Leaf anatomy of the South African Danthonieae (Poaceae). XIV. *Pentameris dregeana*

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ABSTRACT

Transverse sections and abaxial epidermal scrapes of leaf blades of *Pentameris dregeana* Stapf, both of herbarium specimens and of freshly fixed material, were examined by light microscopy. The anatomical structure was found to be basically uniform in a representative sample. A few somewhat atypical specimens, however, showed epidermal similarities with *Pentaschistis colorata* (Steud.) Stapf. A comparison with other danthonoid grasses revealed some specimens identified as *Pentaschistis colorata* var. *polytricha* Stapf which resemble *Pentameris dregeana* very closely in leaf anatomy. A definite gradation in leaf anatomy between *Pentameris dregeana* and *Pentaschistis colorata* appears to exist and, consequently, it is proposed that the affinities of *Pentameris dregeana* lie with this group of *Pentaschistis* species rather than close to any of the other *Pentameris* species.

UITTREKSEL

Dwarssnee en abaksiale epidermale skrapings van blaarlaminas van *Pentameris dregeana* Stapf, beide van herbariumeksemplare en van vrys gefikseerde materiaal, is met behulp van ’n ligmikroskoop ondersoek. Dit is gevind dat die blaaranatomie in ’n verteenoorgedinge monster basies eenvormig was. Nietemin het ’n paar iets afwykende eksemplare epidermale ooreenkomste met *Pentaschistis colorata* (Steud.) Stapf getoon. Sommige eksemplare wat as *Pentaschistis colorata* var. *polytricha* Stapf benaam is, het hoe sterk anatomiese ooreenkomstig getoon met *Pentameris dregeana*. Daar is skynbaar ’n duidelike oorgang tussen die blaaranatomie van *P. dregeana* en die van *Pentaschistis colorata*. Om die rede word voorgestel dat die verwantskappe van *Pentameris dregeana* met hierdie groep *Pentaschistis*-spesies lê eerder as met enige ander *Pentameris*-spesies.

INTRODUCTION

*Pentameris dregeana* Stapf is a densely tufted perennial which is usually not as robust as the other members of this genus. The leaf blades are tightly inrolled and wiry, and the old leaves are characteristically curly. Soft, woolly hairs are particularly common on the leaf sheath but may also occur near the base of the blade. The inflorescence is a panicle with rather small spikelets, the glumes being from 12–15 mm long (*Chippindall 1955*). The spikelets are therefore smaller than in any of the other species of *Pentameris*, where the glumes range from 18–25 mm long.

*Pentameris dregeana* is a species of the mountain fynbos, and is confined to the mountains of the south-western Cape Province, where it occurs from the Clanwilliam District in the north-west to Willowmore in the east. It favours rocky habitats and is often found in rock crevices or cliff faces. The species is even found at high altitudes in the alpine zone but is probably never open and expanded: not permanently infolded type but margins usually almost meet, forming an enclosed, hollow cylinder (*Figures 1–9*); ribs over l’vb/s and 3’vb/s of similar shape and size. No abaxial ribs or furrows although slight undulations may be associated with the vbs (*Figures 3 & 4*). *Median vascular bundle*: structurally identical to lateral 1’vb/s; recognizable by location only. *Vascular bundle arrangement*: 5, 7 or 9 1’vb/s in leaf section; 1 3’vb separates successive 1’vb/s (*Figures 1–9*), although laterally this pattern may be obscured. No 2’vb/s. All vbs located in centre of blade thickness (*Figure 9*) or slightly abaxially (*Figure 6*). *Vascular bundle description*: 3’vb elliptical with well developed phloem. 1’vb elliptical with phloem adjoining the ibs; metaxylem vessels narrow, narrower in diameter than the obs cells (*Figure 6*). *Vascular bundle sheaths*: obs elliptical; interrupted both adaxially and abaxially by bundle sheath extensions intergrading.

