

## Leaf anatomy of the South African Danthonieae (Poaceae). X. *Pseudopentameris*

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### ABSTRACT

The leaf blade anatomy of *Pseudopentameris macrantha* (Schrad.) Conert and *P. brachyphylla* (Stapf) Conert was studied both in transection and in surface view and is illustrated by means of photomicrographs. The leaf anatomy is typically danthonoid. The abaxial epidermis consists of inflated, hexagonal long cells and stomata and micro-hairs are absent. Adaxial micro-hairs were observed. The creation of a new genus to accommodate these two species appears justified but certain species in *Pentameris* Beauv., *Merxmullera* Conert and *Pentaschistis* Stapf show similarities to *Pseudopentameris* and consideration should be given to their inclusion in *Pseudopentameris*.

### INTRODUCTION

*Pseudopentameris* Conert was described as recently as 1971 to accommodate two species previously placed in *Danthonia* DC., namely *Pseudopentameris macrantha* (Schrad.) Conert and *P. brachyphylla* (Stapf) Conert (Conert, 1971). De Wet (1956) was also of the opinion that these two species deserved generic rank but refrained from describing a new genus as a complete comparative anatomical, cytological and morphological study of the genus *Danthonia* was not available.

The species assigned to *Pseudopentameris* have 2-flowered spikelets over 40 mm long and differ considerably from all the other South African species previously referred to the genus *Danthonia*. Several authorities, including Nees, Kunth and Adamson (Chippindall, 1955), were aware of these differences and had placed these species in the genus *Pentameris* Beauv. Conert (1971) notes that *Pseudopentameris* differs from *Pentameris* in having many-nerved glumes, the caryopsis structure is different and the leaf anatomy is distinct. Chippindall (1955) mentions that the style is greatly reduced, whereas in *Pentameris*, it is short but there is little else in the spikelet morphology of *Pseudopentameris macrantha* and *P. brachyphylla* to suggest affinity with *Pentameris*.

De Wet (1956) considers *Pseudopentameris* to be closely related to both *Danthonia* and *Pentameris* but Conert (1971) is of the opinion that the genus occupies an isolated position with no obvious relationships with other danthonoid grasses. This opinion is confirmed by Renvoize (1981) who includes *Pseudopentameris* in the peripheral genera of his Arundineae which includes all the genera here considered as belonging to the Danthonieae. However, in his multivariate analysis *Pseudopentameris* is grouped with the 'core' genera of the Arundinoideae.

*P. macrantha* and *P. brachyphylla* are both rather robust, tufted perennials being easily distinguished from each other by the pronounced rolling or curling

of the lower leaves of *P. brachyphylla*. The genus is confined to the south-western Cape Province from Piketberg in the north to Riversdale in the east. *P. brachyphylla* is very rare and occurs mainly in the Hottentots Holland range where it sometimes occurs together with *P. macrantha*. *P. macrantha* is particularly common on the Cape Peninsula. Both species appear to favour sandy habitats at the base of hill slopes, often in seepage areas but, in the De Hoop area, *P. macrantha* grows in crevices in limestone rock.

The leaf anatomy of *Pseudopentameris* has received scant attention in the past. De Wet (1954, 1960) reported that the chlorophyll is uniformly distributed throughout the mesophyll, bicellular hairs are present, the epidermis consists of thin parenchyma and the costal silica cells are dumb-bell shaped. He is of the opinion (De Wet, 1956) that the species now included in *Pseudopentameris* combine in their leaf anatomy the panicoid type of epidermis (with micro-hairs) and the festucoid type of chlorophyll distribution. Renvoize (1981), on the other hand, considers micro-hairs to be absent in *Pseudopentameris* but does not consider the genus to belong with the pooid grasses because 'the subsidiary cells are low dome-shaped, the silica bodies are saddle-shaped or oblong and the long cells may be straight or sinuous-walled'. These features favour the placing of this genus in the Arundinoideae.

