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Leaf anatomy of the South African Danthonieae (Poaceae). XVI. The genus *Urochlaena*

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ABSTRACT

The leaf blade anatomy of *Urochlaena pusilla* Nees is described and illustrated. The transectional anatomy is non-Kranz with diffuse but uniformly distributed chlorenchyma. The abaxial epidermis has dome-shaped stomata, dumbbell-shaped silica bodies, elongated finger-like microhairs, and cushion-based macrohairs may or may not be present. This type of arundinoid anatomy closely resembles that of *Tribolium* Desv., *Chaetobromus* Nees, *Schismus* Beauv., and certain species of *Pentaschistis* Stapf. *Urochlaena pusilla* is very similar to *Tribolium utriculosum* (Nees) Renv. in leaf anatomy and these two species appear to be closely related.

UITTREKSEL

Die blaaranatomie van *Urochlaena pusilla* Nees word beskryf en geïllustreer. Die anatomie in dwarssnee is nie-Kranz met 'n verspreide maar eweredige samestelling van die chlorenchiem. Die abaksiale epidermis het koepelvormige huidmondjies, murgbeenvormige silikaliggaampies, langwerpige, vingeragtige mikrohare, en makrohare met baie gespesialiseerde epidermisselle aan die basis kan aanwesig of afwesig wees. Hierdie tipe anatomie is kenmerkend van die Arundineae en toon ooreenkomste met dié van *Tribolium* Desv., *Chaetobromus* Nees, *Schismus* Beauv., en sekere species van *Pentaschistis* Stapf. Wat blaaranatomie betref, is *Urochlaena pusilla* baie soortgelyk aan *Tribolium utriculosum* (Nees) Renv. en hierdie twee spesies blyk nou verwant te wees.

INTRODUCTION

Urochlaena Nees is a monospecific genus containing the single species *U. pusilla* Nees, a small annual characterized by a dense spike-like panicle embraced by the inflated uppermost leaf sheath. At maturity the culm disarticulates at the uppermost node, complete with the inflorescence and modified upper sheath, and this whole structure acts as a dispersal unit (Chippindall 1955; Clayton & Renvoize 1986).

Urochlaena is endemic to the Western Mountain Karoo and the Succulent Karoo of the Vanrhynsdorp, Nieuwoudtville and Calvinia Districts of the Cape Province of South Africa. This restricted distribution range is typified by poor soils, low winter rainfall (150 mm or less per annum), and a low karroid dwarf shrub vegetation with very few perennial grasses (Acocks 1975).

The classification of *Urochlaena* has been somewhat inconsistent during the last 30 years. It was initially placed in the Eragrosteae (Chippindall 1955) but its relationships are now considered to lie with the Arundinoideae. Loxton (1976) and Watson *et al.* (1986) include *Urochlaena* in the Danthonieae and Clayton & Renvoize (1986) place it in the Arundineae in which tribe the Danthonieae are included.

Urochlaena pusilla appears to be most closely related to *Tribolium utriculosum* (Nees) Renv. (= *Lasiochloa utriculosa* Nees) (Chippindall 1955; Clayton & Renvoize 1986). Both are small annuals from the drier, northwestern parts of the winter rainfall region, with *T. utriculosum* extending further northwards into Namaqualand. *T. utriculosum* always has hairy leaf blades but those of *Urochlaena pusilla* are either hairy or glabrous except at the bearded sheath mouth (Chippindall 1955).

Little information is available on the leaf anatomy of *Urochlaena*. De Wet (1960) notes that the anatomy is festucoid but that the epidermis is panicoid. Watson *et al.* (1986) note that the anatomy is C_3 without arm and fusoid cells. The microhairs are of the panicoid type, being linear in shape, and the silica bodies are also of the panicoid type, being dumbbell-shaped. It is the purpose of this paper to describe and illustrate the leaf blade anatomy of *Urochlaena* and to compare its structure with that of the other South African danthonioid grass species.

MATERIALS AND METHODS

Plants of *Urochlaena pusilla* were collected in the field in the Nieuwoudtville and Vanrhynsdorp Districts. Herbarium voucher specimens were prepared for verification by the National Herbarium (PRE) where they are housed. Leaf segments were immediately fixed in FAA (Johansen 1940).

