Bothalia 15, 1 & 2: 153–159 (1984)

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

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Keywords: *Asthenatherum glaucum*, C_4, Danthonieae, Kranz, leaf anatomy

ABSTRACT

The leaf blade anatomy of *Asthenatherum glaucum* (Nees) Nevski was studied. Detailed descriptions of the leaf section and abaxial epidermis are given and illustrated by means of photomicrographs. The leaf anatomy of all specimens is undoubtedly Kranz with radiate chlorenchyma and specialized parenchyma bundle sheath chloroplasts. This observation is the most important justification for separating *Asthenatherum* from *Danthonia*, which has non-Kranz anatomy.

Significant epidermal variation was observed, particularly in the form and occurrence of macro-hairs and prickles. These epidermal differences appear to correlate with geographical distribution and growth form of the plants and may be of infraspecific taxonomic significance. The epidermal variation is continuous, but three more or less distinct groups can be recognized: annual plants with unique macro-hairs with corrugated walls; annual or perennial plants without macro-hairs but with large straight prickles without swollen bases; and perennial plants without these large prickles. These groups appear to represent an intergrading cline along an increasing moisture gradient eastwards from the Namib Desert in South West Africa/Namibia.

INTRODUCTION

Asthenatherum glaucum (Nees) Nevski is a densely tufted, coarse perennial with culms much branched from a stout, woody rhizome (Chippindall, 1955; Conert, 1962; Hubbard, 1970; Launert, 1970). The base of the plant is clothed in cataphylls which may be glabrous and papery or hairy.

All the above authors stress the strong perennial nature of *A. glaucum*, yet in the National Herbarium (PRE) a significant proportion of the collection of this species consists of what are undoubtedly annual plants. These specimens all display inflorescences, although obviously only in their first year of growth and it appears to be quite common for this perennial grass to flower in its first year. In common with many other grasses from arid environments, these neotonous plants apparently behave exactly as short-lived annuals unless sufficient moisture is available to allow the establishment of a plant of sufficient critical mass to overcome the regular periods of drought, which frequently occur in the desert regions it inhabits. This phenomenon has resulted in a certain degree of taxonomic confusion and also led to problems with identification within this genus.

A. glaucum is a hardy species which is obviously well-adapted to climatic extremes of moisture, temperature and insolation. It inhabits the desert and semi-desert areas of the Namib, Namaqualand, the Orange River Broken Veld and the Kalahari Thornveld. This grass favours a loose, sandy substrate and occurs almost exclusively on sand dunes of coarse to fine windblown sand.

In the Namib Desert proper, *A. glaucum* is common on the lower parts of the sand dunes. The annual plants that have been collected all come from the Namib Desert and there appears to be a certain degree of niche separation between plants displaying the annual habit and the perennial specimens. Therefore, most collections of annual specimens have been made from the fine gravel plains in the interdune areas. This observation may be relevant in future taxonomic considerations.

Away from the Namib Desert, *A. glaucum* appears to be restricted to areas of deep, loose, red sand, such as the Kalahari sand dunes. Only plants with a perennial growth form have been recorded from these areas.

Asthenatherum was originally described as belonging to the genus *Danthonia* DC. In 1934 Nevski separated it from *Danthonia*, a decision which has now been generally accepted (Conert, 1962; Launert, 1970; Hubbard, 1970), although Hubbard (1937) originally did not adopt Nevski's genus due to practical considerations. However, he did consider the species that had been transferred to *Asthenatherum* as forming a natural group. Chippindall (1955) also retained the genus *Danthonia* for the species presently assigned to *Asthenatherum*.

Asthenatherum can easily be distinguished from typical *Danthonia* by the presence of a long, pungent callus (Conert, 1971) as well as by the many-nerved glumes separated by a distinct internode and the transverse line of hairs on the lemma (Hubbard, 1970). The most meaningful diagnostic character, however, is the presence of radiate chlorenchyma which no other *Danthonia* species possesses. This characteristic of *Asthenatherum* has been known for almost fifty years (Hubbard, 1937) and constitutes the most important justification for separating *Asthenatherum* from *Danthonia*.

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The generic status of *Asthenatherum** is, therefore, now generally accepted but considerable confusion still surrounds the identity of the species assigned to this genus — this in spite of a detailed study of the whole genus by Conert in 1962. Conert (1962) recognized five taxa in the genus (4 species and 1 variety) of which four were recorded as occurring in southern Africa. Launert (1970) and the National Herbarium (PRE) (L. Smook, pers. comm.) recognize only *A. glaucum* and *A. mossamedense* (Rendle) Conert from South West Africa/Namibia and the *Flora of Southern Africa* region. The variety, *A. glaucum* var. *lasiophyllum* (Pilg.) Conert, has not been accepted. *A. forskalii* (Vahl) Nevski, a species distributed throughout North Africa and the Middle East, but also recorded from southern Angola (Conert, 1962, 1971) is not recognized in the *Flora of South West Africa* (Launert, 1970), although it very possibly occurs in this territory.

