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COMPARATIVE ANATOMICAL STUDIES IN DANThONIA SENSU LATO (DANThONIEAE: POACEAE)

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ABSTRACT

Leaf anatomy and lodicule micromorphology were examined for representative species of Danthonia, 12 of its segregate genera, Cortaderia, and Schismus. Major conclusions are: 1) Generic status for the segregates Centropodia, Dregeochloa, Monachather, and Pseudopentameris is supported; these genera appear isolated in the Danthonieae. 2) Rytidosperma appears to be distinct from Danthonia s.s., and from Chionochloa. 3) Suggested close relationships between Merxmuellera and Chionochloa, and between Chionochloa and Cortaderia, are not supported. 4) Karroochloa and Schismus appear to be closely related. 5) Danthonia cachemyriana and D. exilis may be more closely related to Karroochloa than to Danthonia s.s.

Key words: Danthonieae, Gramineae, Poaceae, Danthonia, Rytidosperma, leaf anatomy, lodicules.

INTRODUCTION

Danthonia s.l. comprises well over 100 named species distributed throughout both hemispheres (Conert 1971; Wright 1984). The species are typically characterized by a two-lobed lemma with a geniculate awn arising from between these lobes; the awn is divided into a basal, often dark-colored and tightly spirally twisted portion and an apical, straight or only slightly twisted part. There are two to many florets per spikelet, and the glumes are equal to or longer than the spikelet. This combination of characters occurs in a broad array of grasses.

Danthonia was placed in the tribe Aveneae by early authors (Hooker 1867; Bentham 1881; Stapf 1934; Hitchcock 1951), based on floret number, glume length, and the form of the awns. Two subtribes of Aveneae were generally recognized by these same authors: the Aveninae, mainly Northern Hemisphere species with membranous ligules and lemmas awned from the middle of the back, and the Danthoninae, primarily Southern Hemisphere taxa with ciliate ligules and lemmas awned from an apical notch. Comparative cytological investigations of Avdulov (1931) and leaf anatomical studies by Prat (1932, 1936) were followed by numerous other nontraditional studies (Reeder 1957; Brown 1958; Tateoka 1954, 1957, 1967; inter alia) which led to the realization that the division in the Aveneae was fundamental, and validated Hubbard’s (1948) description of the tribe Danthonieae as a separate entity. This arrangement was further substantiated by Hilu and Wright (1982), who showed on the basis of UPGMA cluster analysis that the arundinoid-danthonioid grasses were distinct from the festucoid group.

DeWet (1954, 1956, 1960) pointed out that Danthonia itself was heterogeneous for a variety of features which had been used in recognizing tribes and subfamilies among the grasses. For example, features of leaf anatomy such as the arrangement and shape of the silica bodies and the structure of the mesophyll, as well as the chromosome base number, were found to differ among the species. DeWet therefore suggested that Danthonia represents a polyphyletic assemblage. Over a dozen
genera have since been segregated from *Danthonia* by various authors (summary in Wright 1984). Most of these have been retained in the Danthonieae. However, the validity of these segregate genera and their relationship to other genera in the Danthonieae remain obscure.

In addition, the delimitation of the Danthonieae itself is problematic. Superficially, the genera of the Danthonieae appear to form a distinctive group. However, upon closer examination, the tribe can be seen to have extremely close ties to the Arundineae, and in fact may be inseparable from it (Renvoize 1982). The closeness of the relationship is particularly evident in the genera *Chionochloa* (Danthonieae) and *Cortaderia* (placed in the Arundineae by most authors, but in the danthonioaid group by Clifford and Watson [1977]). Indeed, *Danthonia archboldii* Hitchc. from New Guinea was placed in *Cortaderia* by Connor and Edgar (1974), and transferred to *Chionochloa* by Conert (1975c), who apparently was unfamiliar with Connor and Edgar's paper. A major impediment to the understanding of relationships within the Danthonieae is the fact that *Danthonia* and its segregates have never been monographed on a worldwide basis, although a number of major regional works have been accomplished: Conert (1971: Africa), Connor and Edgar (1979: New Zealand), DeWet (1954, 1956, 1960: selected species, worldwide), Nicora (1973: Argentina and Chile), Vickery (1956: Australia), and Zotov (1963: New Zealand).

Thus, despite considerable study, the phylogenetic and taxonomic relationships within this group of grasses remain obscure. As part of a study aimed at elucidating these complex relationships, I examined the leaf anatomy and lodicule micromorphology of representative species of *Danthonia* s.s. and 14 of its segregate genera.

**MATERIALS AND METHODS**

Leaf anatomy and lodicule micromorphology were examined for 93 species representing 15 genera (Table I). A complete list of specimens examined is on file in the libraries at RSA and at MO. In addition to taxa comprising *Danthonia* s.l., species of *Cortaderia* and *Schismus* were investigated for comparative purposes. Although never included within *Danthonia*, a close relationship between these two genera and *Danthonia* has been suggested by several authors (Conert 1961; Clifford and Watson 1977; Wright 1984).

From herbarium specimens to be prepared for anatomical investigation I selected leaf material from a section approximately midway along the blade of mature leaves. Flag leaves on flowering culms were not used. The leaf material was first soaked in a 5% solution of Conrad 70 for approximately 24 hr, thoroughly rinsed in water, placed in a weak (ca. 5%) solution of acetic acid in 50% ethanol for 24–48 hr, and then stored in 50% ethanol until examined (Schmid and Turner 1977).