Conflicting reports have, therefore, been made in the past regarding the leaf anatomy of *Pseudopentameris*, particularly as far as the presence or absence of micro-hairs is concerned. This paper reports on a detailed study of a representative sample of 24 specimens, most of which were freshly fixed in the field and, as a result, should enable anatomical characteristics to be confidently evaluated in future considerations of the relationships and taxonomy of *Pseudopentameris*. The standardized terminology of Ellis (1976, 1979) is used in the descriptions together with the following abbreviations:

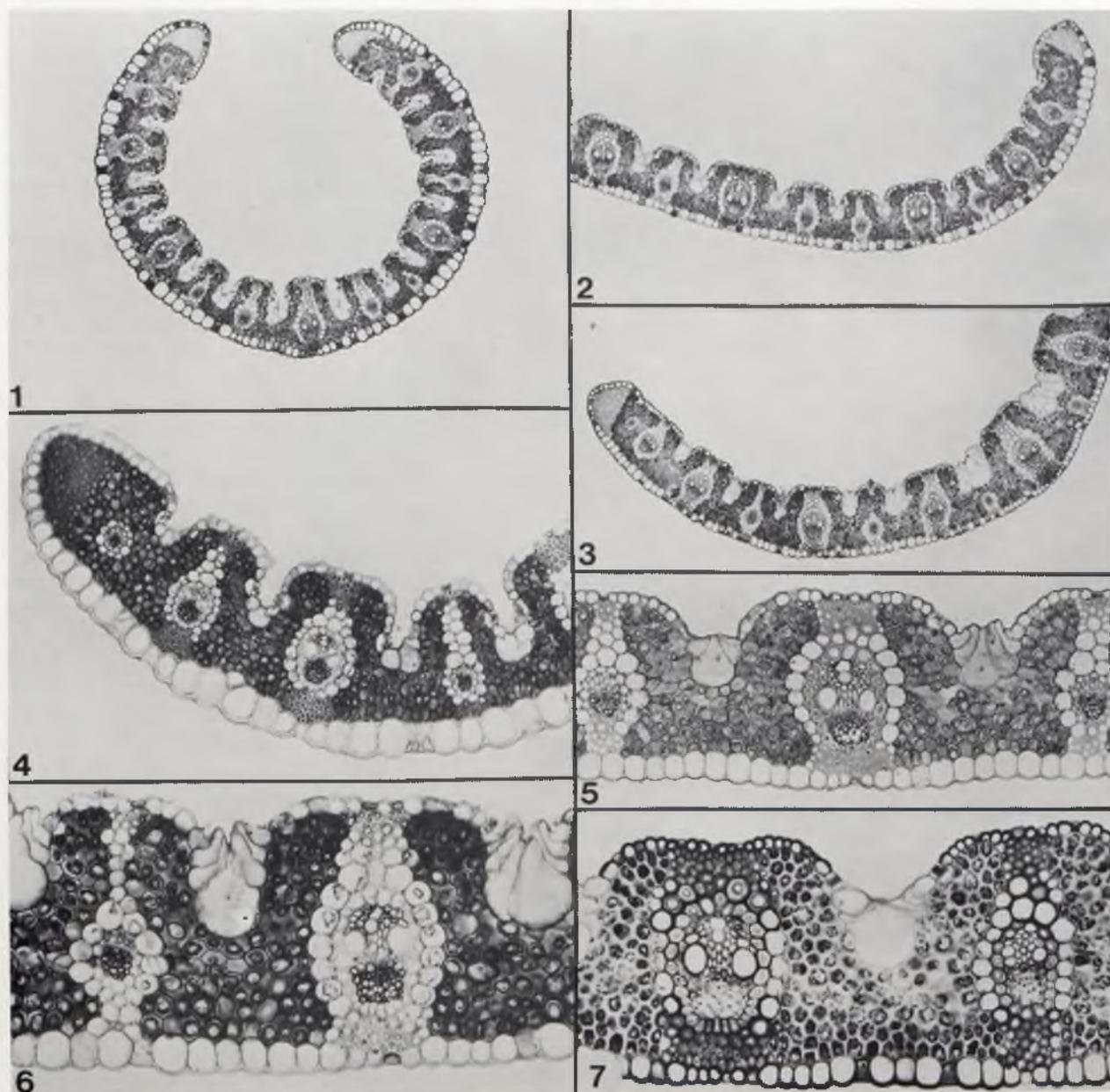
- vb/s — vascular bundle/s
- 1'vb/s — first order vascular bundle/s
- 2'vb/s — second order vascular bundle/s
- 3'vb/s — third order vascular bundle/s
- ibs — inner bundle sheath; mestome sheath
- obs — outer bundle sheath; parenchyma sheath