Disjunct distributions between many arid area species, which occur in the northern as well as in the southern desert areas of Africa, are well documented (Monod, 1971; De Winter, 1971). *A. forskalii* is considered to be an example of a taxon displaying this distributional phenomenon by the above authors as well as Conert (1971). However, Hubbard (1937) comments that the specimens of *A. forskalii* from Angola possess more deeply-lobed lemmas than those from North Africa and one specimen (*Pearson* 2174) has fulvous hairs on the lemmas. The identity of the Angolan specimens requires verification in the light of this statement and because specimens collected in the extreme north of South West Africa/Namibia, in almost identical habitats to those of Mossamedes further north in Angola, have been determined as being *A. glaucum*. Chippindall (1955) also records *A. forskalii* from South West Africa.

Conert (1962, 1971) considered *A. glaucum* as being endemic to South Africa and this view has been confirmed by Monod (1971) and De Winter (1971). However, Hubbard (1970) records *A. glaucum* from the Turkana Desert in northern Kenya. This observation implies that *A. glaucum* also has a widely disjunct distribution. In addition, it also raises the probability that *A. glaucum* and *A. forskalii* are conspecific. It is remarkable that such uncertainty still exists in a genus which has received considerable taxonomic attention relatively recently.

Two other species are included in the genus: *A. fragile* (Guinet & Sauvage) Monod is another species from North Africa and Arabia and *A. mossamedense* (Rendle) Conert is endemic to South West Africa and Angola (Conert, 1971).

In the present study freshly fixed material of only *A. glaucum* was available for study. Leaf anatomy and epidermal characteristics were determined and compared with the anatomy of several preparations prepared from herbarium material. These specimens had been variously identified as *A. forskalii, A. glaucum* var. *lasiophyllum* and *A. mossamedense*. However, the *A. forskalii* specimens were later determined as being var. *lasiophyllum* by Conert in 1973 but cited as *A. glaucum* by Launert (1970). All the specimens previously quoted as being var. *lasiophyllum* are now considered to be *A. glaucum* by the National Herbarium. This study was consequently restricted to *A. glaucum* with a few comparisons being made with material prepared from herbarium material of *A. mossamedense*. In the anatomical descriptions which follow, the terminology of Ellis (1976, 1979) will be followed and the following abbreviations will be used:

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 *ASTHENATHERUM GLAUCUM* (NEES) NEVSKI