Transverse sections, 10 μm thick, were prepared after desilicification in 30 % hydrofluoric acid (Breakwell 1914), dehydration following the method of Feder & O'Brien (1968) and embedding in Tissue Prep (Fischer Scientific). The sections were stained in safranin and fast green (Johansen 1940). The manual scraping method of Metcalfe (1960) was used to prepare scrapes of the abaxial epidermis. The anatomical structure was recorded photographically using a Reicherdt Univar microscope and Ilford Pan F film.

In the anatomical descriptions which follow, the standardized terminology of Ellis (1976, 1979) will be used, 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

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Specimens examined:

Urochlaena pusilla

CAPE.—3118 (Vanrhynsdorp): Vanrhynsdorp (−DA), *Ellis 5346, 5347*. 3119 (Calvinia): Pakhuis Pass, 61 km N of Clanwilliam (−CA), *Ellis 1724;* Botterkloof Pass, 42 km N of Clanwilliam (−CD), *Ellis 2449, 4629*.

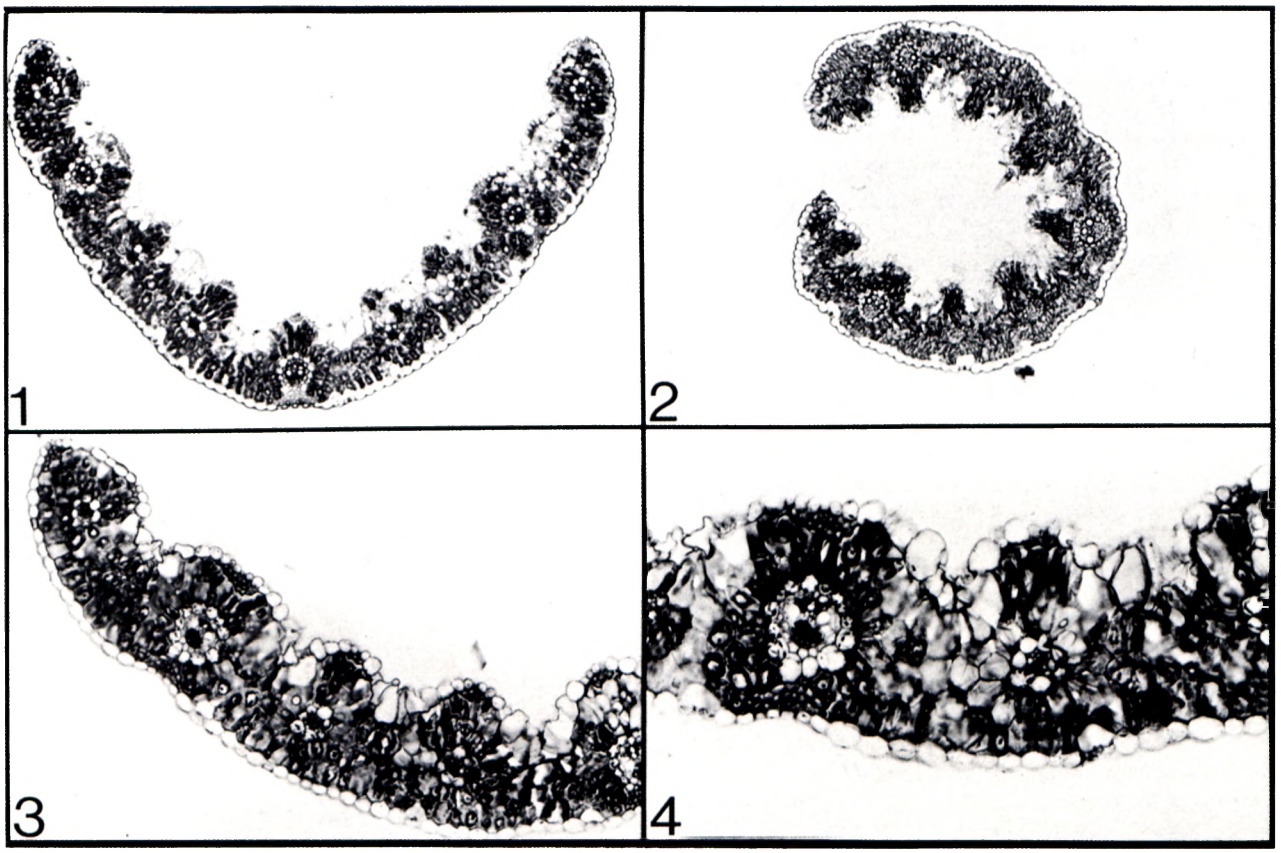
ANATOMICAL DESCRIPTION OF THE GENUS *UROCHLAENA*