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ANATOMICAL DESCRIPTION OF *PSEUDOPENTAMERIS*  
CONERT*Leaf in transverse section*

*Leaf outline*: broadly U-shaped (Figs 2 & 3) with arms of lamina convex (Fig. 1) in *P. macrantha*; leaves tend to be expanded and flat in *P. brachyphylla* (Figs 14 & 17). *Ribs & furrows*: similar adaxial ribs present over and furrows between all vbs; furrows of medium depth, either cleft-like (Fig. 4) or more open (Figs 5 & 6); ribs with rounded sides and flat tops in both species. No abaxial rib development. *Median bundle*: not structurally different from other 1'vbs; distinguishable by location only (Figs 1, 14 & 17). *Vascular bundle arrangement*: always 5 1'vbs in leaf section in *P. brachyphylla* (Figs 14 & 17) but *P. macrantha* has either 5 (Fig. 1) or 7 or 9 (Figs 2 & 3). The arrangement of different orders of vbs

along the width of the blade is regular from midrib to margin with 1 3'vb located between consecutive 1'vbs; sometimes the secondary bundle may be sufficiently developed to be termed a 2'vb (Fig. 17) and irregularities in the pattern of arrangement may appear near the margin (Fig. 4). All vbs are located in the centre of the blade or are slightly displaced abaxially. *Vascular bundle structure*: 3'vbs circular to elliptical with phloem well developed (Figs 5, 6 & 16). 1'vbs elliptical with phloem adjoining the ribs; very narrow metaxylem vessels; lysigenous cavity and protoxylem vessels developed. *Vascular bundle sheaths*: obs elliptical to almost round; entire around some 3'vbs (Figs 6 & 15) or with abaxial interruption (Figs 5 & 16); 1'vbs with both adaxial and abaxial interruptions; no extensions. 10–14 cells comprise obs; cells not well differentiated from chlorenchyma cells although obvious due to absence of chloroplasts



FIGS 1–7. — *Pseudopentameris macrantha*: transverse sections of the leaf blade. 1–3, outline of the leaf,  $\times 100$ : 1, Ellis 2526; 2, Ellis 2512; 3, Ellis 2515; 4, leaf margin structure, Ellis 2526,  $\times 250$ . 5–7, detail of vascular bundles and mesophyll: 5, compact, isodiametric chlorenchyma, Ellis 2338,  $\times 250$ ; 6, isodiametric chlorenchyma, Ellis 2515,  $\times 400$ ; 7, unligified sclerenchyma girders and chloroplast arrangement, Ellis 2265,  $\times 400$ .

and slightly thickened walls. Ibs complete around l'vbs; cells with uniformly thickened walls (Figs 5, 7, 15 & 16). *Sclerenchyma*: adaxial girders associated with all l'vbs; equidimensional in *P. macrantha* (Figs 5, 6 & 7) but T-shaped in *P. brachyphylla* (Figs 15 & 16). Abaxial girders equidimensional in both species. Fibres with thickened walls but composed mainly of cellulose and do not stain red with saffranin. Margins with rounded sclerenchyma cap in *P. macrantha* (Fig. 4) but no sclerenchyma developed in association with the margin in *P. brachyphylla* (Figs 14 & 17). *Mesophyll*: chlorenchyma not radiate; consists of tightly packed, angular, regular, isodiametric cells (Figs 5, 6 & 16); these chlorenchyma cells with characteristic central vacuole with peripheral chloroplasts. No colourless cells. *Adaxial epidermis*: fan-shaped groups of bulliform cells situated at bases of furrows. No macro-hairs, prickles, hooks or papillae seen but adaxial micro-hairs commonly visible in transections of *P. brachyphylla* (Figs 15 & 16). *Abaxial epidermis*: no bulliform cells; consists of very conspicuous large, regular, inflated cells with outer tangential wall slightly thickened. No appendages.