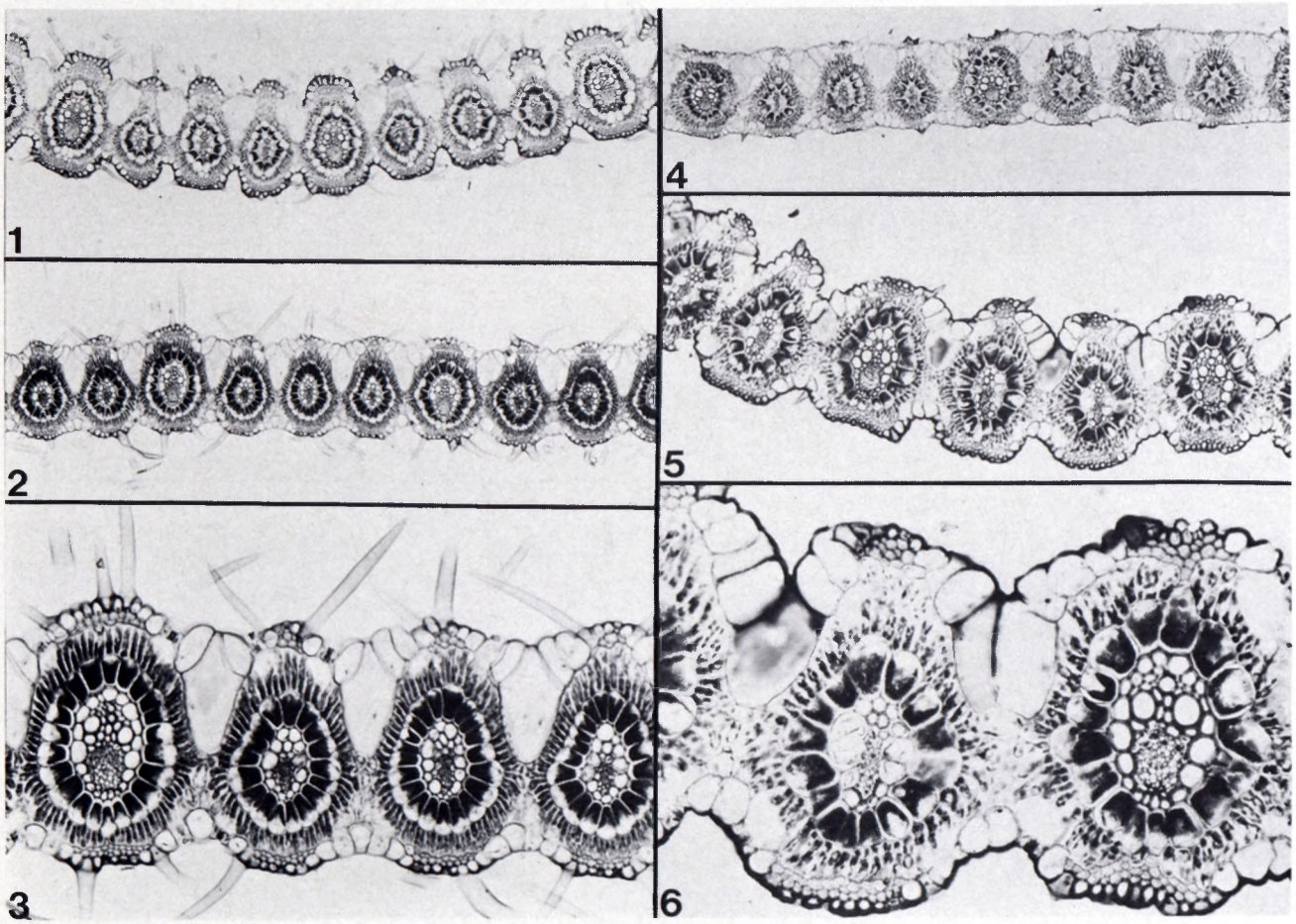
Leaf in transverse section

Leaf outline: broadly U-shaped to expanded and flat; relatively thick (0,30 mm−0,50 mm). *Ribs and furrows:* very slight (Figs 2 & 4) to medium (Figs 1 & 5) adaxial ribs and furrows; furrows between all vbs; adaxial ribs rounded; similar ribs over all vbs. Abaxial ribs and furrows more pronounced than adaxial ones; abaxial ribs somewhat flattened (Figs 1 & 5) and furrows shallow to medium depth. *Median bundle:* not distinguishable structurally from other 1'vbs. *Vascular bundle arrangement:* 7, 9 or 11 1'vbs in section; 3 3'vbs between consecutive 1'vbs (Figs 1−4); seldom 2 (Fig. 5) or 4; no 2'vbs; all vbs centrally located in blade. *Vascular bundle structure:* 3'vbs elliptical to tall and narrow (Figs 3 & 6); well developed xylem and phloem and ibs. 1'vbs elliptical (Figs 3 & 6); phloem adjoins ibs; metaxylem vessels narrow and circular; tend to have smaller diameter than even the ibs cells. *Vascular bundle sheaths:* elliptical to almost rounded; double; both sheaths entire (Figs 1−6); no extensions; parenchyma sheath cells numerous (>15), uniform in size and shape, fan-shaped with straight radial walls and inflated tangential walls (Figs 3 & 6); specialized, centripetal chloroplasts conspicuous (Figs 3 & 6); ibs complete; relatively large, unthickened cells particularly noticeable in 3'vbs (Fig. 3). *Sclerenchyma:* small adaxial strands associated with all vbs (Figs 3 & 6); well developed abaxial strands associated with all vbs; arched, follow shape of ribs (Figs 3 & 6); sometimes with minute contact with obs cells (Fig. 6). Fibres thick walled; cellulose, not lignin, thickening. No sclerenchyma between bundles. Margin with small sclerenchyma cap. *Mesophyll:* radiate chlorenchyma (Figs 3 & 6); tabular cells surround bundles completely (except where girders in contact with bundle sheaths); successive chlorenchyma groups almost completely separated by bulliform cells. No colourless cells associated with bulliform cells. *Adaxial epidermis:* fan-shaped bulliform cell groups with central cell shield-shaped (Fig. 6) or even diamond-shaped (Fig. 3); occupy

* Subsequent to going to press, the name *Asthenatherum* Nevski has been replaced by *Centropodia* Reichb, and the new combinations *C. glauca* (Nees) T.A. Cope and *C. mossamedensis* (Rendle) T.A. Cope have been published by T.A. Cope in *Kew Bull.* 37,4: 657−659 (1983).

about half leaf thickness. Epidermal cell walls unthickened; macro-hairs variable; absent (Figs 4–6) or present (Figs 1–3); slender and elongated; costal; could be classified as prickles; bases superficial (Fig. 3); small hooks present when macro-hairs absent (Fig. 5); no papillae. *Abaxial epidermis:* small fan-shaped bulliform cell groups at bases of furrows; macro-hairs or prickles either absent (Figs 4–6) or common (Figs 1–3); hairs shorter and thicker than adaxial prickles and tend to be interlocking; hooks present on specimens without prickles; no papillae.