Leaf in transverse section

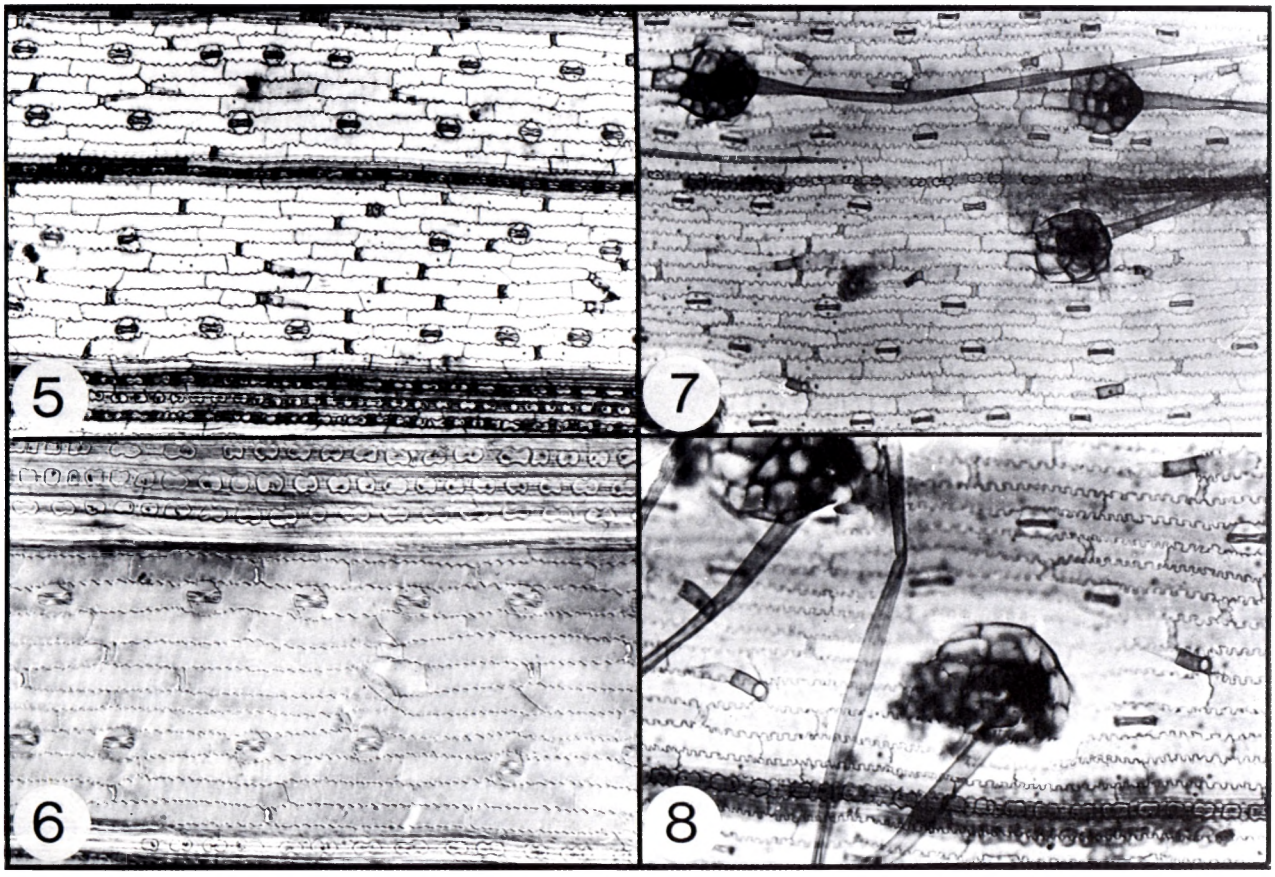
Outline: open, either expanded or variously inrolled, U-shaped (Figures 1 & 2); blade narrow (± 2 mm wide) and ± 200 μm thick. *Ribs and furrows*: rounded adaxial ribs present over all vbs (Figures 1 & 2); furrows shallow and wide (Figure 3). Abaxial surface without undulations associated with the vbs. *Median vascular bundle*: no structurally distinct midrib present (Figures 1 & 2). *Vascular bundle arrangement*: 3 1'vbs in leaf section; 2 3'vbs between consecutive 1'vbs; no 2'vbs. All vbs located in the centre of the blade (Figures 3 & 4). *Vascular bundle description*: 1' and 3'vbs rounded although 3'vbs may tend to be angular in outline (Figure 4); phloem adjoins ibs; metaxylem vessels with very narrow lumens, inconspicuous and less than half the diameter of the obs cells (Figure 4). *Vascular bundle sheaths*: obs round, complete, with no extensions; cells very small, the largest being abaxially located (Figure 4); irregular in size, with thin walls and contain small, unspecialized chloroplasts. Ibs entire, without thickened secondary walls. *Sclerenchyma*: small adaxial strands associated with all vbs (Figure 3); those of the 1'vbs larger than those of the 3'vbs which consist of only 2 or 3 fibres; abaxial girders associated with the 1'vbs only; trapezoidal in shape (Figure 4). Minute sclerenchyma cap in leaf margin (Figure 3). Fibres not lignified. *Mesophyll*: chlorenchyma nonradiate with no pattern of arrangement (Figure 4); diffusely arranged with many air spaces; the chlorenchyma cells parenchymatous, rather large but irregular in size and shape; lateral cell count greater than four. No colourless cells present. *Adaxial epidermal cells*: groups of small bulliform cells located at the bases of the furrows; occupy less than ¼ of the leaf thickness; epidermal cells thin-walled; few prickles associated with the adaxial ribs (Figure 2). *Abaxial epidermal cells*: thin-walled, slightly inflated with a thin cuticle; no epidermal appendages visible.