Preparations of the lower epidermis were made by placing the soaked leaf material on a microscope slide and scraping away the upper epidermis and mesophyll with a razor blade until only the lower epidermis itself remained (Metcalfe 1960). The preparation was then mounted in Hoyer's solution (Johansen 1940) so that the outer surface of the epidermis faced the cover slip. Hoyer's solution has a sufficiently high refractive index to reveal silica bodies, and has the additional advantage of being water-soluble, yet permanent.
Table 1. Species examined.

| Dregiochloa: D. pumila (Nees) Conert. |
| Erythranthera: E. australis (Petrie) Zotov, E. pumila (Kirk) Zotov. |
| Karroochooa: K. curva (Nees) Conert & Türe, K. purpurea (L. f.) Conert & Türe, K. tenella (Nees) Conert & Türe. |
| Monachather: M. paradoxo Steud. |
| Monostachya: M. oreoboloides (F. Muell.) Hitchc. |
| Plinthanthesis: P. paradoxo (R. Br.) S. T. Blake. |
| Pseudotentamis: P. brachyphylla (Stapf) Conert, P. macrantha (Schrad.) Conert. |
| Pyrrhantthera: P. exiguo (Kirk) Zotov. |
| Schismus: S. arabicus Nees, S. barbatus (L.) Thell., S. inermis (Stapf) C. E. Hubbard, S. scaberimus Nees. |

Leaf sections were cut freehand with a razor blade, stained with safranin and counterstained with fast green using Northen’s variation of Foster’s method (Johansen 1940), dehydrated through an alcohol series to xylene, and mounted in Coverbond. Lodicules were dissected from the florets in a drop of alcohol and mounted in Hoyer’s solution. Slides are deposited at RSA.

RESULTS

Terminology used in descriptions of leaf anatomical features follows Ellis (1976, 1979) whenever possible. One major departure, however, is in the description of the shape of the adaxial and abaxial sclerenchyma. Ellis described the sclerenchyma and bundle sheaths separately, whereas I found that in most of the taxa examined these two types of cells intergrade, making any distinction between the two structures arbitrary and frequently misleading.

Stomatal subsidiary cell shape was recorded for most taxa. All shapes were
within the triangular to dome-shaped category; however, the range of shapes within a species and even within a given specimen was great. Furthermore, I was unable to detect meaningful differences between taxa. Another feature examined was the shape and size of the microhairs on the leaf surface. Again, the range of variation within and between species was quite large. In addition, the apical cells of microhairs are only rarely preserved intact in herbarium material, and thus uniform comparisons cannot be made. For these reasons, information on subsidiary cell and microhair shape is not included in the taxon descriptions.

Centropodia

*Leaf transection.*—Adaxial furrows generally wide and open; adaxial ribs present, rounded, similar in shape over all vascular bundles (VBs). Midrib absent. VBs round to elliptical. Outer bundle sheath (OBS) complete, cells much larger than parenchyma cells, conspicuous. Inner bundle sheath (IBS) cell walls not thickened, or very slightly and evenly thickened. Metaxylem vessels much smaller than OBS cells. Phloem not divided. Adaxial and abaxial sclerenchyma associated with all VBs, as strands (abaxially T-shaped in *C. glauca*). Bundle-sheath extensions (BSE) and colorless cells absent. Mesophyll poorly preserved in available material, but reported by DeWet (1954, 1956) to be radiate. Upper epidermal cells unspecialized; syringe-shaped prickle hairs (Fig. 1) absent. Bulliform cells in fan-shaped groups with the center cell enlarged and penetrating deeply into the mesophyll (Fig. 3).

*Leaf abaxial epidermis.*—Microhairs apparently absent. Intercostal long-cell side walls difficult to observe because they lie in deep grooves overarched by prickles, but apparently parallel, with interlocking undulations. Costal short cells mainly paired, with rounded or occasionally cross-shaped silica bodies.

*Lodicule morphology.*—Lodicule preparations unavailable.

Chionochloa

*Leaf transection.*—Adaxial furrows narrow clefts; adaxial ribs present and similar over all VBs, rounded or flat topped (massive [Fig. 4] in *C. frigida*). Midrib present (absent in *C. frigida* and *C. rigida*). Primary VBs round to elliptical (egg shaped in *C. bromoides* and *C. rubra*); secondary VBs round to elliptical. OBS incomplete below (complete in *C. rubra*), cells equal to or smaller than parenchyma cells, generally inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller or larger than OBS cells. Phloem not divided. Adaxial sclerenchyma present over all VBs, T- or anchor shaped (girder in *C. beddiei*, girder narrower toward the bundle in *C. frigida*); abaxial sclerenchyma present under all VBs, T- to anchor shaped or forming girders. BSE present adaxially, present or absent abaxially. Colorless cells present as BSE only, or a layer of colorless, usually silica-filled cells present just above the lower epidermis. Mesophyll not radiate or indistinctly radiate. Upper epidermis composed of broadly papillate cells (Fig. 5); syringe-shaped prickle hairs absent. Bulliform cells absent.