intercostal zones of specimens lacking prickles (Figs 10–12); unbarbed asperites may be present in costal zones (Fig. 12). *Micro-hairs:* not observed on any preparation examined. *Macro-hairs:* extremely elongated, unicellular macro-hairs present on some specimens (Figs 13–16); few specialized epidermal cells associated with base (Fig. 16); base of hair constricted and somewhat superficial (Fig. 14); unique unrecorded type of hair with corrugated cell walls; can be abundant or absent altogether; always associated with specimens with prickles that resemble short macro-hairs; never with specimens with



FIGS 1–6.—*Asthenatherum glaucum:* transverse sections of the leaf blade. 1–3, form with well developed epidermal prickles. 1, *Ellis* 2141, × 100; 2, *Ellis* 2178, × 100; 3, *Ellis* 2178, × 250. 4–6, form without elongated epidermal prickles. 4, *Ellis* 872, × 100; 5, *Ellis* 3605, × 160; 6, *Ellis* 3605, × 400.

Abaxial epidermis in surface view

Intercostal long cells: elongated, side walls parallel; slightly undulating particularly in areas adjoining costal zones (Figs 11 & 12); prickles or hooks between long cells (Figs 8 & 9, 11 & 12). *Stomata:* low to tall dome-shaped (Figs 9, 11 & 12) stomata present in all files of intercostal cells; interstomatal cells elongated; 1 or 2 between successive stomata in a file. *Intercostal short cells:* absent except those associated with hooks on edges of zone (Fig. 11). *Papillae:* no papillae present. *Prickles:* large, straight, sharp-pointed without swollen bases; resemble short macro-hairs; interlocking over intercostal zones (Figs 7–9); not found on all specimens; both costal and along the margins of the costal zones. *Hooks:* small, sharp-pointed hooks in hooks only. *Silica bodies:* vertically elongated (Figs 9 & 12) to cuboid (Figs 9 & 11) and even dumb-bell shaped (Figs 11 & 16); occur throughout costal zones; sometimes associated with cork cells; often not.

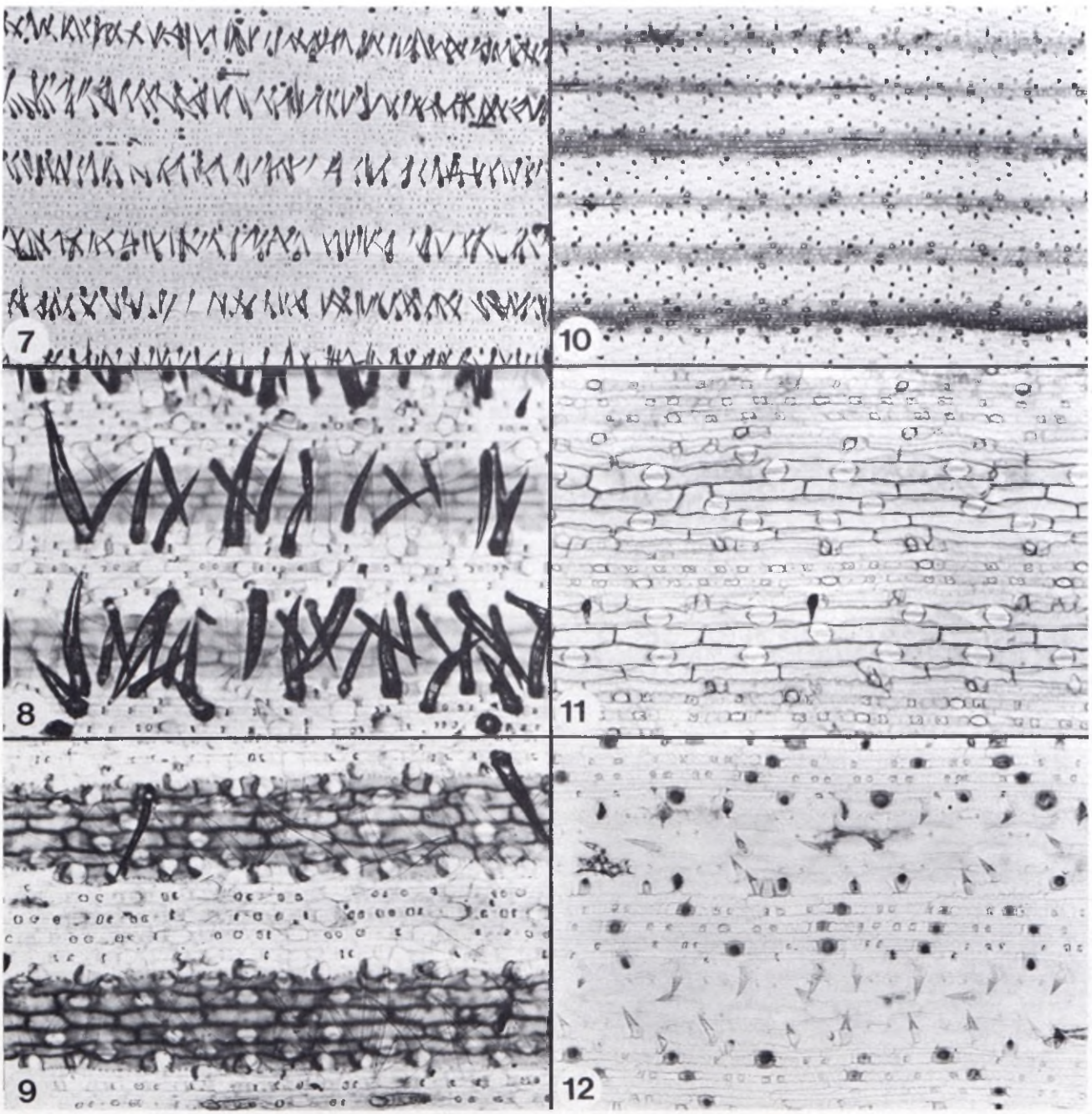
Specimens examined:

A. glaucum

S.W.A. — 2314 (Sandwich Harbour): Gobabeb Research Station, Namib (–BD), *Koch s.n.*; S of Kuiseb River at Gobabeb, *Jensen 163*; Strey 2593**. 2419 (Aranos): Farm Bethel, E of Aranos (–BD), *Van Vuuren & Giess 1124+*. 2615 (Luderitz):

* Specimens personally determined by H. J. Conert in 1973 as being *A. glaucum* var. *lasiophyllum.*

+ Specimens with reduced prickles on both epidermides.



FIGS 7–12.—*Asthenatherum glaucum:* abaxial epidermis in surface view. 7–9, form with well developed epidermal prickles. 7, *Ellis* 2139, × 100; 8, *Ellis* 2178, × 250; 9, *Ellis* 2177, × 250. 10–12, *A. glaucum* form with small epidermal hooks. 10, *Ellis* 872, × 100; 11, *Ellis* 872, × 250; 12, *Van Vuuren & Giess* 1124, × 250.

120 km W of Aus on road to Luderitz (–DB), *De Winter & Hardy 7890**.

CAPE. — 2816 (Oranjemund): 2 km W of Beesbank on road to Alexander Bay (–DA), *Ellis 2177, 2178, 2179*. 2822 (Glen Lyon): Matsap (–DB), *Ellis 3605*+. 2919 (Pofadder): 21 km E of Pofadder on road to Kakamas (–BA), *Ellis 2139, 2140, 2141, 2142*. 2921 (Kenhardt): 12 km from Kakamas turn-off on Kenhardt-Upington road (–AC), *Ellis 872*+; 15 km from Kenhardt on Kakamas road, *Botha & Panagos* 21+.

A. mossamedense

S.W.A. — 1812 (Sanitatas): Orupembe waterhole (–BA), *De Winter & Leistner 5725*. 2016 (Otjiwarongo): 112 km W of Welwitschia on road to Torra Bay (–AA); *De Winter & Hardy 8152*. 2115 (Karibib): 300 km W of Windhoek at Khomas Hochland-Swakopmund junction (–DD), *De Winter & Hardy 8021*.