ANATOMICAL DESCRIPTION OF *PENTAMERIS DREGEANA*

Leaf in transverse section

Outline of lamina: inrolled from both margins; probably never open and expanded: not permanently infolded type but margins usually almost meet, forming an enclosed, hollow cylinder (*Figures 1–9*); ribs over l’vb/s and 3’vb/s of similar shape and size. No abaxial ribs or furrows although slight undulations may be associated with the vbs (*Figures 3 & 4*). *Median vascular bundle*: structurally identical to lateral 1’vb/s; recognizable by location only. *Vascular bundle arrangement*: 5, 7 or 9 1’vb/s in leaf section; 1 3’vb separates successive 1’vb/s (*Figures 1–9*), although laterally this pattern may be obscured. No 2’vb/s. All vbs located in centre of blade thickness (*Figure 9*) or slightly abaxially (*Figure 6*). *Vascular bundle description*: 3’vb elliptical with well developed phloem. 1’vb elliptical with phloem adjoining the ibs; metaxylem vessels narrow, narrower in diameter than the obs cells (*Figure 6*). *Vascular bundle sheaths*: obs elliptical; interrupted both adaxially and abaxially by bundle sheath extensions intergrading.
FIGURES 1–9. — Leaf blade anatomy of Pentameris dregeana as seen in transverse section. 1–6, typical form. 1, Ellis 2480, inrolled outline, × 100; 2, Ellis 2484, inrolled setaceous leaf, × 100; 3, Esterhuysen 27321, × 100; 4, Esterhuysen 21824, strongly inrolled blade, × 100. 5–6, Ellis 2494: 5, outline, × 100; 6, detail of adaxial ribs and furrows, mesopyll and vascular bundles, × 250. 7–9, pubescent form. 7, Ellis 2580, inrolled outline, × 100. 8–9, Ellis 2556: 8, setaceous leaf outline, × 100; 9, detail of leaf margin, × 250.
...cults of a crescentic cork cell and a round to elliptical silicula cell. Intercostal long cells but much narrower; each long zones: Swollen, superficially located between several modi-
...ticles. Not of cushion hair type. Abaxial epidermis: no bulliform cells; epidermal cells small, flattened with a thick continuous cuticle (Figures 6 & 9). No epidermal appendages.

Abaxial epidermis in surface view

Intercostal long cells: rectangular, length 2x – 3x width (Figures 10–17); side walls parallel; end walls vertical; anticlinal walls thickened, without pits, with regular pointed undulations. Arrangement of adjacent files forms brickwork pattern. Adjoining long cells separated by short cells. Intercostal short cells: cork-silica cell pairs separate virtually all adjacent long cells. Cork cell crescentic, enfolding round silica body; narrower than long cells. Stomata: absent. Prickles: absent. Microhairs: none observed. Microhairs: either absent (Figures 10–13) or common in intercostal zones only (Figures 14–17); unicellular, soft, thin-walled and 1–2 mm long; base slightly swollen, superficially located between several modified epidermal cells. Not of cushion hair type. Costal zones: 5–7 files wide. Long cells of similar length to intercostal long cells but much narrower; each long cell separated by a silico-suberose couple consisting of a crescentic cork cell and a round to elliptical silicula cell.

Specimens examined:
CAPE. — 3219 (Wuppertal): Buffelskloof Pass, Koue Bokkeveld Mts (–CA). Ellis 2404; Skoenesig, Ceres (–CC). Hanekom 1275, 3318 (Cape Town): Porterville (–BB). Esterhuysen 21807. 3319 (Worcester): Schorlemberg, Great Witteberg (–AB). Ellis 2484; Leeuwenfontein Peak, Gydoberg (–AD). Ellis 2480; Tarantula Peak, Esterhuysen 21824; Bainskloof (–CA). Esterhuysen 26313; Middagkramberg, Framshoek Pass (–CC). Boucher 2388*, Ellis 666*, 3321 (Ladismith): Toverkop, Swartberg (–AD). Esterhuysen 26751*, 3322 (Outdshoorn): Swartberg Pass (–AC). Ellis 2556*, 2580*, 3325 (Willowmore): Willowmore (–AD). Acocot 19925; Formosa Peak (–DC). Esterhuysen 27400*.

DISCUSSION AND CONCLUSIONS

The 14 examined specimens of Pentameris dregeana were collected at localities throughout the distribution area of the species. Yet their leaf anatomy is remarkably uniform, and both the leaf in transverse section (Figures 1–9) and the abaxial epidermis (Figures 10–17) show negligible variation. This is considered unusual seeing that ecotypic variation is common in many fynbos species in response to the diversity of habitats in this ecologically varied region.

