

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

R. P. ELLIS\*

**Keywords:** Danthonieae, leaf anatomy, *Pentameris*, Poaceae

## 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

Dwarssneë en abaksiale epidermale skrapings van blaarlamina's van *Pentameris dregeana* Stapf, beide van herbariumeksemplare en van vars gefikseerde materiaal, is met behulp van 'n ligmikroskoop ondersoek. Dit is gevind dat die blaaranatomie in 'n verteenwoordigende monster basies eenvormig was. Nietemin het 'n paar ietwat afwykende eksemplare epidermale ooreenkomste met *Pentaschistis colorata* (Steud.) Stapf getoon. Sommige eksemplare wat as *Pentaschistis colorata* var. *polytricha* Stapf benaam is, het ook sterk anatomiese ooreenkomste getoon met *Pentameris dregeana*. Daar is skynbaar 'n duidelike oorgang tussen die blaaranatomie van *P. dregeana* en dié van *Pentaschistis colorata*. Om dié 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 it does not form low, dense cushions with pungent leaf apices as does *P. macrocalycina* (Steud.) Schweick.

Apart from the statement by De Wet (1956) that both the epidermal and internal anatomy are festucoid, no information on the leaf anatomy of *P. dregeana* is available. It is the purpose of this paper to describe and illustrate the leaf anatomy of *P. dregeana* in detail and to compare its structure with that of the other species of the genus as well as the other South African danthonoid grasses. For the anatom-

ical descriptions, the terminology of Ellis (1976, 1979) will be followed and the following abbreviations will be used:

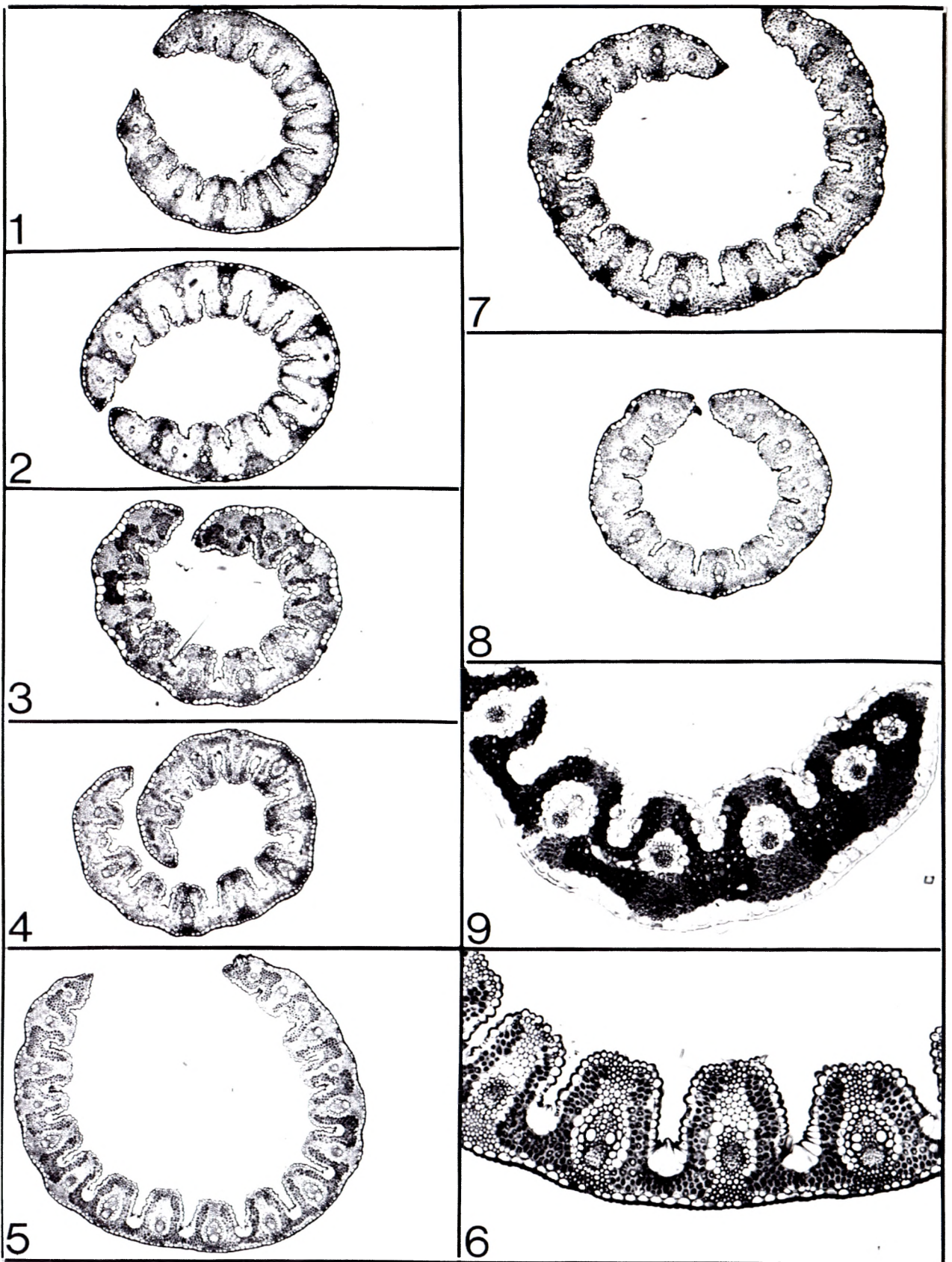
- vb/s – vascular bundle/s
- 1'vb/s – first order vascular bundle/s
- 3'vb/s – third order vascular bundle/s
- ibs – inner bundle sheath; mestome sheath
- obs – outer bundle sheath; parenchyma sheath

