid, freshly fixed specimens of *D. pumila*. This should serve as a caution when anatomical comparisons are made between sections of herbarium and fresh material. Thus, Dinter 4018 (Fig. 1) resembles the sections of *D. calvinensis* (Figs. 9 and 10) and it is only the sequence of the different orders of vascular bundle and the silica bodies and prickly hairs (Figs. 5 and 6) of the epidermis that reveal it to be a typical *D. pumila* specimen.

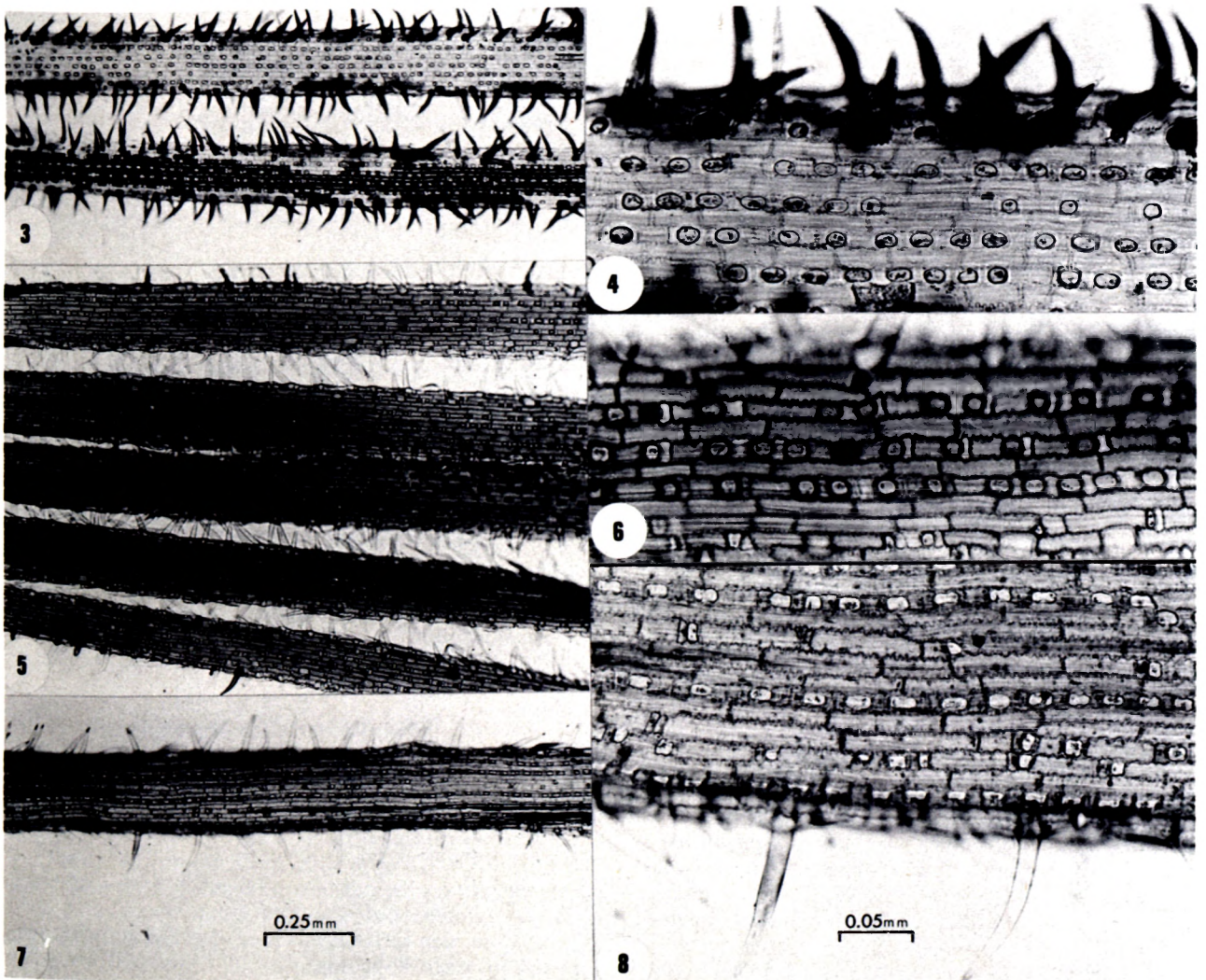
Remarkably little variation in leaf anatomy was evident in the specimens studied which may be expected from a species inhabiting a limited area with uniform climate, and occupying such a specialized niche. This species can readily be recognised by the elongated, deep bulliform cells associated with narrow columns of adaxial chlorenchyma cells, the thickness of the leaf and the abaxial furrows with interlocking prickles.