#### *Abaxial epidermis in surface view*

*Intercostal long cells*: usually elongated but sometimes length is only slightly greater than width (Fig. 12); side walls always angled or bowed outwards giving cells a hexagonal or inflated appearance; end walls vertical; walls either slightly undulating (Fig. 18) or not undulate (Fig. 12) and unthickened. Cell shape and size is noticeably consistent throughout all intercostal zones. Pairs of short cells are present between successive long cells. No abaxial bulliform cells. *Stomata*: absent on abaxial surface of both *P. macrantha* and *P. brachyphylla* in all specimens examined except Ellis 2515 (Fig. 8); low dome-shaped. *Intercostal short cells*: silico-suberose couples with silica cell tall and narrow with smooth outline or kidney shaped (Figs. 12, 18 & 19); short cell larger than silica cell and enfolding it; located between virtually all intercostal long cells. *Papillae*: absent. *Prickles & hooks*: not present on any preparations examined. *Micro-hairs*: not present on abaxial surface. *Macro-hairs*: absent. *Costal silica bodies*: equidimensional to horizontally elongated dumb-bell shaped (Figs 12, 13, 18 & 19); alternate with costal long cells; costal zones narrow (3–5 files wide).

#### Specimens examined:

##### *Pseudopentameris brachyphylla*

CAPE. — 3418 (Simonstown): Platberg, Kogelberg State Forest (-BD), Ellis 2343, 2344, Boucher 357a. 3419 (Caledon): Lebanon Forest Reserve, Grabouw (-AA), Kruger 149; Bredasdorp (-BD), Acocks 22476.

##### *Pseudopentameris macrantha*

CAPE. — 3218 (Clanwilliam): Versveld's Pass, Piketberg (-DC), Ellis 1171. 3318 (Cape Town): Kirstenbosch, Table Mountain (-CD), Ellis 2308, Sandwith 73, White 5518; Heuningvlei, Jonkershoek (-CD), Ellis 2265, 2266. 3418 (Simonstown); Cape Point Nature Reserve (-AD), Ellis 2326, 2327; Cape Hangklip (-BD), Ellis 2338, 2339; Elephant Rock near Bettys Bay, Cleghorn 2495. 3419 (Caledon): 5 km from Kleinmond on road to Hermanus (-AC), Ellis 2515; 10 km from Hermanus on

road to Gansbaai (-AD), Ellis 2512. 3420 (Bredasdorp): De Hoop Nature Reserve (-AD), Ellis 1288, 2526; 5 km from Wydegelegen on road to De Hoop, Ellis 1660; Breede River mouth (-BD), Ellis 1673; 3 km from Arniston on road to Bredasdorp (-CA), Ellis 1274. 3421 (Riversdale): Albertina (-BA), Ellis 2551.

#### DISCUSSION AND CONCLUSIONS

The contradictory statements in the literature regarding the presence or absence of micro-hairs in *Pseudopentameris* deserve comment in the light of the observations of the present study. No micro-hairs were observed on the abaxial epidermis of any of the 24 specimens examined in this study and this observation is in agreement with the statement by Renvoize (1981) that micro-hairs are absent. However, in the leaf transections of all the specimens of *P. brachyphylla*, and in many of the sections of *P. macrantha*, micro-hairs are clearly evident on the sides of the furrows of the adaxial epidermis. (Figs 15 & 16). The emphasis placed on the absence of micro-hairs by Renvoize (1981), therefore, is not justified and *Pseudopentameris* can be considered as belonging to the Arundineae together with all the other South African genera previously placed in the Danthonieae. Considering it as a peripheral genus, together with the other anomalous arundinoid genera, is no longer necessary in the light of the observations of the present study.