A number of species show a more or less complete abaxial band of subepidermal sclerenchyma. Zotov (1963) used this as a key character; however, the degree of completeness appears to vary within species.
Fig. 1-6.—1. *Merxmuella macowanii*, leaf XS. Syringe-shaped prickle hairs.—2. *M. macowanii*, leaf XS. Phloem evenly divided by fibers into two groups of conductive strands; syringe-shaped prickle hairs.—3. *Monachather paradoxa*, leaf XS. Bulliform cell groups with center cell enlarged and penetrating deeply into mesophyll.—4. *Merxmuella papposa*, leaf XS. Massive ribs and extensive development of colorless cells.—5. *Chionochloa bromoides*, leaf XS. Broadly papillate upper epidermal cells.—6. *Merxmuella macowanii*, lower epidermis. W-shaped undulations of intercostal long-cell walls. (Fig. 1-5: bar = 50 μm; Fig. 6: bar = 10 μm.)
Abaxial leaf epidermis.—Microhairs apparently absent. Intercostal long-cell side walls parallel; undulations U-shaped (W-shaped [Fig. 6] in *C. beddiei* and sometimes in *C. rigida*). Costal short cells paired, with rounded silica bodies. Zotov (1963) reported dumbbell-shaped silica bodies in *C. bromoides*. In contrast, I found only elongate, rounded silica bodies.

Lodicule morphology.—Lodicules cuneate to diamond shaped or apically lingulate (Fig. 7), hairy (glabrous in *C. rigida* and occasionally in *C. rubra*). Microhairs present in *C. beddiei*, *C. flavescens*, *C. frigida*, and *C. rigida*, 2–4 celled; absent in *C. bromoides*, *C. conspicua*, and *C. pallens*.

Danthonia s.s. (including Sieglingia)

Leaf transection.—Adaxial furrows broad and open or steep sided; adaxial ribs present, rounded or flat topped, generally similar in shape over all VBs. Midrib present or absent. Primary and secondary VBs round or occasionally egg shaped. OBS generally incomplete, sometimes complete above, cells equal to or smaller than parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller or larger than outer bundle-sheath cells. Phloem not divided (divided into two even groups [Fig. 2] in *D. cirrata*, *D. malacantha*, and *D. montana*). Adaxial sclerenchyma present over all VBs (absent over third-order VBs in *D. chaseana*, *D. cirrata*, and occasionally in *D. sericea*); T- or anchor shaped or forming girders; abaxial sclerenchyma present under all VBs or lacking under third-order VBs; T- or anchor shaped or forming girders. Adaxial and abaxial BSE present or absent. Colorless cells absent or present only as BSE (a few colorless, generally silica-filled cells sometimes present in mesophyll in *D. parryi*, *D. domingensis*, and *D. montevidensis*). Mesophyll not radiate (sometimes inconspicuously radiate in *D. intermedia* and *D. cirrata*). Upper epidermal cells generally unspecialized (somewhat enlarged in *D. montana*, *D. dusenii*, and occasionally in *D. secundiflora* and *D. montevidensis*; broadly papillate in *D. chaseana*); syringeshaped prickle hairs absent. Bulliform cells present as simple fan-shaped groups (absent in *D. chaseana*).

Abaxial leaf epidermis.—Microhairs present (none seen in *D. unispicata*, *D. chaseana*, and *D. malacantha*). Intercostal long-cell side walls parallel or bowed, with variously shaped undulations. Costal short cells usually in long rows (mainly paired in *D. domingensis*, *D. cirrata*, and *D. malacantha*); costal silica bodies cross to dumbbell shaped.

Lodicule morphology.—Lodicules generally cuneate, glabrous (hairy, diamond shaped with thinner apical portion in *D. shrevei*), and without microhairs. A single, 2-celled microhair was found on one otherwise typical lodicule of *D. alpina*. This appears to be an abnormal development, but more extensive investigation should be conducted.

Danthonia cachemyriana and *D. exilis*

Leaf transection.—Adaxial furrows broad and steep sided or narrow clefts; adaxial ribs present, rounded, similar over all VBs. Midrib present or absent. VBs round to elliptical. OBS incomplete, cells equal to or smaller than parenchyma cells, inconspicuous. IBS cells unevenly thickened. Metaxylem vessels smaller than (*D.*
exilis) or larger than (D. cachemyriana) OBS cells. Phloem not divided. Adaxial and abaxial sclerenchyma associated with all VBs, T- to anchor shaped in D. cachemyriana; lacking in association with third-order VBs in D. exilis, forming strands adaxially and girders narrower toward the bundles abaxially. BSE and colorless cells lacking. Mesophyll not radiate. Upper epidermal cells unspecialized or slightly enlarged; syringe-shaped prickly hairs absent. Bulliform cells present as simple fan-shaped groups.

*Leaf abaxial epidermis.*—Microhairs present in D. cachemyriana, not seen in D. exilis. Intercostal long-cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

*Lodicule morphology.*—Lodicules cuneate, hairy, with 2–3 celled microhairs.