## ANATOMICAL DESCRIPTION OF *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). 11, 13, 15 or 17 vbs in blade section. **Ribs and furrows:** flat-topped, square adaxial ribs present over all vbs; deep, cleft-like furrows between all vbs (Figure 6); ribs over 1'vbs and 3'vbs 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'vbs; recognizable by location only. **Vascular bundle arrangement:** 5, 7 or 9 1'vbs in leaf section; 1 3'vb separates successive 1'vbs (Figures 1–9), although laterally this pattern may be obscured. No 2'vbs. All vbs located in centre of blade thickness (Figure 9) or slightly abaxially (Figure 6). **Vascular bundle description:** 3'vbs elliptical with well developed phloem. 1'vbs 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

\* Botanical Research Institute, Department of Agriculture and Water Supply, Private Bag X101, Pretoria 0001.



FIGURES 1-9. — Leaf blade anatomy of *Pentameris dregeana* as seen in transverse section. 1-6, typical form. 1, *Ellis 2480*, inrolled outline,  $\times 100$ ; 2, *Ellis 2484*, inrolled setaceous leaf,  $\times 100$ ; 3, *Esterhuysen 27321*,  $\times 100$ ; 4, *Esterhuysen 21824*, strongly inrolled blade,  $\times 100$ . 5-6, *Ellis 2494*: 5, outline,  $\times 100$ ; 6, detail of adaxial ribs and furrows, mesophyll and vascular bundles,  $\times 250$ . 7-9, pubescent form. 7, *Ellis 2580*, inrolled outline,  $\times 100$ . 8-9, *Ellis 2556*: 8, setaceous leaf outline,  $\times 100$ ; 9, detail of leaf margin,  $\times 250$ .

into sclerenchyma girders (Figures 6 & 9). Obs cells small, rounded, with thin walls and no chloroplasts. Ibs entire; composed of rounded cells with thicker inner tangential cell walls. *Sclerenchyma*: all vbs with prominent adaxial and abaxial girders; narrow towards bundles; girders either intergrade with thick-walled collenchyma of bundle sheath extensions (Figure 6) or sclerenchyma fibres abut on the ibs abaxially and the obs adaxially (Figure 9). Very small sclerenchyma cap in margin (Figure 9). *Mesophyll*: homogeneous chlorenchyma consisting of regular, tightly packed, isodiametric cells, not radiate (Figures 6 & 9); forming U-shaped groups on sides and bases of furrows. No colourless cells. *Adaxial epidermis*: small, fan-shaped groups of bulliform cells occur at the bases of the furrows (Figures 6 & 9). Epidermal cells small, slightly inflated with a continuous cuticle (Figure 9); prickles present on edges of ribs. *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  $2 \times -3 \times$  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 on abaxial surface (Figures 10–17). *Papillae*: absent. *Prickles*: absent. *Microhairs*: none observed. *Macrohairs*: 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 silica cell.