This confirmation of the presence of micro-hairs on *Pseudopentameris* agrees with De Wet's (1954, 1956, 1960) observations. However, De Wet (1956) considers the epidermis of *Pseudopentameris* to be panicoid and similar to that of genera such as *Schismus* Beauv., *Chaetobromus* Nees and many species of *Pentaschistis* Stapf. This is not the case, however, as *Pseudopentameris* does not possess numerous abaxial micro-hairs as do all the above genera. The abaxial epidermis of *Pseudopentameris* actually resembles that of *Pentameris* Beauv. and *Merxmuellera* Conert. more closely. These are considered as being festucoid by De Wet (1956) and the characterization of the epidermis of *Pseudopentameris* as panicoid does not agree with the observations of the present study. Of all the South African danthonoid genera, *Pseudopentameris* resembles most closely *Pentameris*, *Merxmuellera* and those *Pentaschistis* species considered by De Wet (1956) as having the festucoid type of epidermis. All these taxa lack abaxial micro-hairs, costal zones are often not clearly defined and stomata are often absent from this surface.

Superficial morphological similarities between *Pseudopentameris* and *Pentameris* undoubtedly exist and Nees, Kunth and Adamson considered these two genera to be congeneric (Chippindall, 1955). Numerous morphological characteristics distinguish these two genera (Chippindall, 1955; De Wet, 1956), however, and Conert (1971) considered these differences to be of sufficient magnitude to warrant the establishment of a new genus. He is of the opinion that no close and obvious relationship exists between *Pseudopentameris* and any other genera known to him.

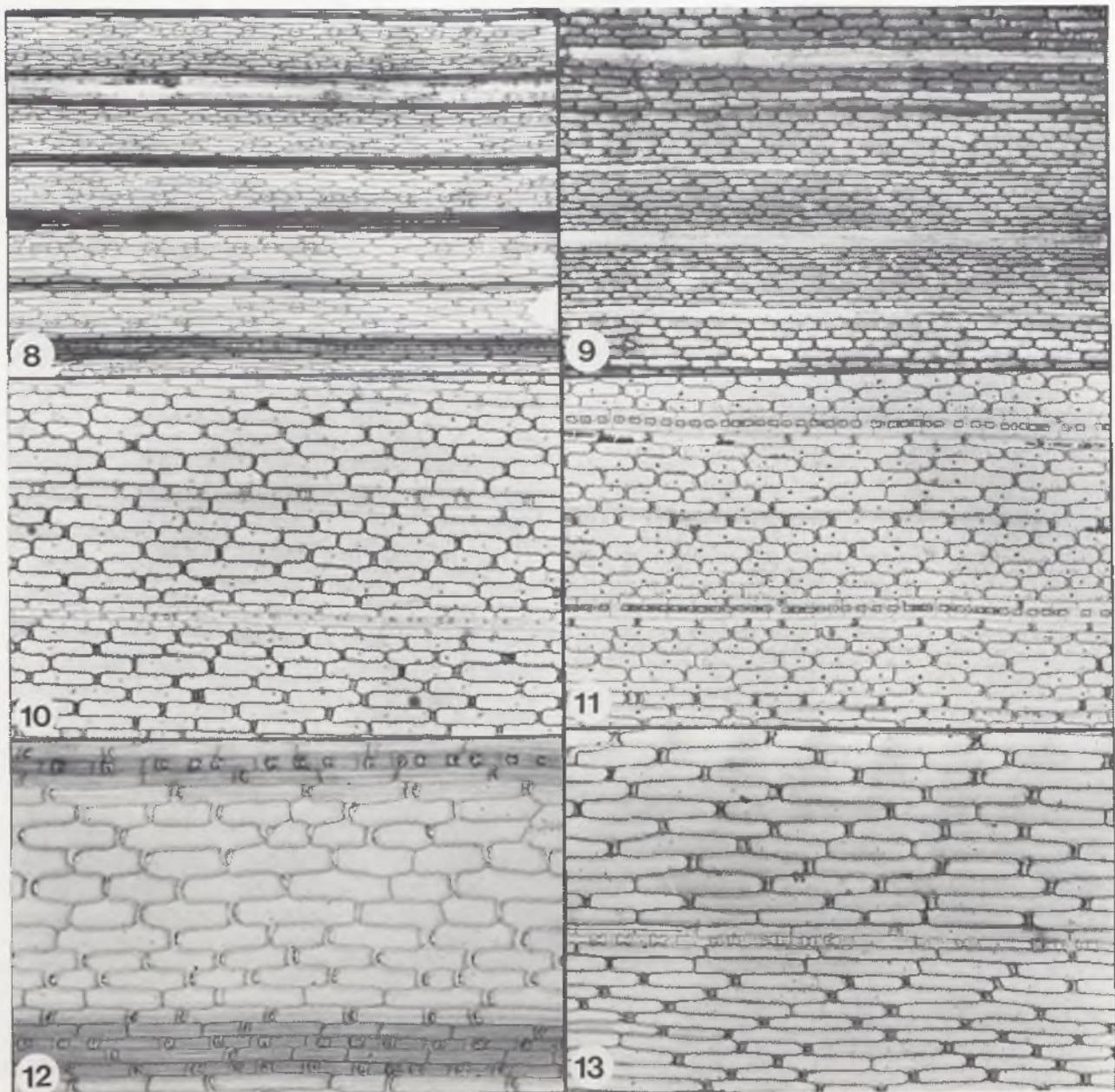
The leaf anatomy corroborates Conert's (1971) decision. The anatomy of *Pseudopentameris* differs