**Dregeochloa**

*Leaf transection.*—Adaxial furrows wide, shallow, open; adaxial ribs present, similar over all VBs, very tall and narrow, rounded to flat topped. Midrib absent. VBs round or elliptical. OBS complete, cells larger than parenchyma cells, conspicuous. IBS not thickened. Metaxylem vessels smaller than OBS cells. Phloem not divided. Adaxial and abaxial sclerenchyma associated with all VBs, forming strands. BSE and colorless cells absent. Mesophyll indistinctly radiate. Upper epidermal cells unspecialized; syringe-shaped prickly hairs absent. Bulliform cells present, center cell very large, straight sided; bulliform groups occupying more than half the leaf thickness.

*Leaf abaxial epidermis.*—Microhairs not seen. Intercostal long cells difficult to observe because of deep abaxial grooves between veins overarched by prickles; side walls apparently parallel, straight or slightly undulating. Costal short cells mostly paired or in short rows, silica bodies cross to dumbbell shaped.

*Lodicule morphology.*—Lodicule preparations unavailable; lodicules reported by Conert (1966) to be cuneate and glabrous.

**Erythranthera**

*Leaf transection.*—Adaxial furrows wide, open (E. pumila) or broad, steep sided (E. australis); adaxial ribs present, similar over all VBs, rounded (E. pumila) or flat topped (E. australis). Midrib present. VBs round to elliptical. OBS incomplete above and below, cells smaller than or equal to parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma forming girders, lacking over third-order VBs; abaxial sclerenchyma forming girders narrower toward bundles, lacking under third-order VBs. BSE absent. Colorless cells apparently absent. Mesophyll not radiate. Upper epidermal cells rounded, slightly inflated (E. pumila) or broadly papillate (E. australis); syringe-shaped prickly hairs absent. Bulliform cells absent.

*Leaf abaxial epidermis.*—Microhairs present. Intercostal long-cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped (E. australis) or rounded (E. pumila) silica bodies.

Available leaf material of E. pumila was poorly preserved and leaf transection
preparations unclear, so observations of this species are ambiguous. Epidermal preparations were adequate.

*Lodicule morphology.*—Lodicules glabrous, with 2-celled microhairs (*E. pumila*) or without microhairs (*E. australis*).

**Karroochloa**

*Leaf transection.*—Adaxial furrows wide, open (broad, steep sided in *K. curva*); adaxial ribs present, similar, and rounded over all VBs. Midrib present. VBs round to elliptical. OBS incomplete above and below, cells equal to or smaller than parenchyma cells. IBS evenly thickened. Metaxylem vessels smaller than or equal to OBS cells (larger in *K. curva*). Phloem not divided. Adaxial and abaxial sclerenchyma associated with all VBs, forming girders narrower toward the bundles (T- or anchor shaped adaxially in *K. curva*). BSE and colorless cells absent. Mesophyll not radiate. Upper epidermis unspecialized (mainly of rounded, slightly inflated cells in *K. curva*); syringe-shaped prickle hairs absent. Bulliform cells absent (*K. curva*) or present as simple fan-shaped groups.

*Leaf abaxial epidermis.*—Microhairs present. Intercostal long-cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

*Lodicule morphology.*—Lodicules more or less cuneate, hairy in *K. purpurea*, hairy or glabrous in *K. curva*, and glabrous in *K. tenella*. Two- to three-celled microhairs present in all species.

**Merxmuellera**

*Leaf transection.*—Adaxial furrows narrow clefts (broad and open in *M. rufa* and *M. stricta*, absent in *M. guillarmodae*); adaxial ribs present and generally similar in shape over all VBs (none in *M. guillarmodae*), rounded or flat topped (massive in *M. arundinacea, M. papposa*, and sometimes in *M. macowanii*). Midrib present (absent in *M. arundinacea* and *M. dura*). Primary VBs round to elliptical or egg shaped; secondary VBs round to elliptical. OBS complete to incomplete; cells equal to or smaller than parenchyma cells, conspicuous or inconspicuous. IBS cells evenly or unevenly thickened. Metaxylem vessels smaller or larger than OBS cells. Phloem not divided or evenly divided by fibers into two groups (*M. stricta, M. davyi, M. macowanii, M. stereophylla, M. drakensbergiensis, and M. guillarmodae*; Fig. 2). Adaxial sclerenchyma present over all VBs (lacking over third-order bundles or absent in *M. guillarmodae*), mainly T- or anchor shaped (strands in *M. papposa*; girders in *M. stricta*); abaxial sclerenchyma present under all VBs, T- or anchor shaped (girders in *M. rufa, M. drakensbergiensis, and M. guillarmodae*; girders narrower toward bundles in *M. dura, M. decora*, and *M. stricta*). BSE present or absent adaxially and abaxially. Colorless cells absent or present as BSE only (extensive in *M. papposa*). Mesophyll not radiate. Upper epidermal cells unspecialized (*M. rufa, M. dura, M. decora, M. drakensbergiensis, and M. arundinacea*), slightly inflated (*M. guillarmodae*), broadly papillate (*M. stricta* and *M. stereophylla*), broadly papillate or fingerlike (*M. macowanii*), or fingerlike (*M. papposa, M. disticha*, and *M. davyi*; Fig. 9); syringe-shaped prickle hairs absent (present in *M. davyi* and *M. macowanii*; Fig. 1). Bulliform cells present as simple fan-shaped groups or absent.
Leaf abaxial epidermis.—Microhairs apparently absent (present in *M. dura, M. stricta,* and *M. guillarmodae*). Intercostal long-cell walls parallel, undulations W-shaped (*M. davyi, M. macowanii, M. stereophylla,* and *M. drakensbergiensis;* Fig. 6) or mainly U-shaped. Costal short cells mainly paired (in short to long rows in *M. stricta* and *M. guillarmodae*), with rounded silica bodies (dumbbell shaped in *M. guillarmodae*).