#### Specimens examined:

CAPE. — 3219 (Wuppertal): Buffelshoek Pass, Koue Bokkeveld Mts (–CA), *Ellis 2494*; Skoongesig, Ceres (–CC), *Hanekom 1275*, 3318 (Cape Town); Porterville (–BB), *Esterhuysen 21907*, 3319 (Worcester); Schurftberg, Great Witzenberg (–AB), *Ellis 2484*; Leeuwfontein Peak, Gydoberg (–AD), *Ellis 2480*; Tarantula Peak, *Esterhuysen 21824*; Bainskloof (–CA), *Esterhuysen 26313*; Middagkransberg, Franschoek Pass (–CC), *Boucher 2388\**, *Ellis 686\**, 3321 (Ladismith); Toverkop, Swartberg (–AD), *Esterhuysen 26751\**, 3322 (Oudtshoorn); Swartberg Pass (–AC), *Ellis 2556\**, 2580\*, 3323 (Willowmore); Willowmore (–AD), *Acocks 19925*; Formosa Peak (–DC), *Esterhuysen 27400\**.

#### DISCUSSION AND CONCLUSIONS

The 14 examined specimens of *Pentameris dregeana* were collected at localities throughout the dis-

tribution 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 ecotypical variation is common in many fynbos species in response to the diversity of habitats in this ecologically varied region.

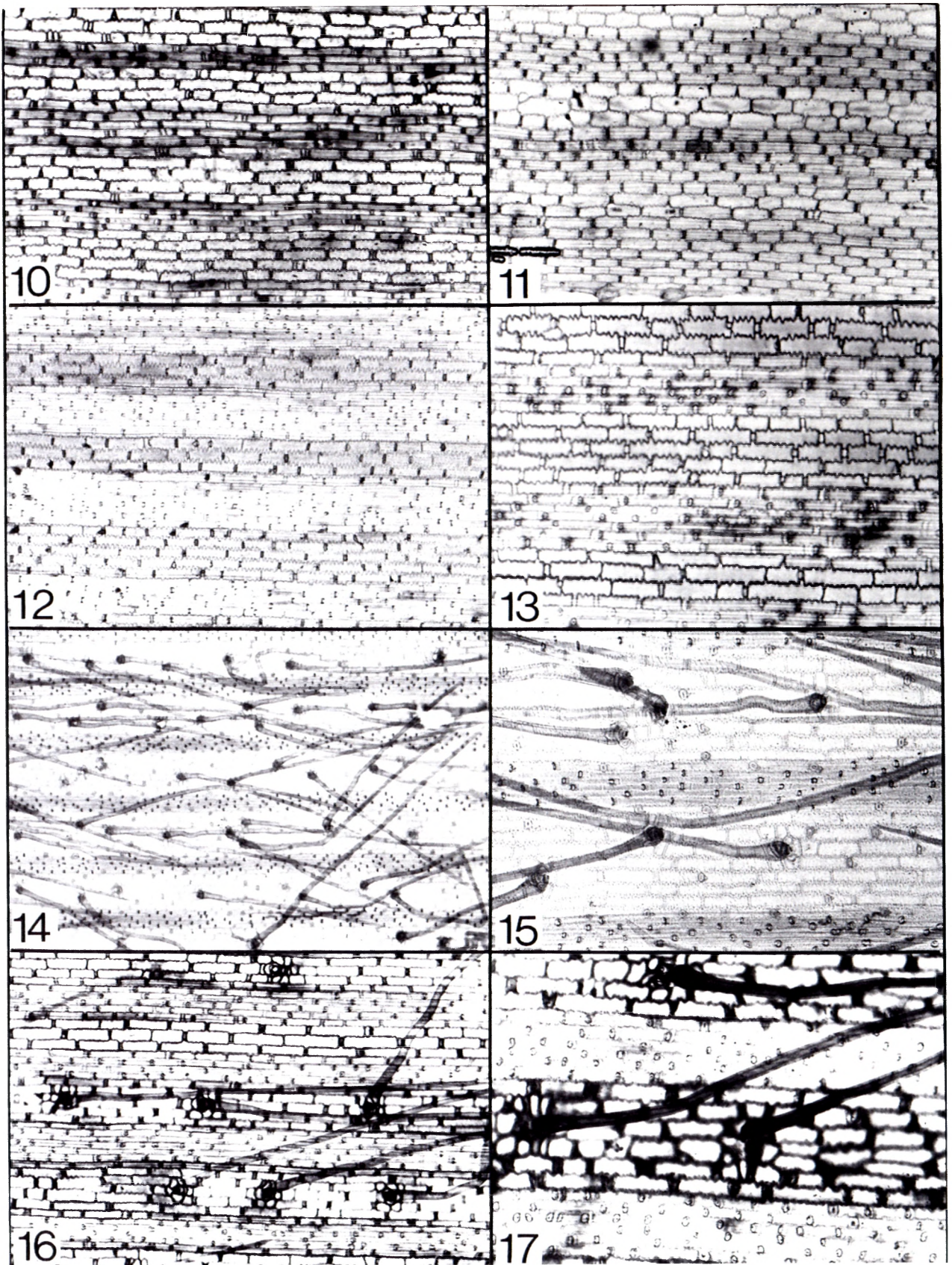
A superficially striking difference, however, is the presence of conspicuous, long, soft macrohairs on some of the specimens of *P. dregeana* studied (Figures 14–17). Although this appears to be a significant difference, it must be remembered that all specimens of *P. dregeana* have this type of macrohair 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 transections 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* (Steud.) Stapf