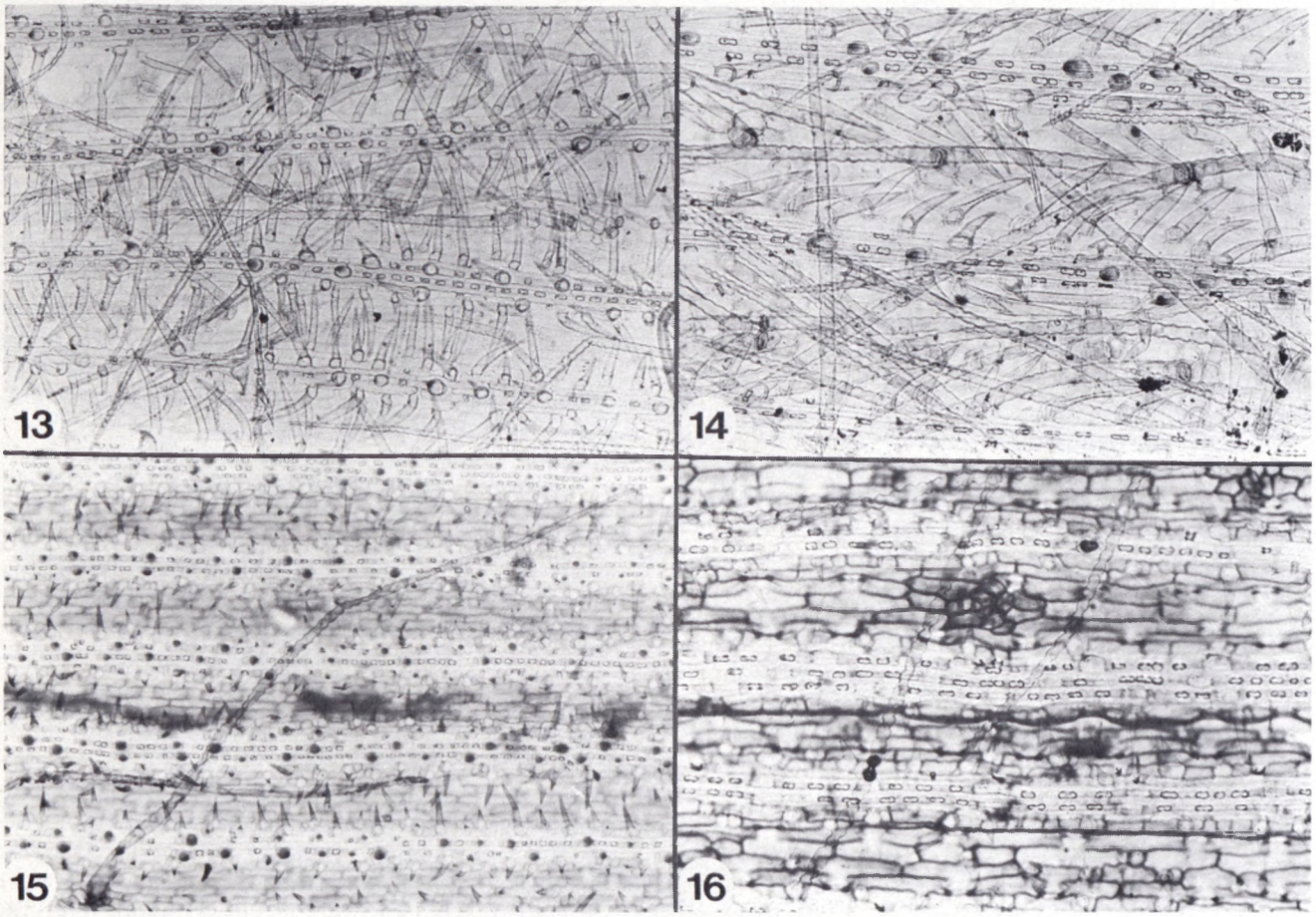
* Specimens personally determined by H. J. Conert in 1973 as being *A. glaucum* var. *lasiophyllum*.

\+ Specimens with reduced prickles on both epidermides.

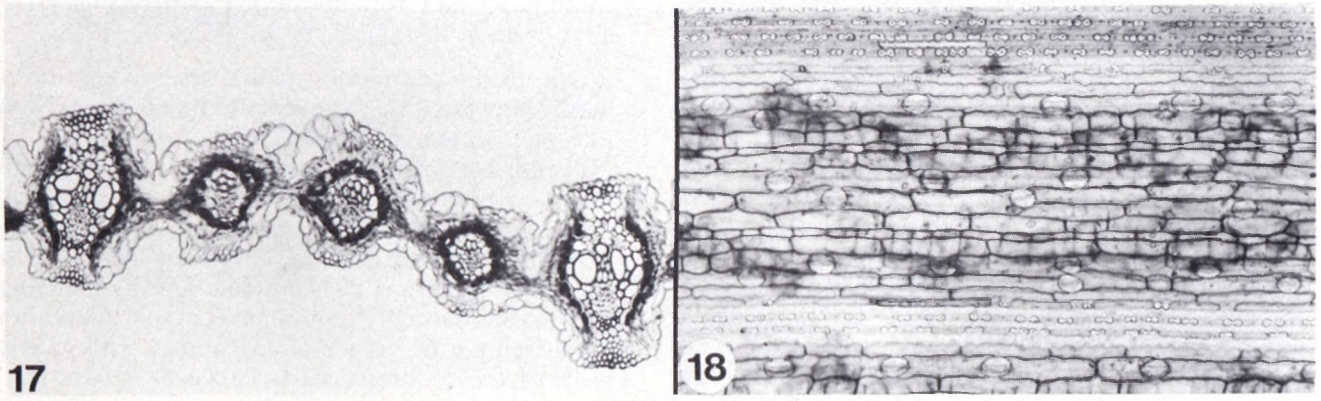
DISCUSSION AND CONCLUSIONS

Taxonomically the most significant features of the leaf anatomy of *A. glaucum* are the radially arranged chlorenchyma and the specialized chloroplasts in the outer bundle sheath cells. This characteristic Kranz anatomy implies that *A. glaucum* possesses the C_4 photosynthetic pathway. This has been confirmed by the determination of $^{12}C/^{13}C$ ratios of representative specimens ($\delta = -15{,}1‰$, Ward 161; $\delta = -14{,}1‰$, Leistner 2006). These ratios are typical of C_4 grasses and corroborate the anatomical indications.

A. mossamedense also has Kranz anatomy (Fig.



FIGS 13–16.—Abaxial epidermis of *Asthenatherum glaucum* var. *lasiophyllum* specimens with elongated macro-hairs. 13–14, *Jensen* 163; 13, × 160; 14, × 250. 15 – 16, *Strey* 2593; 15, × 160; 16, × 250.