Lodicule morphology.—Lodicules quite variable; cuneate to diamond shaped or apically lingulate; hairy (hairs very sparse and pricklelike in *M. papposa*). Microhairs present in some species, absent in others (either present or absent in *M. macowanii* and *M. arundinacea*). 

Monachather

Leaf transection.—Adaxial furrows wide, open; adaxial ribs present, similar, flat topped over all VBs. Midrib present. VBs round to elliptical. OBS incomplete above, cells equal to or smaller than parenchyma cells, inconspicuous. IBS cells evenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem
not divided. Adaxial sclerenchyma present over all VBs, T- or anchor shaped; abaxial sclerenchyma present under all VBs, forming girders narrower toward bundle. BSE present adaxially, absent abaxially. Colorless cells present as BSE only. Mesophyll not radiate. Upper epidermal cells unspecialized; syringe-shaped prickle hairs absent. Bulliform cells in fan-shaped groups, with center cell of each group enlarged (Fig. 3).

**Leaf abaxial epidermis.** — Micro hairs present on lower leaf epidermis; intercostal long-cell walls parallel, with undulating walls. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

**Lodicule morphology.** — Lodicules cuneate, glabrous, without microhairs.

**Monostachya**

**Leaf transection.** — Adaxial furrows wide, open; adaxial ribs present, similar, rounded over all VBs. Midrib present. VBs round to elliptical. OBS incomplete below, cells smaller than or equal to parenchyma cells. IBS unevenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma forming girders, lacking over third-order VBs; abaxial sclerenchyma present under all VBs, forming girders narrower toward the bundles. BSE present adaxially, lacking abaxially. Colorless cells present as BSE only. Mesophyll not radiate. Upper epidermal cells fingerlike; syringe-shaped prickle hairs absent. Bulliform cells absent.

**Leaf abaxial epidermis.** — Micro hairs not seen. Intercostal long-cell walls parallel, with U-shaped or interlocking undulations. Costal short cells mainly paired, with rounded silica bodies.

**Lodicule morphology.** — Lodicules variable in this genus, generally cuneate, hairy or glabrous, with or without 2-celled microhairs.

**Plinthanthesis**

**Leaf transection.** — Adaxial furrows broad, steep sided; adaxial ribs present, similar, rounded over all VBs. Midrib present. VBs round to elliptical. OBS incomplete above and below, cells smaller than or equal to parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels larger than OBS cells. Phloem not divided. Adaxial sclerenchyma present over all VBs, T- or anchor shaped. Abaxial sclerenchyma present under all VBs, forming girders. BSE lacking. Colorless cells absent. Mesophyll not radiate. Upper epidermis unspecialized; syringe-shaped prickle hairs absent. Bulliform cells absent.

**Leaf abaxial epidermis.** — Micro hairs present on abaxial epidermis. Intercostal long-cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

**Lodicule morphology.** — Lodicules cuneate, glabrous, without microhairs.

**Pseudopentameris**

**Leaf transection.** — Adaxial furrows broad, steep sided; adaxial ribs present, rounded, similar in shape over all VBs. Midrib present. VBs round to elliptical. OBS
complete, cells larger than parenchyma cells, conspicuous. IBS evenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma lacking over third-order VBs, present under all VBs, forming girders. BSE present or absent. Colorless cells absent or present only as BSE. Upper epidermal cells unspecialized. Bulliform cells present as simple fan-shaped groups.

Seen in transection, the abaxial epidermal cells in this genus are considerably larger than those of the adaxial epidermis, and are often somewhat inflated.

**Leaf abaxial epidermis.**—Microhairs not seen. Intercostal long-cell side walls thin, bowed out and inflated in *P. brachyphylla*, more or less parallel and not inflated in *P. macrantha*, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

**Lodicule morphology.**—Lodicule preparations unavailable.

**Pyrrhanthera**

**Leaf transection.**—Adaxial furrows wide, open; adaxial ribs lacking over third-order VBs, similar in shape, rounded. Midrib present. VBs round to elliptical. OBS incomplete below, cells equal to or smaller than parenchyma cells. IBS unevenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma forming girders, lacking over third-order VBs; abaxial sclerenchyma forming girders narrower toward the bundles, lacking under third-order VBs. BSE present adaxially, absent abaxially. Colorless cells present as BSE only. Mesophyll not radiate. Upper epidermal cells unspecialized or rounded and somewhat enlarged; syringe-shaped prickles absent. Bulliform cells absent.

**Leaf abaxial epidermis.**—Microhairs present on abaxial leaf epidermis; intercostal long cells with walls parallel and with U-shaped undulations; costal short cells in long rows, silica bodies cross to dumbbell shaped.