significantly from that of most *Pentameris* species and anatomical indications are that *Pseudopentameris* undoubtedly warrants separate generic status and that it occupies a somewhat isolated phylogenetic position nearest to *Pentameris* and *Merxmuellera*. This contention appears to be substantiated by the fact that there are some species in both the latter genera possessing a large degree of anatomical similarity to *Pseudopentameris*, indicating a somewhat intermediate relationship for *Pseudopentameris*.

*Pentameris dregeana* Stapf, *P. macrocalycina* (Steud.) Schweick., *P. obtusifolia* (Hochst.) Schweick. and *P. thurarii* Beauv. show little anatom-

ical similarity to *Pseudopentameris*. However, *Pentameris longiglumis* (Nees) Stapf and an undescribed species represented by *Ellis* 2342, *Taylor* 3023 and *Haynes* 770, bear rather close resemblances to *Pseudopentameris*. Both these species have large, inflated abaxial epidermal cells which are hexagonal in shape in surface view. Stomata and micro-hairs are also absent and the costal zones are somewhat indistinct. However, the silica bodies are not dumb-bell shaped as in *Pseudopentameris*.

Both these two *Pentameris* species have been found only in the Caledon District in the Kogelberg State Forest. They grow together in the same com-



FIGS 8-13. — *Pseudopentameris macrantha*: abaxial epidermis. 8-9, arrangement of costal and intercostal zones.  $\times 100$ : 8, costal and intercostal zones overlying first and third order vascular bundles, note presence of stomata. *Ellis* 2515; stomata absent, *Ellis* 2526. 10-11, regular intercostal long cells and narrow costal zones,  $\times 160$ : 10, *Ellis* 1288; 11, *Ellis* 1673. 12-13, detail of epidermal cells.  $\times 250$ : 12, intercostal long cells separated by silico-suberose couples and costal silica bodies irregularly dumb-bell shaped. *Ellis* 2551; 13, silica bodies dumb-bell shaped and long cells slightly sinuous. *Ellis* 2265.