2. *Dregeochloa calvinensis* Conert*Leaf in transverse section*

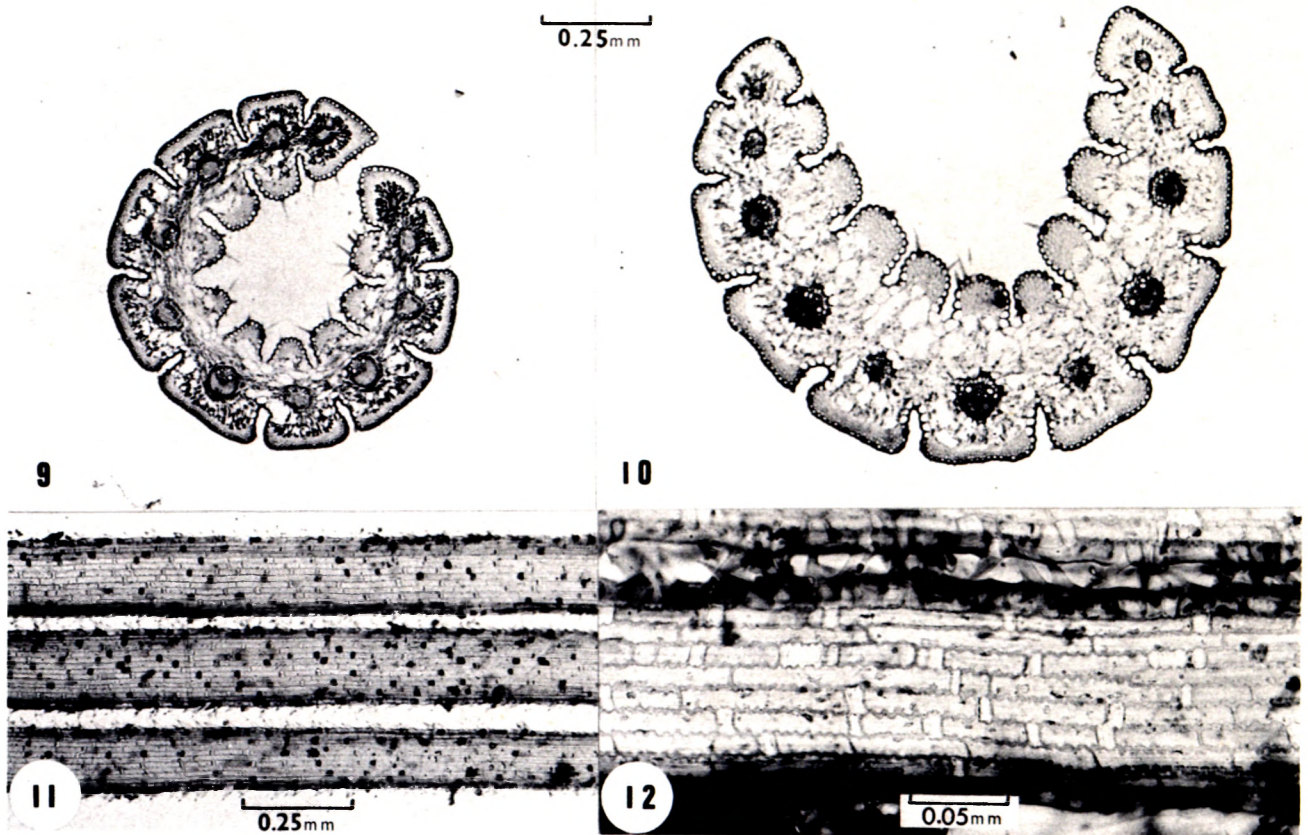
Leaf outline: U-shaped with base and sides equal in length to hollow cylindrical condition where margins almost meet. Generally more tightly inrolled than *D. pumila*; width from 1,60 mm to 2,30 mm in dried material. **Ribs and furrows:** adaxial furrows of medium depth and at least $\frac{1}{4}$ of leaf thickness. (This greater depth may be due to shrinkage in the herbarium material examined). Furrows narrow, cleft-like. Adaxial ribs same height as abaxial ribs although shaped differently; not moniliform; interlocking prickles small and infrequent. **Vascular bundle arrangement:** one 3'vb on either side of the median



FIGS 1 & 2.—*Dregeochloa pumila*: transverse sections of the leaf blade; 1, *Dinter* 4018; 2, *Ellis* 2174.



