Bothalia 15, 3 & 4: 579–585 (1985)

Leaf anatomy of the South African Danthonieae (Poaceae). XIII. *Pentameris macrocalycina* and *P. obtusifolia*

R. P. ELLIS*

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

ABSTRACT

The leaf blade anatomy of *Pentameris macrocalycina* (Steud.) Schweick. and *P. obtusifolia* (Hochst.) Schweick. is described and illustrated. The leaf anatomy of these two species shows many similarities suggesting a close relationship between them. A slight problem appears to exist with the circumscription of *P. obtusifolia* and a minor taxonomic adjustment may result in a classification which agrees totally with that based on leaf anatomy. This would result in details of the leaf outline being diagnostic for these two taxa. The nomenclature of *P. obtusifolia* is also very confusing and clarification is needed by reference to the relevant type specimens. *P. macrocalycina* and *P. obtusifolia* together with *P. longiglumis* (Nees) Stapf, appear to form a distinct genus and do not bear close anatomical resemblances to either *P. thuarri* Beauv. or *P. dregeana* Stapf.

INTRODUCTION

Pentameris macrocalycina (Steud.) Schweick. and *P. obtusifolia* (Hochst.) Schweick. are two grass species which are common in the mountain fynbos of the mountain ranges of the extreme southern Cape. Their distribution ranges from the Cedarberg in the west to the Great Winterhoek Mountains in the east. Both species prefer rocky habitats on Table Mountain Sandstone, often occurring on very steep slopes with a cool, south-facing aspect. They are true montane species capable of withstanding extreme climatic conditions and *P. obtusifolia*, in particular, is found on even the highest peaks in alpine conditions. At these higher altitudes (above 1 650 m) this species may form low, dense, cushion-like plants, possibly in response to regular snowfalls.

These two species appear to be well adapted to fire and most collectors note that they are conspicuously common soon after fires. However, after several seasons of regeneration of the fynbos sclerophyllous vegetation they may die out and be replaced by ericaceous and proteaceous species. On the other hand, *P. macrocalycina* may remain common for many years even in the absence of burning. This is obvious on extremely rocky substrates such as crevices in rocks, even in mature fynbos communities.

Both species are strongly tufted perennials with rigid and woody culms. The leaf sheaths are glabrous except at the woolly mouth and the leaf blades are wiry, filiform, plicate and terete. These blades are finely pointed or pungent, very hard, glabrous and smooth outside and densely but minutely tomentose inside. The leaves of an individual plant may be either flexuous and strongly curled or erect and very straight. Plants with both leaf types often occur in the same population and, consequently, this difference does not appear to be taxonomically or ecologically significant although it has a very strong visual impact. In *P. obtusifolia* the leaf blades are usually shorter, more rigid and exceptionally pungent (Chippindall, 1955).

The ecological requirements, as well as vegetative and spikelet morphology, of these two species are very similar and they appear to be closely allied. Chippindall (1955) notes a close relationship between *P. obtusifolia* and *P. dregeana* Stapf but this was not borne out by field observations or leaf anatomy (Ellis, in press). In this study, the leaf anatomy of *P. macrocalycina* and *P. obtusifolia* will be compared to ascertain whether the leaf anatomy confirms these indications of a close relationship. The anatomy of these species has not been published in the literature and it will be described and illustrated in detail using standardized terminology (Ellis, 1976, 1979). The following abbreviations will be used:

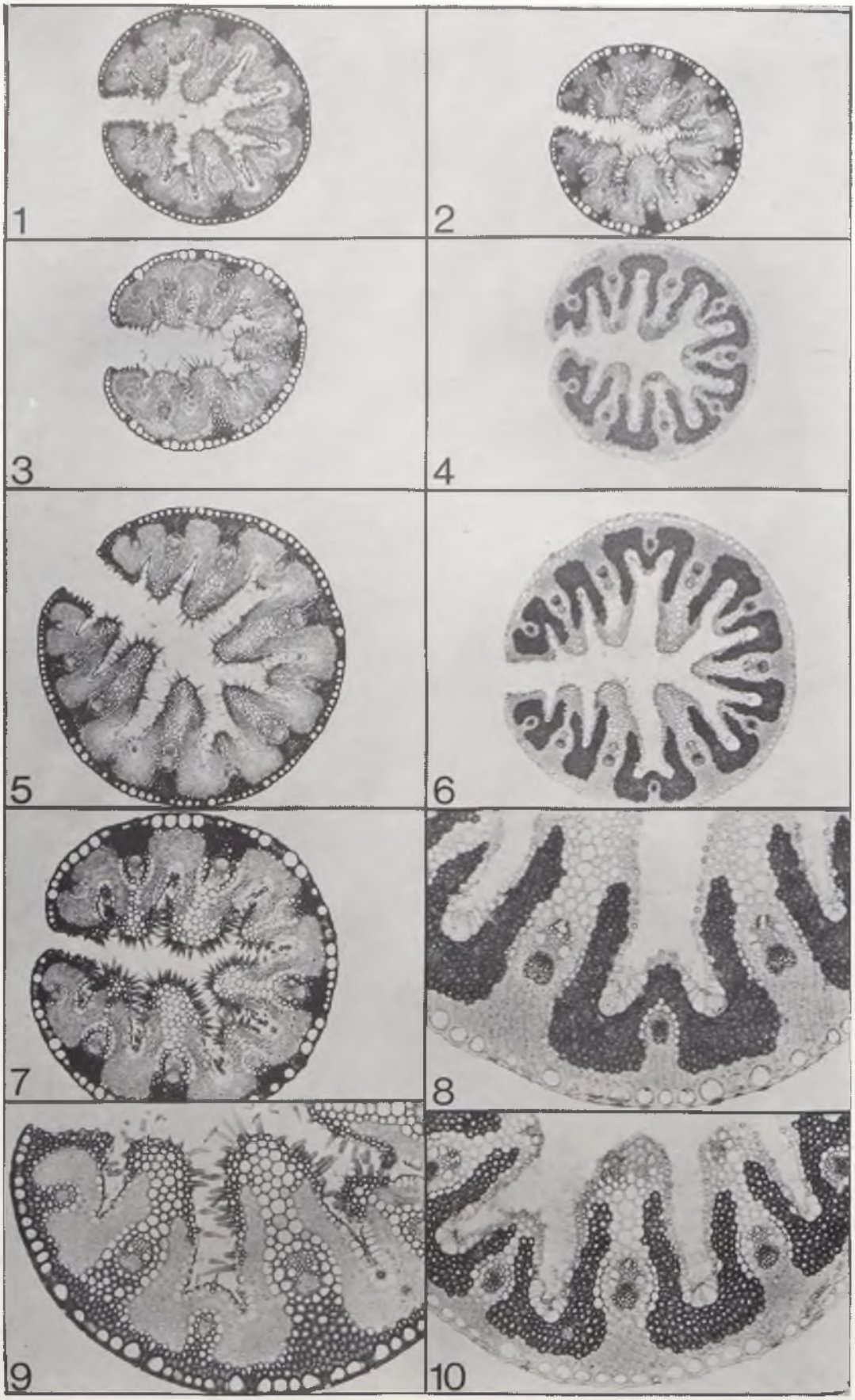
vb/s — vascular bundle/s
1'vb/s — first order vascular bundle/s
3'vb/s — third order vascular bundle/s
ibs — inner bundle sheath; mestome sheath
obs — outer bundle sheath; parenchyma sheath