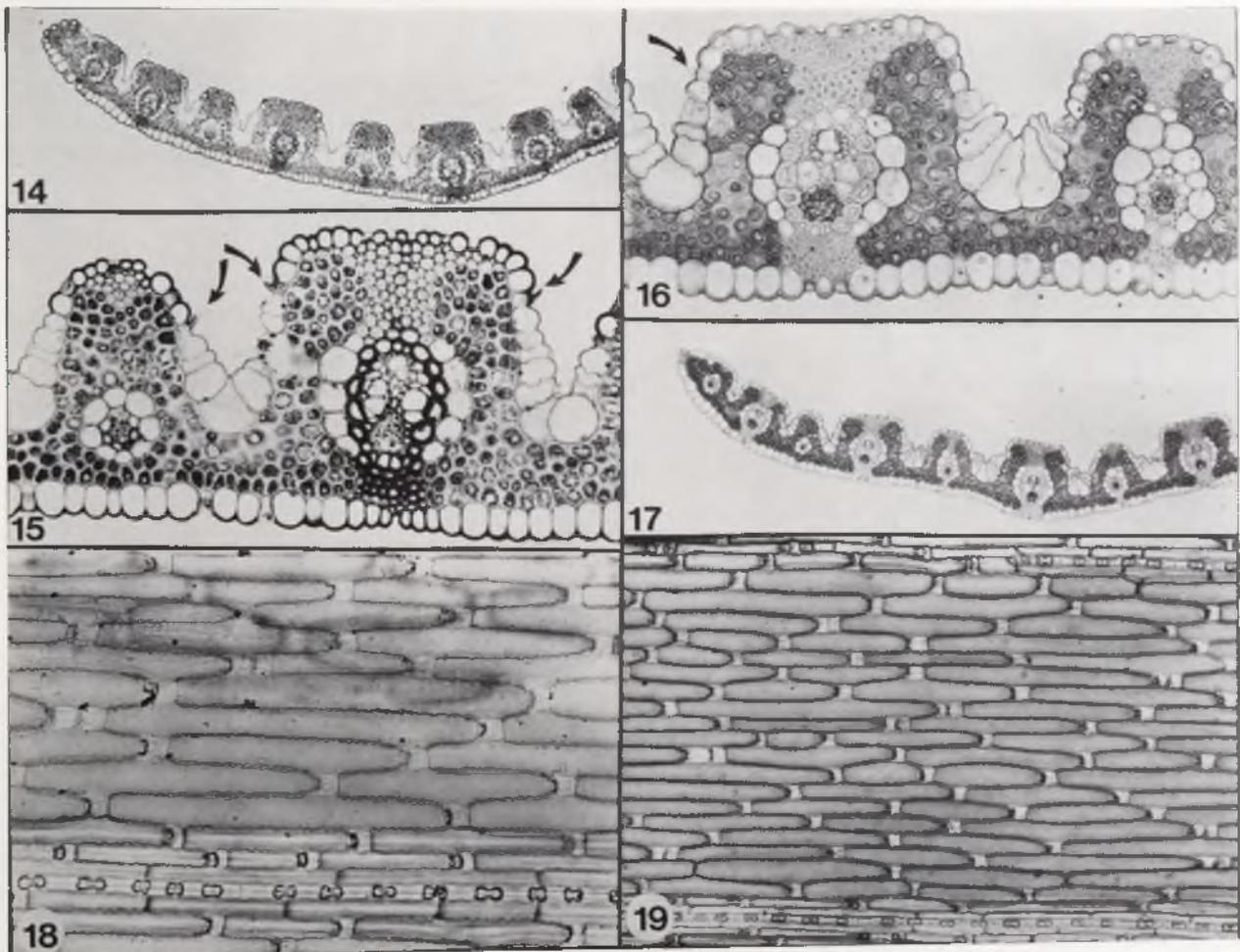
munity, often also in association with both *Pseudopentameris brachyphylla* and *P. macrantha*. The undescribed species, in particular, appears to be intermediate between *Pentameris longiglumis* and *Pseudopentameris* and a hybrid origin appears most likely. The spikelet morphology of *Pentameris longiglumis* requires detailed reassessment in order to establish its true relationships with either *Pentameris* or *Pseudopentameris*.