**Lodicule morphology.**—Lodicules cuneate, glabrous, with 2-celled microhairs.

**Rytidosperma**

**Leaf transection.**—Adaxial furrows of various shapes; adaxial ribs present over all VBs (absent in *R. penicillatum*, absent over third-order VBs in *R. procerum, R. clavatum*, and *R. corinum*); rounded or flat topped, generally similar in shape over all VBs. Midrib present or absent. Primary VBs round to elliptical (egg shaped in *R. longifolium* and occasionally in *R. caespitosum*); secondary VBs round to oval. OBS complete to incomplete, cells smaller than or equal to parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller or larger than OBS cells. Phloem not divided. Adaxial sclerenchyma associated with all VBs or lacking over third-order VBs; T- to anchor shaped or forming girders; abaxial sclerenchyma associated with all VBs (lacking under third-order VBs in *R. clavatum* and occasionally in *R. setifolium*); forming girders or girders narrower toward the bundle. BSE present or absent adaxially, absent abaxially (present in *R. glabra*). Colorless cells absent or present only as BSE. Mesophyll not radiate (indistinctly radiate in *R. clavatum*). Upper epidermal cells unspecialized, rarely
slightly inflated (broadly papillate to fingerlike in *R. pauciflorum*, *R. corinum*, and *R. setifolium*); syringe-shaped prickle hairs absent. Bulliform cells present as simple fan-shaped groups or absent.

*Leaf abaxial epidermis.*—Microhairs present or apparently absent. Intercostal long-cell side walls parallel or bowed, with variously shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies (mainly paired, with rounded silica bodies in *R. virescens* and *R. glabra*).

*Lodicule morphology.*—Lodicules cuneate or diamond shaped, hairy (glabrous in *R. corinum*), microhairs present, 2–3(–4) celled.

Cortaderia

*Leaf transection.*—Adaxial furrows variously shaped; adaxial ribs present and similarly shaped over all VBs; flat topped (rounded in *C. modesta* and *C. archboldii*). Midrib present or absent. VBs round to elliptical. OBS complete, cells equal to or smaller than parenchyma cells but conspicuous (*C. araucana*, *C. pilosa*, and *C. modesta*); or incomplete, cells equal to or smaller than parenchyma cells, inconspicuous (*C. hapalotricha*, *C. pungens*, and *C. archboldii*). IBS cells unevenly thickened (evenly thickened in *C. modesta* and *C. archboldii*). Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided by fibers (*C. archboldii*, *C. hapalotricha*, and *C. pungens*), or divided irregularly into two or more groups (Fig. 9). Adaxial sclerenchyma present over all VBs, T- or anchor shaped; abaxial sclerenchyma present under all VBs, T- or anchor shaped (girder narrower toward bundle in *C. araucana*, girder in *C. archboldii*). BSE present adaxially except in *C. hapalotricha* and *C. pungens*; extensions present abaxially except in *C. hapalotricha*, *C. pungens*, and *C. archboldii*. Colorless cells absent or present as BSE only (extensive in *C. araucana*). Mesophyll not radiate. Upper epidermal cells unspecialized (broadly papillate in *C. pungens*, fingerlike in *C. archboldii*); syringe-shaped prickle hairs absent. Bulliform cells absent (present as simple fan-shaped groups in *C. hapalotricha* and *C. archboldii*).

*Leaf abaxial epidermis.*—Microhairs apparently absent (present in *C. modesta*). Intercostal long cells with parallel side walls and generally U-shaped or interlocking undulations (occasionally W-shaped in *C. pungens* and *C. modesta*). Costal short cells in long rows (*C. hapalotricha*, *C. pungens*, and *C. archboldii*) or mainly paired (*C. araucana*, *C. pilosa*, *C. modesta*) with cross- to dumbbell-shaped silica bodies (rounded in *C. pilosa*).

*Lodicule morphology.*—Lodicules cuneate or with a distinct apical lobe; hairy, with 2–3-celled microhairs in *C. hapalotricha*; hairy, without microhairs in *C. pilosa* and *C. modesta*; glabrous, with microhairs in *C. pungens*; glabrous, without microhairs in *C. archboldii*.

Schismus

*Leaf transection.*—Adaxial furrows wide, open; adaxial ribs present, similar, and rounded over all VBs (lacking over third-order VBs in *S. scaberrimus*). Midrib lacking (present in *S. barbatus*). VBs round to elliptical. OBS complete (incomplete below in *S. scaberrimus*); cells equal to or smaller than parenchyma cells, inconspicuous. IBS unevenly thickened (evenly thickened in *S. scaberrimus*). Meta-
xylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma present as strands over all VBs in S. inermis, absent over third-order VBs in S. arabicus and S. scaberrimus, and absent altogether in S. barbatus; abaxial sclerenchyma present, or absent under third-order VBs, as strands (T- or anchor shaped in S. scaberrimus). BSE absent. Colorless cells absent. Mesophyll not radiate. Upper epidermal cells unspecialized; syringe-shaped prickle hairs absent. Bulliform cells absent (apparently present as simple fan-shaped groups in S. scaberrimus).

Conert and Türe (1974) note no bulliform cells in S. scaberrimus, though they do occur in S. pleuropogon, which was not included in the present study. Available material of S. scaberrimus was poorly preserved, and consequently the leaf transections are not entirely clear; nevertheless, bulliform groups appear to be present.