FIGS 3–8.—*Dregeochloa pumila*: abaxial epidermis; 3 & 4, *Ellis* 2173; 5 & 6, *Dinter* 4018; 7 & 8, *Giess & Van Vuuren* 653.



FIGS 9–12.—*Dregeochloa calvinienensis*. 9 & 10, transverse sections of the leaf blade; 11 & 12, abaxial epidermis. 9, Erasmus s.n.; 10, 11 & 12, Dekkers s.n.

vascular bundle; lateral two 1'vbs adjacent to one another with no 3'vbs present between them. *Vascular bundle sheath*: obs cells inflated and rounded; chloroplasts appear specialized and concentrated near inner tangential wall (Figs. 9 and 10). (This observation needs confirmation using freshly fixed material). Ibs well developed and distinct around both 1' and 3'vbs, complete, composed of small thickened cells often with inner tangential and radial walls markedly thickened. Around 1'vbs the walls of cells adjacent to the phloem very thick with narrow lumen. Adaxial cells of ibs larger than lateral cells of sheath. *Adaxial sclerenchyma*: well developed strand; usually arched following shape of rib; similar over all vascular bundles. *Mesophyll*: indistinctly radiate with the chlorenchyma surrounding each individual bundle being divided by abaxial and adaxial furrows. *Adaxial epidermis*: bulliform cells appear absent, or small and present on sides and bases of furrows (Fig. 10). Costal epidermal cells all with outer wall slightly thickened. *Abaxial epidermis*: bulliform cells absent or only very small; situated on the sides and bases of furrows. Costal epidermal cells with distinct, thick cuticle on outer wall; thickness of cuticle and outer wall being equal to, or greater, than depth of epidermal cell. Interlocking prickles with very short barbs at sides of costal zones.

Abaxial epidermis

Prickles: short, hook-like base; barbs short (± 0.05 mm), developed from apex of base; all barbs point irregularly in direction of leaf apex. *Silica-bodies*: Tall and narrow to square; outline smooth, regular (Fig. 12).

Specimens examined

CAPE.—3019 (Loriesfontein): Handelkraal, E.N.E. of Loriesfontein (-CD), Dekkers s.n. (PRE, iso). 3022 (Carnarvon): Brandewynskuil, between Vosburg and van Wyksvlei (-DB), Erasmus s.n.

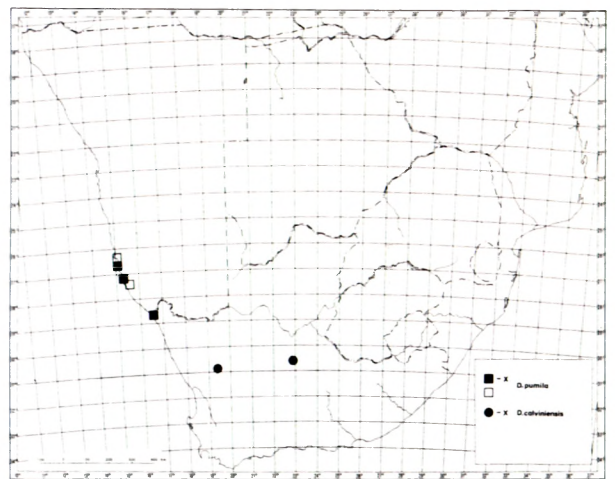


FIG. 13.—Distribution of *Dregeochloa pumila* and *D. calvinienensis* compiled from specimens at the National Herbarium, Pretoria (PRE). X indicates localities of specimens studied anatomically.

Discussion

This rare, perennial species is known only from the above two localities and collections. At Handelkraal, on the margin of the Western Mountain Karroo, it is locally frequent on limestone. In contrast to *D. pumila*, this species forms small, dark green, dense and erect tufts from 15–25 cm high.

Vegetatively *D. calvinienensis* bears little resemblance to *D. pumila*, but the leaf anatomy is strikingly similar as seen in transverse section. Small differences occur in the shape and size of the bulliform cells (this may have been accentuated by the fact that only herbarium specimens were studied), the size and thickening of the epidermal cells and the prickles and possibly the arrangement of the different orders of

vascular bundles. The abaxial epidermis, however, shows important differences, especially in the shape of the silica bodies. Although *D. calvinensis* has tall and narrow silica bodies (Fig. 12) and *D. pumila* circular or oblong bodies (Figs. 4 and 6), both these shapes, and the fact that the silica cells and short cells are solitary or paired, and not in long rows, are typical festucoid characters (Metcalf, 1960). This difference, although striking, can thus be expected even in two closely related taxa.