In the genus *Merxmuellera* there is also a group of species which differs significantly from the remainder of the genus in possessing epidermal long cells with outwardly bowed walls. This group includes *M. decora* (Nees) Conert, *M. lupulina* (Thunb.) Conert and *M. rufa* (Nees) Conert and their anatomy has been described in detail (Ellis, 1983). All these species differ from *Pseudopentameris* in having abaxial stomata and micro-hairs. However, stomata are absent from some specimens of *Merxmuellera decora* and micro-hairs are exceedingly rare in all three species. It must also be mentioned that the inflated nature of the abaxial long cells is only evident in surface view and in transection the epidermal cells are not as large and inflated as in *Pseudopentameris*. All the above species do, however, have very little lignin present in the fibres of the sclerenchyma gir-

ders — a noticeable feature shared with *Pseudopentameris* but not with other danthonoid grasses in general.

Finally, *Merxmuellera lupulina*, in particular, bears a strong anatomical resemblance with *Pentaschistis involuta* (Steud.) Adamson and *P. viscidula* (Nees) Stapf (Ellis, 1983). These species also have inflated epidermal cells and are exceptional in the genus due to this fact. They, therefore, deserve consideration together with *Merxmuellera lupulina* and its allies.

Anatomical criteria, therefore, suggest that the above-mentioned *Merxmuellera*, *Pentameris* and *Pentaschistis* species require taxonomic re-evaluation in conjunction with *Pseudopentameris*. This is essential in order to establish the true relationships of *Pseudopentameris* and to define the limits of the above genera. This study of the leaf anatomy of *Pseudopentameris* fully supports the creation of a separate genus to accommodate these two very closely related species which bear little resemblance to the majority of the taxa previously classified in *Danthonia* as well as *Pentameris* and *Pentaschistis*. However, *Pseudopentameris* does share certain anatomical characters with a few species from each of



FIGS 14-19. — *Pseudopentameris brachyphylla*: leaf anatomy and epidermal structure. 14-17. leaf in transverse section: 14, outline of leaf, Ellis 2344,  $\times 100$ ; 15, detail of mesophyll and vascular bundles, note presence of adaxial micro-hairs (arrowed), Ellis 2344,  $\times 400$ ; 16, mesophyll, vascular bundles and micro-hair (arrowed), Ellis 2343,  $\times 250$ ; 17, outline, Ellis 2343,  $\times 100$ . 18-19, detail of abaxial epidermis: 18, sinuous intercostal long cells and dumb-bell shaped silica bodies, Ellis 2344,  $\times 400$ ; 19, intercostal long and short cells, Ellis 2343,  $\times 250$ .

these genera but the taxonomic and phylogenetic significance of these shared characteristics is not certain at this stage and awaits cytogenetical confirmation. A possible practical solution, that is suggested by the leaf anatomy, is the incorporation of all these taxa with anomalous anatomy in a single genus together with *Pseudopentameris*. This would result in the creation of a genus, which would be anatomically homogeneous, and would be easily distinguishable from all the other South African danthonoid genera on the basis of leaf anatomy.

#### UITTREKSEL

*Die anatomiese struktuur van die blaar van Pseudopentameris macrantha (Schr.) Conert en P. brachyphylla (Stapf) Conert is bestudeer. Beskrywings van die blaaranatomie in dwarsnee en van die abaksiale epidermis word gegee en geïllustreer deur middel van fotomikrograwe. Die blaaranatomie is tipies van die Danthonieae maar die abaksiale epidermis bestaan hoofsaaklik uit geswolle, seshoekige langselle en huidmondjies en mikrohare is afwesig. Adaksiaal mikrohare is wel waargeneem. Die beskrywing van 'n nuwe genus vir die twee spesies, wat huidiglik in Pseudopentameris gehuisves word, blyk geregverdig*

*te wees maar sekere spesies van Pentameris Beauv., Merxmuellera Conert en Pentaschistis Stapf toon ooreenkomste met Pseudopentameris en behoort oorweeg te word vir moontlike insluiting in hierdie genus.*

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