\* Specimens have abaxial macrohairs.



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,  $\times 160$ ; 11, *Esterhuysen 27321*, without a clear distinction between costal and intercostal zones,  $\times 160$ ; 12, *Ellis 2484*, costal and intercostal zones distinguishable,  $\times 160$ ; 13, *Ellis 2480*, detail of intercostal long cells and costal files,  $\times 250$ . 14–17, pubescent form. 14–15, *Ellis 2556*: 14, numerous long, soft macrohairs,  $\times 100$ ; 15, detail of intercostal macrohairs and their basal cells,  $\times 250$ . 16, *Boucher 2388*, macrohairs common,  $\times 160$ ; 17, *Ellis 2580*, detail of costal zones, intercostal long cells and macrohairs,  $\times 250$ .

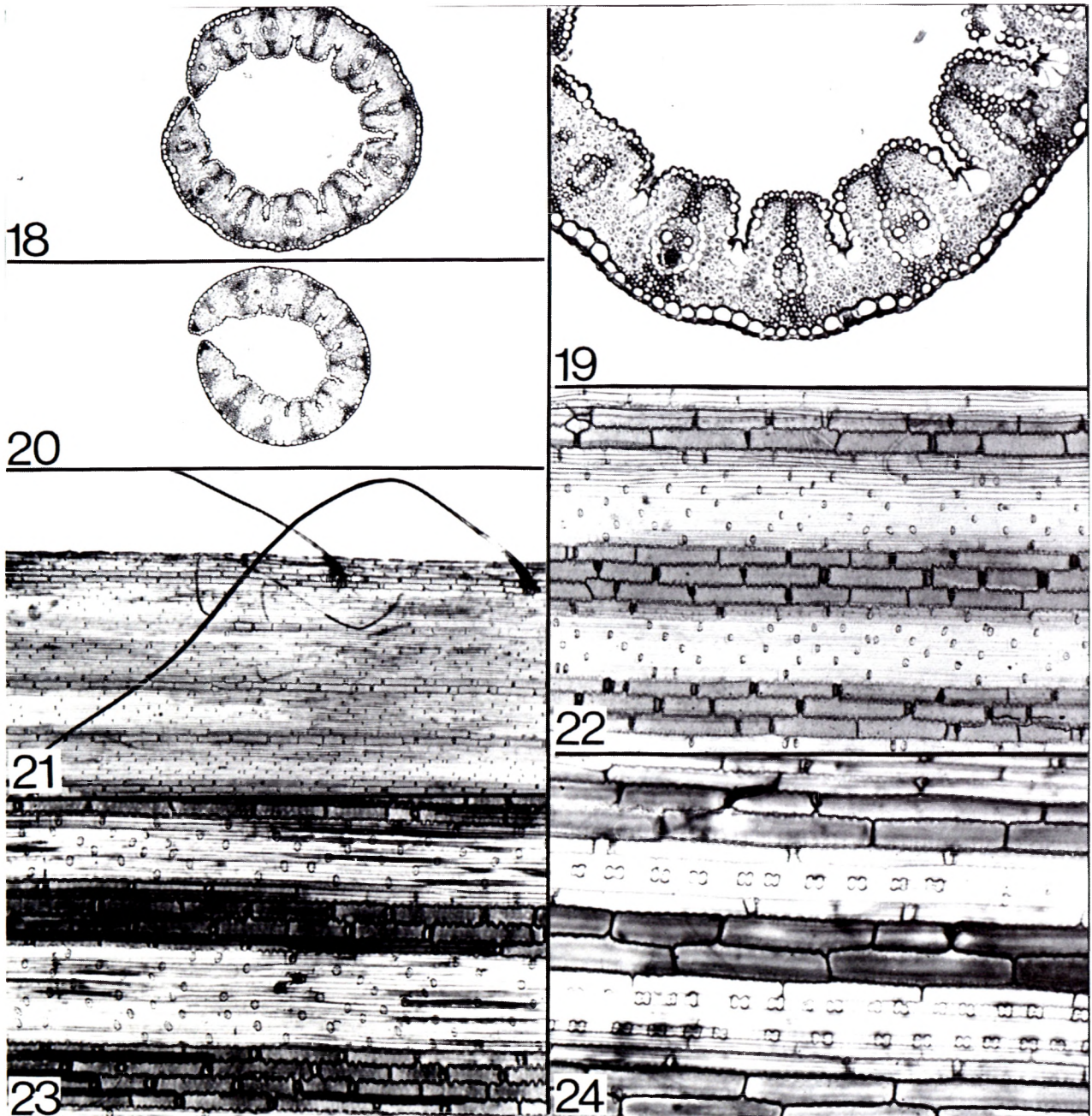
(Figures 25–32). This possible relationship is not evident in leaf transections, because *Pentastichis colorata* and its close allies have very characteristic abaxial epidermal cells between the bundles alternating with small, fibrous cells overlying the bundles. Nevertheless, relationships of *P. dregeana* appear to lie with this group of *Pentastichis* 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 *Pentastichis colorata*.

