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Leaf anatomy of the South African Danthonieae (Poaceae). XVIII. *Centropodia mossamedensis*

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ABSTRACT

The leaf blade anatomy of *Centropodia mossamedensis* (Rendle) T. A. Cope [= *Asthenatherum mossamedense* (Rendle) Conert] is described and illustrated. This description is based on freshly fixed material and confirms that this species has Kranz anatomy with the C_4 photosynthetic pathway. The anatomy differs little from that of *C. glauca* and both undoubtedly belong to the same genus which is justifiably separated from the other danthonoid genera.

UITTREKSEL

Die blaaranatomie van *Centropodia mossamedensis* (Rendle) T. A. Cope [= *Asthenatherum mossamedense* (Rendle) Conert] word beskryf en geïllustreer. Hierdie beskrywing is gebaseer op vars gefikseerde materiaal en bevestig dat hierdie spesie die Kranz-tipe anatomie en C_4-fotosintese besit. Die blaaranatomie wyk weinig af van dié van *C. glauca* en albei spesies behoort ongetwyfeld aan dieselfde genus. Hierdie studie bevestig dat *Centropodia* van die ander genera in die Danthonieae geskei behoort te word.

INTRODUCTION

In a previous paper (Ellis 1984) in this series the anatomy of *Centropodia mossamedensis* (Rendle) T. A. Cope [= *Asthenatherum mossamedense* (Rendle) Conert] (Cope 1983) was briefly described. This description was based on herbarium material and the anatomical preparations were not of a very high quality. Subsequent to the above study, fresh material of *C. mossamedensis* was collected and fixed in the field, yielding good quality leaf blade transverse sections. The results are described, illustrated and compared with the leaf anatomy of *C. glauca* (Nees) T. A. Cope [= *Asthenatherum glaucum* (Nees) Nevski].

MATERIALS AND METHODS

Plants of *C. mossamedensis* were collected in South West Africa/Namibia. Herbarium voucher specimens were prepared for verification by the National Herbarium (PRE) where they are now housed.

Leaf blade segments were removed and immediately fixed in FAA. Leaf blade transverse sections and abaxial epidermal scrapes were prepared following the methods outlined in a previous paper in this series (Ellis 1988).

The standardized terminology of Ellis (1976, 1979) was used for the anatomical descriptions together with the following abbreviations:

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

Specimens examined:

Centropodia mossamedensis

SWA/NAMIBIA.—2014 (Welwitschia): Damaraland, 60 km W of Khorixas on road to Skeleton Coast (–AB), *Ellis 4750*. 2116 (Okahandja): Okahandja Dist.; 26 km W on road to Swakopmund, Otjitundu River crossing (–DD), *Ellis 4725, 4726*.

ANATOMICAL DESCRIPTION OF *CENTROPODIA MOSSAMEDENSIS*

Leaf in transverse section

Leaf outline: expanded and flat lamina (Figure 1A & E). *Ribs and furrows*: very slight adaxial ribs (Figure 1B & F); slight furrows between all vbs; ribs rounded. Abaxial ribs and furrows more pronounced than adaxial ones (Figure 1B & F); furrows between all vbs and ribs rounded. *Median vascular bundle*: structurally indistinguishable from lateral 1'vbs. *Vascular bundle arrangement*: 9 or 13 1'vbs in leaf section: 3, 4 or 5 3'vbs between consecutive 1'vbs except laterally where fewer 3'vbs are present (Figure 1A & E); 2'vbs absent; all vbs centrally located in blade. *Vascular bundle structure*: 3'vbs slightly elliptical with well developed xylem and phloem tissue and an ibs (Figure 1B, C & F); 1'vbs elliptical (Figure 1B, C & F); phloem adjoins the ibs; metaxylem vessels narrow, with a diameter slightly less than that of the obs cells; diameter greater than that of the ibs cells. *Vascular bundle sheaths*: double; slightly elliptical to almost rounded; both sheaths entire around all vbs (Figure 1C); no extensions although a few Kranz cells may be located outside the outer sheath (Figure 1C); parenchyma sheath cells very numerous (15–26), regular in size and shape, fan-shaped with straight radial walls and inflated outer tangential walls; specialized, large, centripetally situated chloroplasts conspicuous; ibs complete around 1' and 3'vbs; cells with slight secondary thickening. *Sclerenchyma*: small adaxial girders associated with all 1'vbs and strands with the 3'vbs; taper toward the bundles; similar abaxial girders and strands