FIGS 17–18.—Anatomy and epidermal structure of *Asthenatherum mossamedense, De Winter & Leistner* 5725. 17, × 250, leaf in transverse section; 18, × 250, abaxial epidermis.

17) and a C_4 $^{12}C/^{13}C$ ratio ($\delta = -12{,}6‰$, De Winter & Hardy 8021). The anatomy of *A. forskalii* is similar to that of *A. glaucum* (Conert, 1962) and, therefore, it can be concluded that *Asthenatherum* is a Kranz genus which exhibits the C_4 pathway.

This observation is important because, in the Danthonieae, virtually all genera are non-Kranz (Brown, 1977; Renvoize, 1981) and the C_4 pathway is primarily associated with all the genera of the Eragrostoideae and most of the Panicoideae. Of the African representatives of the Danthonieae, De Wet (1956) considered both *Asthenatherum* and *Alloeochaete* to have panicoid anatomy and, consequently, to be C_4. Brown (1977) followed De Wet but did not actually examine any material of *Alloeochaete*. When this was done by Renvoize (1981), this genus was found to have non-Kranz anatomy. *Asthenatherum* is, therefore, the only South African genus of the Danthonieae which is Kranz and, consequently, is of particular phylogenetic significance.

On a worldwide basis, *Asthenatherum*, together with *Pheidochloa* of Australia, are the only C_4 genera of the Danthonieae recognized by Brown (1977). Renvoize (1981) widened the concept of this tribe (which he included in the Arundineae) and incorporated several other Kranz genera such as

Triraphis, *Eriachne* and *Neyraudia*. In the sub-family Arundinoideae, *Aristida* and *Stipagrostis* are additional C_4 genera placed in the tribe Aristideae (Renvoize, 1981).

The classification of *Asthenatherum* is, therefore, critical to a better understanding of the derivation of the Kranz syndrome and the taxonomy of this interesting genus requires careful consideration. The Arundinoideae, with the predominance of the C_3 photosynthetic pathway, their rather limited ecological success and their unspecialized spikelet morphology appear to be a relatively primitive group (Renvoize, 1981) and may have given rise to some of the more modern sub-families. They probably evolved from the ancestral grass type before the other major sub-families became established and from these pioneer Arundinoideae the grasses radiated into the three most successful groups extant today (Renvoize, 1981).

The leaf anatomy of *Asthenatherum*, with a Kranz outer, parenchymatous sheath with centripetally arranged chloroplasts resembles many of the Eragrostoideae, some Paniceae and *Stipagrostis* (Brown, 1977; Ellis, 1977). In the Eragrostoideae these Kranz parenchyma sheath cells are, in paradermal view, short and radially wide, whereas in *Asthenatherum* they are longer than they are wide (Brown, 1974). In addition, the silica cells of the Eragrostoideae differ considerably from those of *Asthenatherum* and any affinities with this sub-family appear remote. *Panicum* species with centripetal chloroplasts also have short and radially wide Kranz cells and differ from *Asthenatherum* in this respect. *Stipagrostis*, however, has elongate Kranz sheath cells which resemble those of *Asthenatherum*. This observation supports the placement of both these genera in the same sub-family.

Micro-hairs are uniform in shape and consistent in occurrence and provide useful characters in grass classification (Renvoize, 1981). De Wet (1954) considered bicellular micro-hairs to be absent in *A. glaucum* and *A. forskalii* but noted their presence on *A. mossamedense*. Unfortunately no micro-hairs were observed on the epidermis of any of the 18 specimens of *Asthenatherum* examined in this study (including 3 of *A. mossamedense)*. They, therefore, appear to be of very infrequent occurrence. Fortunately Palmer & Tucker (1981) give very clear scanning electron photomicrographs of micro-hairs on both the abaxial and adaxial epidermis of *A. glaucum* (*Rains & Yalala* 22, Botswana). These micro-hairs are finger-like with a noticeably longer basal cell. The apical cell is much shorter, usually deflated and with a rounded apex.

The ratio of distal to basal cell length, together with the rounded apex, are similar to the condition in the danthonoid grasses studied by Tateoka *et al.* (1959) and appears to lend weight to the classification of *Asthenatherum* in the Arundinoideae. This micro-hair shape is definitely not of the eggshape type characteristic of the Eragrostoideae and the rounded apex makes panicoid relationships unlikely. *Stipagrostis* also has a more tapering distal cell than illustrated for *A. glaucum*.

Leaf anatomy, therefore, does not appear to suggest alternative affinities for *A. glaucum* and it seems to be best placed in the Arundinoideae together with the danthonoid grasses. However, the presence of the Kranz syndrome in *Asthenatherum* implies that, in the Danthonieae, the Kranz syndrome must have evolved at least once and probably on several independent occasions to produce *Pheidochloa* and the other genera currently classified with the danthonoid group. Eragrostoideae, on the other hand, probably all derive from a single evolution of the syndrome.