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

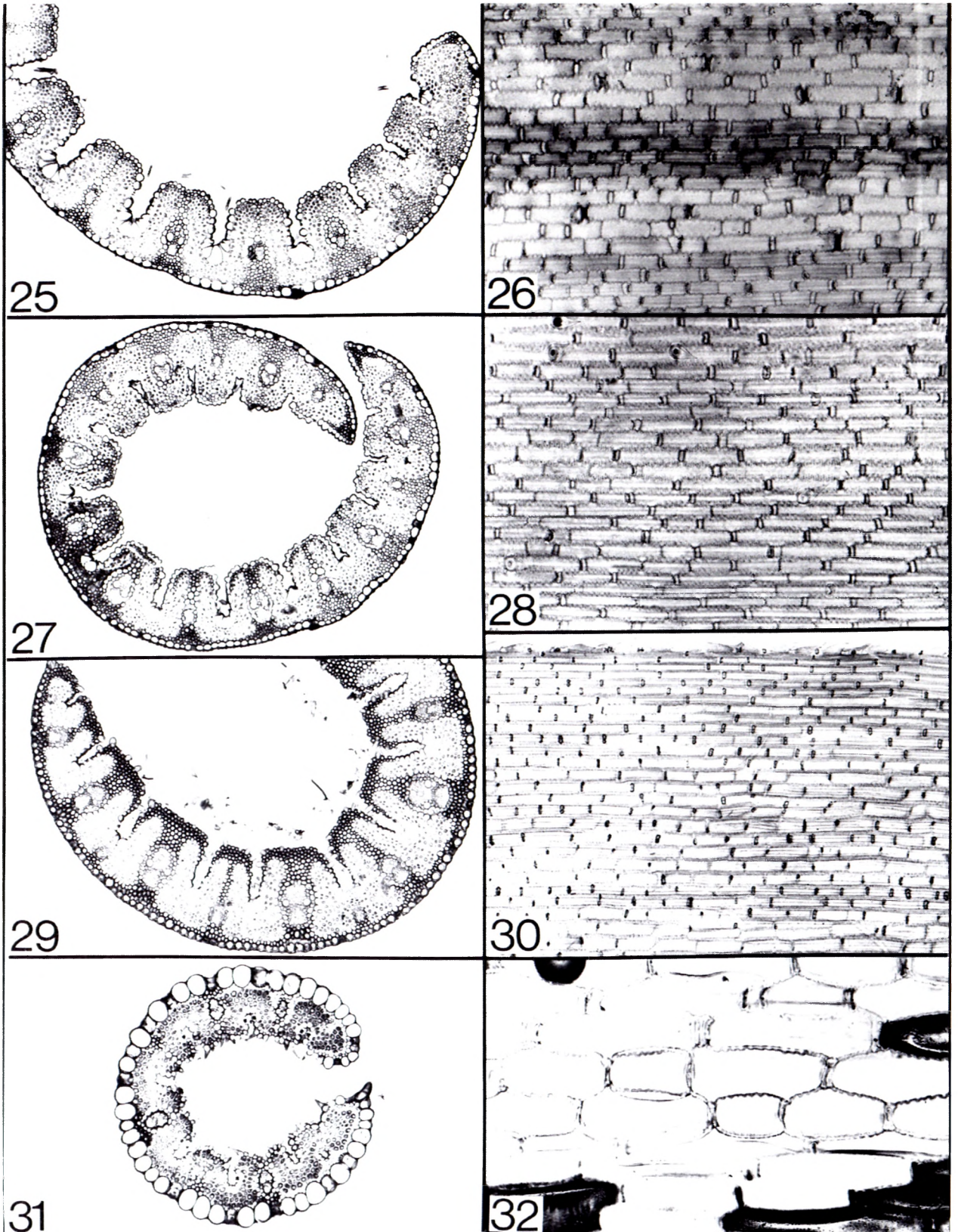
CAPE. — 3219 (Wuppertal): Buffelshoek Pass. Koue Bokkeveld Mts (–CA). *Ellis* 2495, 2497, 3319 (Worcester): Leeuwfontein Peak, Gydoberg (–AD). *Ellis* 2477.