Leaf abaxial epidermis.—Microhairs present (none seen in S. inermis). Intercostal long cells with parallel walls, undulations generally U-shaped. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies (mainly paired, with rounded silica bodies in S. inermis).

Lodicule morphology.—Lodicules cuneate, hairy, with 2-celled microhairs (glabrous or hairy, without microhairs in S. arabicus).

DISCUSSION

Danthonia has been subdivided by various authors because of obvious heterogeneity in morphological and anatomical features (e.g., DeWet 1954, 1956; Zotov 1963; Conert 1971). However, the data presented here reveal that extensive variation in leaf anatomy and lodicule morphology remains within the segregate genera themselves. Four of the segregate genera investigated are distinct anatomically, as well as morphologically. They are clearly isolated in the Danthonieae.

Centropodia

Members of this African genus have the outer bundle sheath complete, with the cells very large and conspicuous, radiate parenchyma, and bulliform cells with the central cell much enlarged. The abaxial leaf surface is deeply grooved, with the grooves overarched by prickles. This combination of characters is not found elsewhere in the study group. The genus also differs from the rest of the Danthonia complex in morphological characters, such as its 5–11-nerved glumes, and its very small chromosomes (DeWet 1954, 1956; Conert 1962; Wright 1984).

Dregeochloa

Leaf anatomy of this African genus of two species is distinctive, especially in its deeply grooved lower surface and its bulliform cells which occupy over half the depth of the leaf. Morphologically it is equally distinctive, particularly in the form of the mature caryopsis. Ellis (1977) and Conert (1966, 1971) have expressed the opinion that this genus occupies an isolated position in the Danthonieae.

Monachather

Anatomically, this monotypic genus is unusual in this study group in having bulliform cells in fan-shaped groups but with the center cell enlarged and pene-
trating deeply into the mesophyll. This feature also occurs in *Centropodia*. *Monachather* also has the inner bundle sheath evenly thickened, a feature which is relatively uncommon. Morphologically, it is distinctive and apparently isolated (Vickery 1956). Johnson and Watson (1981) noted the presence of a germination flap in the lemma, a feature which is uncommon among the danthonioid grasses and which was not found among any of the species of *Rytidosperma* which they investigated. In addition, the chromosomes of this species are much smaller than those of species of *Rytidosperma* (Abele 1959). Therefore, based on all available evidence, *Monachather* warrants generic status, and occupies an isolated position in the tribe.

**Pseudopentameris**

Like *Dregeochloa* and *Centropodia*, *Pseudopentameris* has large and distinct outer bundle sheath cells. Additionally, the lower epidermal cells are larger than those of the upper epidermis and often inflated, a condition not found elsewhere in this study group. Its morphology is also distinctive, especially the structure of the caryopsis and the stigmatic hairs which are decurrent and join over the top of the ovary (DeWet 1954, 1956; Conert 1971). This combination of specializations suggests that the closest relationships of this African genus lie outside the core group of the Danthonieae.

The remaining taxa in the study group show more similarities to one another than to any other taxa. Nevertheless, their interrelationships are not clear based on either anatomy or overall morphology.

**Chionochloa**

This genus, which contains the widespread and important snowgrasses of Australia and New Zealand, is relatively uniform in leaf anatomy. Species of *Chionochloa* possess broadly papillate upper epidermal cells, generally have a well-developed abaxial subepidermal band of sclerenchyma, and lack bulliform cells; the costal short cells in the abaxial epidermis are paired, with rounded silica bodies. In combination, these features distinguish *Chionochloa* from *Rytidosperma*. Zotov (1963) found similar uniformity in morphological characteristics within *Chionochloa*. He noted that the variation which occurs is clinal in nature, rendering it difficult to separate the genus into species groups, or even to discover features differentiating species with \(2n = 36\) from those with \(2n = 42\). Anatomical variation which occurs is not necessarily paralleled by morphological differences. For example, *C. bromoides* and *C. beddiei*, both coastal New Zealand rock-dwelling species and morphologically very similar, differ in primary VB shape, adaxial sclerenchyma shape, the type of intercostal long-cell wall undulations, and in the presence or absence of microhairs on the lodicules. These differences suggest the possibility of convergent evolution in these two species.

**Cortaderia**

Anatomical data strongly support the inclusion of *C. archboldii*, a distinctive New Guinean member of this genus, in section *Bifida* (Connor and Edgar 1974). Despite its unusual appearance (Fig. 8), it shows marked similarities to *C. hapalotricha* and *C. pungens*, the other representatives of this section, in features of the outer bundle sheath and extensions, presence of bulliform cells, phloem un-
Chionochloa and Cortaderia show a number of anatomical similarities, as pointed out by Zotov (1963) and Conert (1971). For instance, the overall outline of the leaf and shape of the ribs as seen in transection are similar (Fig. 8), and broadly papillate upper epidermal cells are found in all Chionochloa and some Cortaderia. However, Cortaderia differs substantially in many other features. The bundle-sheath extensions are more strongly developed in Cortaderia, and in some species the outer bundle sheath is also thickened, a feature not found in Chionochloa. The silica bodies are nearly always cross to dumbbell shaped in Cortaderia, and rounded in Chionochloa. In addition, all species of Cortaderia are gynodioecious, a condition rare in the Poaceae and not found in Chionochloa (Connor 1963, 1970, 1974, 1981). Thus, the two genera appear distinct and not particularly closely related. This conclusion is supported by Wright (1984), who found no evidence of cladistic relationship between these two genera.