There appears to be a specialization and a centripetal concentration of chloroplasts in the parenchyma sheath cells of both *D. calvinensis* specimens examined (Figs. 9 and 10) and it is unfortunate that no fresh material was obtained to confirm this. In addition, the mesophyll, which is also poorly preserved, appears to consist of two layers of more or less radially arranged chlorenchyma cells. This configuration is typical of the Kranz syndrome but the $^{13}\text{C}/^{12}\text{C}$ ratios are typical non-Kranz ($\delta = -26, 32$; Dekkers s.n.) as are those for *D. pumila* ($\delta = -25, 93$; de Winter & Giess 6235). The possibility that *D. calvinensis* represents a very early stage in the acquisition (or late stage in the loss) of the Kranz syndrome still exists, and this warrants further investigation. If this is in fact the case then the relationship of *Dregeochloa* to *Asthenatherum*—a Kranz genus in the Danthoniaceae—becomes much clearer.

DISCUSSION AND CONCLUSIONS

In the past the leaf anatomy of this genus has, to a large extent, been misinterpreted. Thus, de Wet (1954) grouped *D. pumila* with the species now included in the genus *Asthenatherum*—all of which have “chloroplasts localized around the bundles.” This, together with morphological criteria, he interpreted as indicating that *D. pumila* belonged to the genus *Asthenatherum*. Jacques-Felix (1962) stated that *D. pumila* had typical panicoid structure and also included this species with *Asthenatherum*. Conert (1962) noted that *D. pumila* did not have elongated radially arranged mesophyll cells. His observations led him to disagree with the above authors and he suggested that *D. pumila* occupied an isolated position in the Danthoniaceae near *Danthonia*.

In a later paper, de Wet (1960) grouped *D. pumila* with those species where the chlorophyll is not localized around the bundles but uniformly distributed throughout the mesophyll and which possess a thin-walled outer bundle sheath. These new observations led him to postulate that *D. pumila* formed a direct link between *Danthonia* and *Asthenatherum*. He was still of the opinion that in all other respects these two genera resembled one another very closely but Conert (1962) noted that the formation of the callus differed in addition to anatomical differences. This influenced Conert's (1962) proposal of an isolated position for *Dregeochloa* (= *D. pumila*).

Certain epidermal features have also been confused. De Wet (1954) described the silica bodies of *D. pumila* as being spherical and stated that micro-hairs were absent. In the 1960 publication de Wet described the

silica bodies as dumbbell-shaped and micro-hairs were observed. In the present study no micro-hairs were found but it must be stressed that, in this genus, the intercostal zones are difficult to preserve and study due to the deep adaxial furrows. On all preparations of *D. pumila* the silica bodies are horizontally elongated and oblong in shape although some silica bodies on Giess and van Vuuren 653 (Fig. 8) have indentations in the centre and could be described as being dumbbell-shaped.

The observations of this study, based solely on leaf anatomy, confirm that these two species closely resemble one another and constitute a unique, distinct group. Their structure is unique amongst the Danthoniaceae and they show little anatomical resemblance to any other South African members of this tribe. This supports Conert's (1966; 1971) conclusions that this genus occupies an isolated position within the tribe. However, *Dregeochloa* has certain similarities in common with *Asthenatherum* (abaxial furrows and prickles, spikelet structure and distribution) which may indicate that these two genera had a common ancestor which gave rise to Kranz and non-Kranz groups. The region where these genera occur is a zone where Kranz genera (*Aristida*, *Stipagrostis*, *Eragrostis* etc.) and non-Kranz genera (*Schismus*, *Karoochloa*, *Chaetobromus* and *Merxmüllera*) are equally abundant. *Dregeochloa* shows no anatomical affinities with the genus *Merxmüllera* (= *Danthonia*) and its removal from *Danthonia* appears justified.

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UITTREKSEL

Die anatomiese struktuur van die blaar in dwarsnee en die abaxiale epidermis van Dregeochloa pumila en D. calvinensis word beskryf en geïllustreer. 'n Genus beskrywing is ingesluit en die verwantskappe van die genus word kortliks bespreek.

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