Abaxial epidermis in surface view

Intercostal long cells: elongate rectangular; anticlinal walls unthickened and slightly to moderately undulating (Figures 6 & 8); cell shape and size constant throughout intercostal zones (Figures 5 & 7); long cells adjoin one another or separated by single short cells (Figures 5 & 7). *Stomata*: dome-shaped subsidiary cells (Figures 5−8); either evenly distributed throughout intercostal zones in the hairy specimens (Figures 7 & 8) or in 1 or 2 rows laterally situated in the intercostal zones in specimens lacking macrohairs (Figures 5 & 6); stomatal files separated by more than one file of intercostal long cells; one interstomatal long cell between successive stomata. *Intercostal short cells*: solitary, tall and narrow cork cells present between long cells (Figure 5); common but not present between all adjoining long cells. *Papillae*: absent. *Prickles*: absent. *Microhairs*: bicellular hairs common and conspicuous; basal and distal cells about equal



FIGURES 1–4.—Leaf transections of *Urochlaena pusilla*. 1, *Ellis 2449*, slightly infolded outline, × 160; 2, *Ellis 1724*, inrolled outline, × 160; 3–4, *Ellis 2449*: 3, lateral part of lamina showing mesophyll and vascular bundle arrangement, × 250; 4, detail of vascular bundles and diffuse chlorenchyma, × 400.



FIGURES 5–8.—Abaxial epidermis of *Urochlaena pusilla*. 5–6, *Ellis 2449*: 5, costal and intercostal zones showing stomatal distribution, × 160; 6, interference contrast showing dumbbell-shaped silica bodies, stomata and intercostal long cells, × 400. 7–8, *Ellis 1724*: 7, macrohairs with cushion bases, × 250; 8, detail of macrohair bases, microhairs and silica bodies, × 400.

in length, both cells elongated, finger-like, the hair length being about twice that of the stomatal complexes (Figure 8); located between long cells, particularly in the central files of the intercostal zones. *Macrohairs*: either present (Figures 7 & 8) or absent (Figures 5 & 6), unicellular, flexible with raised cushion bases of many specialized epidermal cells (Figure 8); common in intercostal zones only. *Silica bodies*: short dumbbell-shaped bodies with wide central portions and rounded ends predominate (Figures 6 & 8); somewhat irregular in shape; confined to costal zones; granules present in silica bodies. *Costal zones*: silica cells alternating with short costal cells (Figures 6 & 8); files with silica cells alternate with files of elongated, rectangular costal long cells; costal zones of 3, 5 or 7 files.