Within the Danthonieae, *Asthenatherum* appears to occupy an isolated and peripheral position. Its closest relative is apparently *Dregeochloa*, with which it shares certain anatomical characters (Ellis, 1977a). *Dregeochloa*, is a non-Kranz genus, however, but does share similar desert habitats, in the Namib and Namaqualand, with *Asthenatherum*.

Considerable variation in epidermal structure was observed within the sample of *A. glaucum* specimens studied. Structures which contributed to this variation were the unique corrugated macro-hairs which were either present or absent and the length of the interlocking prickle hairs. These were sometimes reduced to unbarbed appendages or even typical hooks. The quantitative nature of the presence of macro-hairs represents a continuum with the hairs being either abundant (Figs 13 & 14), infrequent (Figs 15 & 16) or absent (Figs 7–12). Similarly, variation in prickle hair length is continuous and well-developed barbs (Figs 7–9) intergrade with typical hooks (Figs 10–12).

Due to the continuous nature of the variation of these characters, there appears to be no justification for recognition of infraspecific taxa within *A. glaucum*. Nevertheless, it seems that the epidermal variation observed represents a definite ecological trend associated with a moisture gradient from the very arid Namib eastwards into the Kalahari. This clinal variation may not be taxonomically meaningful, but undoubtedly represents ecotypic adaptation to differing environmental conditions. The genetic basis of these differences is, however, unknown.

Three groups within *A. glaucum* can be recognized on the basis of this epidermal structure. The first group possesses long macro-hairs with corrugated walls as well as interlocking prickles (Figs 13–16). It must be noted, however, that the epidermal preparations examined in this study were prepared from the mid-lamina region of the leaf blade and only the abaxial surface was studied. Nevertheless, the specimens that possessed these unique macro-hairs had all been determined by Conert (1962) as being var. *lasiophyllum* using these hairs as a diagnostic criterion. It must be pointed out, however, that these hairs occur on the leaf sheaths of many of the *A. glaucum* specimens examined in this study but are absent on the leaf blades. However, those specimens with cushion hairs on the blades are all genuine annual plants and occur only in the true

Namib Desert where they are found in the fine gravel soils of the dune strates.

A. glaucum specimens with interlocking prickles but lacking cushion hairs (Figs 7–9) are usually perennial plants but may flower in their first year of growth and thus appear annual. They also occur in the Namib Desert but seem to favour the lower parts of sand dunes in a sandy substrate. This form also has a wider distribution than the first, occurring southwards as far as Namaqualand and the Orange River Broken Veld and extending eastwards into the pre-Namib areas. Away from the Namib Desert proper, only perennial plants have been collected.

Further to the east, in the Kalahari and northern Cape, *A. glaucum* is restricted to Kalahari dunes on deep, loose, red sand. All these plants are densely tufted perennials. Specimens collected from these areas show a considerable reduction in the length of the interlocking prickles which, in these cases, can only be termed intercostal hooks and unbarbed costal asperites (Figs 10–12).

Superficially the epidermal structure of these three groups is distinct but it must be remembered that they gradually intergrade into one another and the variation is not disjunct. Recognition of infraspecific taxa does, therefore, not seem justified but cognizance of this variation must be taken for purposes of microscopic identification for applied purposes.

A. mossamedense was not studied in detail during this study because no freshly fixed material was available. However, the leaf anatomy appears to be similar to that of *A. glaucum* (Figs. 17) with the epidermis exhibiting a further reduction in the presence of prickles until they are totally absent (Fig. 18). Some specimens have numerous unbarbed costal prickles. In this respect, *A. mossamedense* may merely represent a continuation of the reduction trend described in *A. glaucum*. It is distinct morphologically, however, (Conert, 1962), and the silica bodies are much more regularly dumb-bell shaped than in *A. glaucum* and, consequently, its specific status is not questioned.

ACKNOWLEDGEMENTS

The author is grateful to Miss H. Botha for technical assistance, to Mrs A. J. Romanowski for the photography and Mrs S. M. Thiart for typing the manuscript. Dr J. C. Vogel of the Natural Isotopes Division, NPRL, CSIR, kindly did the $^{12}C/^{13}C$ determinations.

UITTREKSEL

Die anatomiese struktuur van Asthenatherum glaucum *(Nees) Nevski blare is bestudeer. Beskrywings van die blaaranatomie in dwarssnee en van die abaksiale epidermis word gegee en geïllustreer deur middel van fotomikrograwe. Alle monsters wat ondersoek is, toon duidelike Kranz anatomie met chlorenchiem radiaal gerangskik en gespesialiseerde chloroplaste in die parenchiem bondelskede. Hierdie waarneming regverdig die skeiding van* Asthenatherum *vanaf* Danthonia *wat nie-Kranz anatomie toon.*

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