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rated by short cells or stomata. *Stomata*: low dome-shaped (Figure 1D & G); not in regular files and occur in most long cell files; 1 or 2 interstomatal cells between successive stomata in a file. *Intercostal short cells*: absent or very rare (Figure 1D) or irregular (Figure 1G); no cork or silica cells but just very short epidermal cells. *Papillae*: absent. *Prickles*: costal, either very common (Figure 1D & H) or rare (Figure 1G); barbs either well developed or virtually absent. *Hooks*: absent. *Microhairs*: present on all specimens but rare (Figure 1H); both cells elongated but distal cell not tapering to a pointed apex; two cells about equal in length. *Macrohairs*: absent. *Silica bodies*: variable, irregular dumbbell-shaped (Figure 1G), short and narrow (Figure 1H) or horizontally elongated rectangular (Figure 1D); occur throughout costal zones; sometimes associated with cork cells but often not.

DISCUSSION AND CONCLUSIONS

The transectional leaf anatomy compares very closely with that of *C. glauca* (Ellis 1984). Both are undoubtedly Kranz with radiate mesophyll, and no chlorenchyma cells are more than one cell distant from a Kranz cell. This indicates the presence of the C_4 photosynthetic pathway which is confirmed by a $12_C/13_C$ ratio of $-12{,}6$ ‰ *(De Winter & Hardy 8021)*. The outer bundle sheath has a regular outline and is Kranz with centripetally located specialized chloroplasts. This structure is typical of that characteristic of the NAD-me subtype of the C_4 photosynthetic pathway but this has yet to be confirmed as *Centropodia* has not yet been biochemically typed (Hattersley 1987).

Anatomical differences between *C. mossamedensis* and *C. glauca* are only minor, particularly the leaf in transverse section. Vessel element diameter is proportionally greater in *C. mossamedensis* where they are slightly wider than the inner bundle sheath cells but they are, nevertheless, still relatively narrow. The bulliform cells occupy less than half the leaf thickness in *C. mossamedensis* but in *C. glauca* they are equal to at least half the leaf thickness. In transection no elongated prickle hairs are evident as in many *C. glauca* specimens.

Superficially the abaxial epidermis differs considerably from that of *C. glauca*. No interlocking prickles resembling macrohairs are present and the unique macrohairs with corrugated cell walls, as in *C. glauca* var. *lasiophyllum*, were not observed.

These epidermal differences are visually very striking but it must be remembered that *C. glauca* exhibits continuous anatomical variation from those specimens with conspicuous interlocking prickle hairs to specimens without this hair type (Ellis 1984). This variation pattern is associated with an ecological cline from the extremely arid Namib Desert eastward to the Kalahari. The anatomy of *C. mossamedensis* appears to be a northward expression of this cline along a moisture gradient and *C. mossamedensis* may merely represent a continuation of this reduction trend evident in *C. glauca*.

The two species are distinct morphologically (Conert 1962) and also appear to occupy different niches. *C. glauca* is a species of the loose red sands of the Kalahari dunes whereas *C. mossamedensis* is confined to gravelly or coarse waterborne sands in dry watercourses. Their separation at species level is, therefore, not questioned by this study even though these two species do not exhibit significant leaf anatomical differences.