Conert (1961) suggested a relationship between Cortaderia and Merxmuellera. This relationship is not strongly supported by the anatomical data presented here. Differences exist in sclerenchyma and bundle-sheath extension development, as well as in costal short-cell arrangement and silica-body shape. However, Merxmuellera is extremely variable anatomically and further study is clearly required before any conclusions can be reached.

Danthonia s.s.

The North American and European species of this genus are uniform anatomically as well as morphologically, as pointed out by De Wet (1954). West Indian and South American species tend to possess anatomical specializations, notably the division of the phloem and the paired arrangement of the costal short cells in some species, which are not found in other Danthonia s.s. Perhaps the most interesting finding is the distinction between D. domingensis and D. shrevei, which were combined as subspecies by Conert (1975a). These two species show many anatomical differences, including the shape and the presence of hairs on the lodicules. Clearly, closer study is needed. However, in spite of the variation within Danthonia s.s., no clear-cut divisions are possible. Wright (1984) found that all these species appeared to form a monophyletic group.

Danthonia cachemyriana and D. exilis

These two species have not been formally removed from Danthonia, though morphological differences (notably the tufted arrangement of the lemma hairs) as well as anatomical features such as the complete absence of bundle-sheath extensions, sclerenchyma shape, and lodicule morphology, indicate a closer relationship to other taxa such as Karroochloa. Wright (1984) found evidence that these two species may represent sister groups of Karroochloa; this possibility is under investigation.

Karroochloa and Schismus

Leaf anatomical data presented here are inconclusive, but generally support the suggested close relationship between these two genera (Conert and Türpe 1969, 1974). Both genera lack colorless cells, bundle-sheath extensions, and, in some
species, bulliform cells; *Karroochloa* and *S. scaberrimus* have the inner bundle-sheath cell walls evenly thickened. The two genera differ primarily in sclerenchyma development. The features they share, however, are found elsewhere in the study group. Lodicule morphology is variable in both genera, and is not helpful in resolving the problem.

**Merxmuellera**

The anatomy of this genus is extremely variable, and no clear-cut patterns are as yet detectable. One aberrant species is *M. guillarmodae*. Conert (1975b) suggested that this species is most closely related to *M. macowanii* or to *M. stricta*. Although neither hypothesis is strongly supported by the anatomical data presented here, a relationship with *M. stricta* appears more plausible.

Wright (1984) indicated that the genus appears to be polyphyletic. More extensive investigations of these species are in progress in an effort to clarify their relationships to each other and to other taxa within the Danthonieae.

**Erythranthera, Plinthanthesis, and Pyrrhanthera**

The anatomical data provide little support for the separation (Zotov 1963; Blake 1972) of these genera from *Rytidosperma*. However, transection preparations of several species were marginal or inadequate due to poor preservation of the leaf material, and further investigation is needed. Lodicules in these genera are glabrous, a condition rare in *Rytidosperma*.

**Monostachya**

Leaf anatomy of this genus is similar to that of *Rytidosperma*. In the presence of paired costal short cells with rounded silica bodies it resembles the South American *R. virescens* and *R. glabra*. Morphologically it differs from *Rytidosperma* in its small size, tiny spikelets, and the extreme reduction of the lemma awn. Jacobs (1982) has argued convincingly for the recognition of this genus, particularly in view of the base chromosome number of \( x = 5 \) (or 10).

**Rytidosperma**

The Australian species of this genus are uniform in leaf anatomy and lodicule morphology, which is consistent with the observation that these species hybridize readily and appear to form a polyploid complex (Brock and Brown 1961; Wright 1984). The New Zealand species such as *R. corinum*, *R. clavatum*, and *R. setifolium*, and the South American species *R. glabra* and *R. virescens*, show greater differences in anatomy.

*Rytidosperma* appears to be distinct from *Danthonia* s.s. both on morphological and anatomical grounds (Wright 1984). Though leaf anatomy in these taxa is similar, lodicule morphology is distinctive for each genus. Lodicules in *Rytidosperma* are hairy except in rare cases and have microhairs, while in *Danthonia* s. str. they are almost exclusively glabrous and lack microhairs. The most critical area for study in these two genera appears to be the West Indies and South America, where species of both appear to be most variable.

This study points out the broad similarities present in the anatomy of this group
of grasses. Renvoize (1982) found that anatomical features were not reliable in delimiting tribal groups within the Arundinoideae, and suggested that characters which could be used in delimiting such subgroups would have to be morphological. However, the variation in anatomical features which does occur in the Danthonieae is not necessarily correlated with morphological differences. This fact is the major source of difficulty in the development of an internally consistent taxonomic system for the group. The evolutionary history of the Danthonieae must have involved extensive convergences and parallelisms which have obscured its pattern. Distinguishing characteristics may exist which would enable us to decipher the evolutionary relationships among these species, but are not yet recognized, just as the characteristics now used to separate the Poeae and the Eragrosteae were known long before they were considered significant. Further studies of these taxa are underway, and it is hoped that they will lead to breakthroughs in the systematics of this fascinating group.

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LITERATURE CITED