A superficially striking difference, however, is the presence of conspicuous, long, soft macrohairs on some of the specimens of P. dregeana studied (Figures 14–17). Although this appears to be a significant difference, it must be remembered that all specimens of P. dregeana have this type of macrohair on the leaf sheath, particularly at the sheath mouth (Chippindall 1955). These hairs are possibly also present on the leaf blades of all P. dregeana specimens but normally confined to those parts of the blade below the central third which was sampled in this study. In the pubescent specimens examined, this type of hair merely extends somewhat higher up the leaf blade than is normal. In addition, the leaf transsections of these pubescent specimens (Figures 7–9) are identical to those of the typical specimens (Figures 1–6). No taxonomic significance is therefore, attached to the presence or absence of these hairs, although pubescent leaf blades were found almost exclusively in specimens from the eastern parts of the distribution area of P. dregeana. This may, however, represent clinal variation.

A less obvious difference is that on some epidermal preparations costal and intercostal zones are not differentiated (Figures 10–11). On others this zonation is clearly distinguishable by differences in cell structure and arrangement (Figures 12–17). The intercostal long cells are rectangular with wavy anticlinal walls and the cells of a file are all separated by small, narrow short cells. The long cells of the costal zones are much narrower and the interspaced silica bodies are of the same width as the long cells.

Although the leaf anatomy of P. dregeana is consistently uniform and stable, a few specimens identified as P. dregeana deviate from the typical structure to varying degrees (Figures 18–24). In transverse section these atypical specimens display typical P. dregeana anatomy (Figures 18–20) but the epidermal structure differs somewhat. The differences are not discrete, however, and a continuum exists from those specimens where the costal and intercostal zones are almost indistinguishable to the situation in Figure 24 (Ellis 2477) where costal and intercostal long cells are significantly different. This particular specimen also differs from all others in that the silica bodies are dumbbell-shaped and microhairs occur between the intercostal long cells (Figure 24). In transverse section this anomalous specimen is indistinguishable from typical P. dregeana specimens (Figures 18 & 19), and it is of interest to note that it was collected at the same locality on the Gydoberg as Ellis 2480, which has typical P. dregeana anatomy (Figures 1 & 13).

These atypical specimens, and Ellis 2477 in particular, seem to indicate a link between Pentameris dregeana and Pentaschistis colorata (Stapf.) Stein. — 3219 (Wuppertal): Buffelshoek Pass, Koue Bokkeveld Mts (–CA). Ellis 2404; Skoenesig, Ceres (–CC). Hanekom 1275, 3318 (Cape Town): Porterville (–BB).
FIGURES 10-17. — Abaxial epidermis of *Pentameris dregeana* as seen in surface view. 10-13, typical form: 10. *Esterhuysen 26313*, showing distribution of costal and intercostal zones. × 160; 11. *Esterhuysen 27321*, without a clear distinction between costal and intercostal zones. × 160; 12. *Ellis 2484*, costal and intercostal zones distinguishable. × 160; 13. *Ellis 2489*, detail of intercostal long cells and costal files. × 250. 14-15. Pubescent form. 14. *Ellis 2556*: numerous long, soft macrohairs. × 100; 15. Detail of intercostal macrohairs and their basal cells. × 250. 16. *Boucher 2388*, macrohairs common. × 160; 17. *Ellis 2580*, detail of costal zones, intercostal long cells and macrohairs. × 250.
(Figures 25–32). This possible relationship is not evident in leaf transections, because *Pentaschistis colorata* and its close allies have very characteristic abaxial epidermal cells between the bundles alternating with small, fibrous cells overlying the bundles. Nevertheless, relationships of *P. dregeana* appear to lie with this group of *Pentaschistis* species rather than with any of the other *Pentameris* species. All these ‘atypical’ *P. dregeana* specimens should undoubtedly be retained in *P. dregeana* on gross morphological features and have been artificially separated here only to accentuate the anatomical link between *P. dregeana* and *Pentaschistis colorata*.

The following *P. dregeana* specimens display atypical leaf anatomy to varying degrees:

CAPE. — 3219 (Wuppertal): Buffelshoek Pass. Koue Bokkeveld Mts (–CA). *Ellis 2495, 2497, 3319* (Worcester): Leeuwenstein Peak. Gydoberg (–AD). *Ellis 2477*.

The anatomical gradation of *Pentameris dregeana* into the *Pentaschistis colorata* species complex appears to be substantiated by the observation that some specimens identified as *Pentaschistis colorata* (Steu.) Stapf var. polytricha Stapf are virtually identical to *P. dregeana* in leaf anatomy e.g. *Ellis 2347, 2509* (Figures 25–28).