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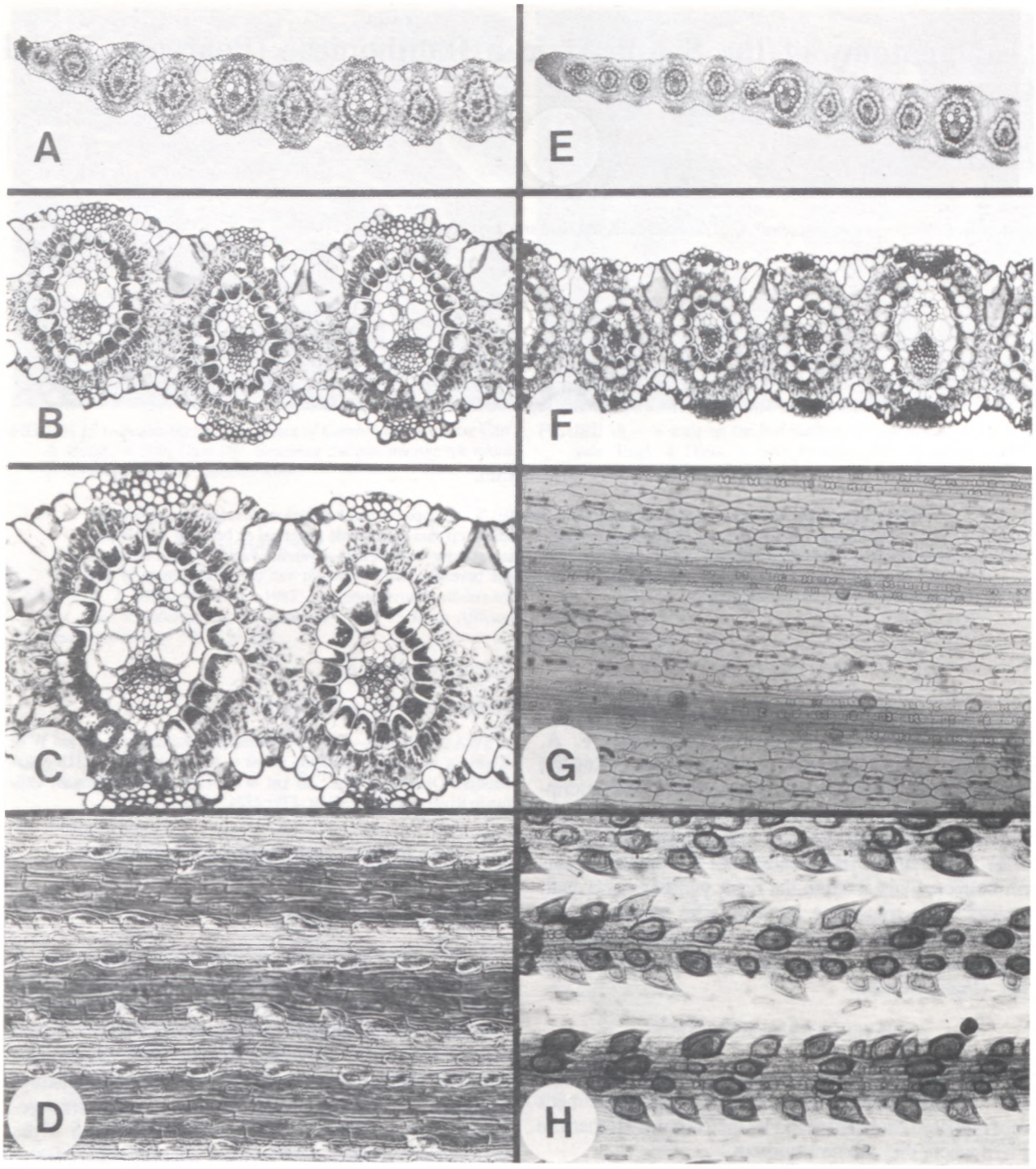

FIGURE 1.—Leaf anatomy of *Centropodia mossamedensis*. A–D, *Ellis 4726*: A, outline of flat, expanded blade, × 100; B, transectional anatomy, × 250; C, anatomical detail showing Kranz anatomy with centripetal specialized parenchyma sheath chloroplasts, × 400; D, abaxial epidermis with costal prickles and intercostal stomata, interference contrast, × 250. E–G, *Ellis 4750*: E, blade outline, × 100; F, Kranz transectional anatomy, × 250; G, abaxial epidermis with few costal prickles, × 250. H, *Ellis 4725*, abaxial epidermis with well developed prickles and intercostal microhairs, × 250.

associated with all vbs except that strands sometimes also associated even with 1'vbs (Figure 1B & C); fibres thick-walled (Figure 1F) or thin-walled (Figure 1B & C) but never lignified. No sclerenchyma between bundles. Small sclerenchyma cap in margin. *Mesophyll*: radiate chlorenchyma (Figure 1B, C & F); single layer of tabular cells surround bundles completely (Figure 1B & C) or with small interruptions due to girders (Figure 1F); lateral cell count 2 or 3. No colourless cells associated with the bulliform cells. *Adaxial epidermis*: fan-shaped bulliform cell groups with central cell shield-shaped; occupy less than half the leaf thickness; epidermal cells with slightly thickened outer walls; macrohairs not present; small costal hooks present (Figure 1B) or absent (Figure 1F); no papillae. *Abaxial epidermis*: small bulliform-like cells at bases of furrows; macrohairs absent; costal prickles present (Figure 1B) or absent (Figure 1F); no papillae.

Abaxial epidermis in surface view

Intercostal long cells: elongated with side walls almost parallel (Figure 1D) to inflated, fusiform (Figure 1G); walls not sinuous; cells adjoin one another or sepa-