The anatomical gradation of *Pentameris dregeana* into the *Pentastichis colorata* species complex appears to be substantiated by the observation that some specimens identified as *Pentastichis colorata* (Steud.) 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 *Pentastichis 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,  $\times 100$ ; 19, detail of adaxial ribs, mesophyll and vascular bundles,  $\times 250$ . 20, *Ellis* 2495, setaceous, inrolled blade,  $\times 100$ . 21–24, abaxial epidermal anatomy. 21–22, *Ellis* 2495: 21, note very long soft macrohairs associated with margin,  $\times 100$ ; 22, clear distinction between costal and intercostal long cells,  $\times 250$ . 23, *Ellis* 2497, with distinct costal and intercostal zones,  $\times 250$ ; 24, *Ellis* 2477, costal zones with dumbbell shaped silica bodies and very different intercostal long cells,  $\times 250$ .



FIGURES 25–32. — Leaf anatomy of *Pentaschistis colorata* var. *polytricha* for comparison with the anatomy of *Pentameris dregeana*. 25–26, *Ellis 2347*: 25, transverse section similar to that of *P. dregeana*,  $\times 160$ ; 26, abaxial epidermis identical to typical *P. dregeana* type,  $\times 250$ . 27–28, *Ellis 2509*: 27, typical inrolled outline,  $\times 160$ ; 28, epidermis differing somewhat from *P. dregeana* type,  $\times 250$ . 29–30, *Ellis 2506*: 29, outline of blade showing conspicuous sclerenchyma girders and thick cuticle,  $\times 160$ ; 30, abaxial epidermis without distinction between costal and intercostal zones,  $\times 160$ . 31–32, *Ellis 2546*: 31, leaf outline showing inflated epidermal cells,  $\times 160$ ; 32, entire abaxial epidermis consists of inflated long cells,  $\times 400$ .

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* (Steud.) 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*. Its 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*.

#### ACKNOWLEDGEMENTS

Miss L. Smook is thanked for identifying the voucher specimens, Mrs H. Ebertsohn for technical assistance, Mrs A. Romanowski for the photography and Mrs M. van der Merwe for typing the manuscript.

#### REFERENCES

- CHIPPINDALL, L. K. A. 1955. In D. Meredith. *The grasses and pastures of South Africa*. Central News Agency, Johannesburg.
- DE WET, J. M. J. 1956. Leaf anatomy and phylogeny in the tribe Danthoneae. *American Journal of Botany* 43: 175–182.
- ELLIS, R. P. 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. *Bothalia* 12: 65–109.
- ELLIS, R. P. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. *Bothalia* 12: 641–672.
- ELLIS, R. P. 1985a. Leaf anatomy of the South African Danthoneae (Poaceae). XI. *Pentameris longiglumis* and *Pentameris* sp. nov. *Bothalia* 15: 567–571.
- ELLIS, R. P. 1985b. Leaf anatomy of the South African Danthoneae (Poaceae). XII. *Pentameris thuarii*. *Bothalia* 15: 573–578.
- ELLIS, R. P. 1985c. Leaf anatomy of the South African Danthoneae (Poaceae). XIII. *Pentameris macrocalycina* and *P. obtusifolia*. *Bothalia* 15: 579–585.