*Ellis 2506* (Figures 29–30), collected at the same locality as *Ellis 2509* (Figures 27–28), has a leaf anatomy very closely resembling that of a specimen identified as *Pentaschistis aristidoides* (Thunb.) Stapf (*Ellis 2488*). The anatomy of *Ellis 2506* is dissimilar

FIGURES 18–24. — Leaf anatomy of atypical specimens of *Pentameris dregeana*. 18–20. leaf in transverse section. 18–19. *Ellis 2477*: 18. inrolled outline, × 100; 19. detail of adaxial ribs, mesophyll and vascular bundles, × 250. 20. *Ellis 2495*: setaceous, inrolled blade, × 100. 21–24. abaxial epidermal anatomy. 21–22. *Ellis 2495*: 21. note very long soft macrohairs associated with margin, × 100; 22. clear distinction between costal and intercostal long cells, × 250. 23. *Ellis 2497*: with distinct costal and intercostal zones, × 250; 24. *Ellis 2477*: costal zones with dumbbell shaped silica bodies and very different intercostal long cells, × 250.
FIGURES 25–32. — Leaf anatomy of *Pentachistis colorata* var. *polytricha* for comparison with the anatomy of *Pentameris dregeana*. 25–26, Ellis 2347: 25, transverse section similar to that of *P. dregeana*. × 160; 26, abaxial epidermis identical to typical *P. dregeana* type, × 250. 27–28, Ellis 2599: 27, typical inrolled outline, × 160; 28, epidermis differing somewhat from *P. dregeana* type, × 250. 29–30, Ellis 2506: 29, outline of blade showing conspicuous sclerenchyma girders and thick cuticle, × 160; 30, abaxial epidermis without distinction between costal and intercostal zones, × 160. 31–32, Ellis 2546: 31, leaf outline showing inflated epidermal cells, × 160; 32, entire abaxial epidermis consists of inflated long cells, × 400.
to that of both *Pentameris dregeana* and *Pentaschistis colorata*, and this example demonstrates the definite interface between *Pentameris dregeana* and the genus *Pentaschistis*. It is clear that the affinities of *Pentameris dregeana* are closer to some species currently placed in *Pentaschistis* than they are to any of the *Pentameris* species.

*Ellis 2546* (Figures 31–32) is another specimen identified as *Pentaschistis colorata* var. *polytricha*, but its leaf anatomy differs from that of all other danthonoid grasses known to the author. Further collections of this taxon are needed before it can be positively identified, but indications are that this specimen represents a new and undescribed species, possibly belonging to *Pentameris*. It is mentioned here because it emphasizes the extreme heterogeneity of *Pentaschistis colorata* var. *polytricha*, a taxon which presently accommodates some specimens matching *Pentameris dregeana* as well as specimens which resemble neither *P. dregeana* nor *Pentaschistis colorata*. *Pentaschistis colorata* var. *polytricha* is therefore a heterogeneous entity which appears to substantiate the anatomical indications found in this study, namely that *Pentameris dregeana* grades into *Pentaschistis* and shows closer affinities to this genus than it does to any other *Pentameris* species.

The following specimens examined during this study were identified as *Pentaschistis colorata* var. *polytricha* by the staff of the National Herbarium:

**CAPE.** — 3219 (Wuppertal): Cedarberg Pass, Algeria State Forest (−AC). *Ellis 2506, 2509, 3319* (Worcester): Franschoek Pass (−CC). *Ellis 2347, 3322* (Oudtshoorn): Robinson’s Pass, Outeniqua Mts (−CC). *Ellis 2546*.

*Pentameris dregeana* resembles some of these specimens linked to *Pentaschistis colorata* more than it does the other species of *Pentameris* such as *P. longiglumis* (Nees) Stapf (*Ellis 1985a*), *P. thuarii* Beauv. (*Ellis 1985b*), *P. macrocalycina* (Staud. Schweick. (*Ellis 1985c*) and *P. obtusifolia* (Hochst.) Schweick. (*Ellis 1985c*). The anatomical affinities of *P. dregeana* are undoubtedly closer to *Pentaschistis colorata* and its allies than to the other members of the genus *Pentameris*. It’s leaf anatomy appears to be somewhat intermediate between these two genera and a final decision on the classification of this interesting species awaits a thorough revision and re-evaluation of the genus *Pentaschistis*.

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