DISCUSSION AND CONCLUSIONS

The leaf anatomy, as described here, agrees with the anatomical details given by De Wet (1960). The transectional anatomy of *Urochlaena* is typically 'festucoid' whereas the abaxial epidermis is panicoid in several respects. The outer bundle sheath consists of a single layer of small, inconspicuous parenchyma cells which do not contain specialized chloroplasts. The chlorenchyma is uniformly and diffusely distributed throughout the mesophyll between the bundles, with no definite pattern of arrangement and with a lateral cell count greater than four. This structure is typical of the non-Kranz anatomy of the pooid grasses and *Urochlaena* undoubtedly is C_3 as reported by Watson *et al.* (1985). The abaxial epidermis, on the other hand, differs significantly from the pooid type. Microhairs are present, the silica bodies are dumbbell-shaped and not nodular, the long cells have sinuous and not straight walls and the stomata are dome-shaped and not parallel-sided. No pooid grass is known to possess microhairs (Watson *et al.* 1985) and those of *Urochlaena* are of the panicoid type, being elongated finger-like. The leaf anatomy, therefore, indicates arundinoid affinities and is in full agreement with the classification of the genus in the Arundineae (Clayton & Renvoize 1986).

The anatomy of *Urochlaena*, with a uniformly distributed and diffuse chlorenchyma of typical parenchyma cells with large intercellular air spaces and an epidermis with stomata and microhairs, resembles that of some other danthonioid genera from South Africa. Examples are *Tribolium* Desv., *Chaetobromus* Nees, *Schismus* Beauv., *Karroochloa* Conert & Türpe and some species of *Pentaschistis* Stapf. The anatomy of these taxa differs significantly from other Cape danthonioid genera such as *Merxmuellera* Conert, *Pentameris* Beauv., *Pseudopentameris* Conert and other *Pentaschistis* species. All these taxa have acicular leaves in which the chlorenchyma consists of small isodiametric cells which are compactly arranged with very small air spaces. The abaxial epidermis also usually lacks stomata and microhairs, and zonation is not evident. This latter type of anatomy has been described in most of the previous papers of this series (Ellis 1980a, 1980b, 1983, 1985a, 1985b, 1985c, 1986).

These two different anatomical types appear to be associated with differing ecological conditions. Danthonioid grasses with acicular leaves and compact mesophyll are all mountain fynbos species growing in oligotrophic soils derived from Table Mountain Sandstone. The unique vegetation of this veld type is characterized

by sclerophyllous leaves, and this anatomical type may reflect an equivalent response by these grass taxa to these particular environmental conditions. *Urochlaena* and the other danthonioid grasses with diffuse mesophyll, on the other hand, favour more fertile soils, such as those of the lowland fynbos and Renosterveld, those derived from granite in the Namaqualand region and several of the Karoo veld types. The Mediterranean pooid exotics, which have a very similar transectional anatomy, have also colonized this latter type of environment. Among danthonioids it is only in taxa with the latter type of anatomy that annuals occur, *Urochlaena* being an example.

Although the leaf anatomy of these two ecological groupings of danthonioid grasses is distinct, it is difficult to ascribe phylogenetic significance to the differences. *Pentaschistis* is the only genus which includes both anatomical types and which has species occurring in both these environments. However, the taxonomy of *Pentaschistis* is very poorly understood and it would be unwise to draw phylogenetic conclusions from these observations. These two different environments, however, may have exserted diverging evolutionary pressures on these two groups of danthonioid grasses; the relationships of *Urochlaena* may therefore reasonably be sought among danthonoid grasses with diffuse mesophyll.

Indeed, the leaf anatomy of *Urochlaena pusilla* resembles that of *Tribolium utriculosum* and *T. echinatum* (Thunb.) Renv. very closely indeed. Both always have prominent cushion-based macrohairs which are often also present on *U. pusilla*. In all other respects the leaf anatomy of these taxa is virtually identical and their affinities appear to lie with each other.

This conclusion based solely on anatomy, is corroborated by morphological indications. Chippindall (1955) and Clayton & Renvoize (1986) suggest that *U. pusilla* and *T. utriculosum* are closely related because both have tubercle-based hairs as well as capitate hairs on the glumes and lemmas. In *T. echinatum* the hairs of the glumes are slender and tapering. *T. utriculosum* has the inflorescence partly enclosed in the uppermost leaf sheath, a condition developed further in *U. pusilla*.

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