ANATOMICAL DESCRIPTION OF *PENTAMERIS MACROCALYCINA*

Leaf in transverse section

Outline of lamina: permanently infolded with very round outline (Figs 1–6); adaxial channel a deep, narrow cleft (Figs 5–7); 9, 11 or 13 vbs in blade; diameter of leaf section 3,0–4,0 mm and leaf thickness ± 2,0 mm. *Ribs and furrows*: adaxial ribs and furrows between all vbs; furrows very deep and cleft-like; rounded, massive ribs over 1'vbs, smaller ribs over 3'vbs (Figs 8–10). No abaxial ribs or furrows. *Median vascular bundle*: structurally identical to 1'vbs or may be smaller than lateral 1'vbs; no midrib or keel developed. *Vascular bundle arrangement*: 5 or 7 1'vbs in blade; one 3'vb usually separates consecutive 1'vbs (Figs 1 & 2) but lateral 1'vbs may be adjacent to one another (Figs 3–7). No 2'vbs. All bundles located closer to the abaxial surface. *Vascular bundle description*: 3'vbs elliptical with well-de-

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



FIGS. 1 – 10. — Transverse sections of the leaf blade of *Pentameris macrocalycina*. 1, *Ellis* 2500 × 100; 2, *Ellis*, 2557, × 100; 3, *Ellis* 2540, × 100; 4, *Ellis* 2499, × 100; 5–6, *Ellis* 2508, × 160; 7, *Ellis* 2548, × 160; 8, *Ellis* 2508, × 250; 9, *Ellis* 2275, × 250; 10, *Ellis* 2499, × 250. Figs 4, 6, 8 & 10 taken with a red filter to enhance cellulose cell walls and for the remainder a green filter was used resulting in the lignified walls being accentuated.

veloped phloem. 1'vbs elliptical; phloem adjoins ibs; metaxylem vessels very narrow, narrower even than the ibs cells (Fig. 9). *Vascular bundle sheaths*: obs elliptical; reduced to two lateral columns of cells on either side of each 1'vb (Figs 8–10); incomplete with wide adaxial and abaxial interruptions; intergrades adaxially with a conspicuous extension/girder composed of thickened parenchyma (Figs 8–10). Obs cells small, irregular in shape, with thin walls and with no chloroplasts. Ibs entire; consists of relatively large cells with inner tangential and radial walls thickened. *Sclerenchyma*: 1'vbs with adaxial, inversely anchor-shaped girders of thickened parenchyma joined to the vbs by long, thick obs extensions (Figs 9 & 10). 3'vbs may lack girders (Fig. 8). All vbs with conspicuous, abaxial, sclerenchymatous girders linked laterally to form a continuous, subepidermal layer of sclerenchyma (Figs 8–10). Fibres lignified (Figs 5 & 6) and thick-walled. No additional sclerenchyma cap developed in the leaf margin but abaxial hypodermal layer extends around the margin to the apex of the first adaxial rib (Fig. 9). *Mesophyll*: homogeneous chlorenchyma consisting of small, tightly packed, isodiametric cells irregularly arranged. The cells occupy the sides and bases of furrows and form either U-shaped (Fig. 10) or W-shaped (Fig. 8) groups. No colourless cells in the mesophyll. *Adaxial epidermis*: small, indistinct groups of bulliform cells at bases of furrows (Figs 8 & 10); epidermal cells very small with individual cuticles; prickles very common. *Abaxial epidermis*: no bulliform cells; epidermis of large, uniform cells with continuous, thick cuticle (Fig. 9). No macrohairs, prickles or papillae.

Abaxial epidermis in surface view

Intercostal long cells: rectangular, length about twice width (Figs 11–18); side walls parallel, end walls vertical; walls heavily thickened and pitted (Figs 15–18). Cell shape and size very consistent throughout abaxial epidermis; costal zones not easily distinguishable. Adjacent horizontal files arranged so that long cells and short cells are opposite one another in a brick-work pattern. Long cells separated by short cells in a single file. *Intercostal short cells*: silico-suberose couples between all long cells; cork cell crescentic, enfolding rounded silica body (Figs 15 & 16). Narrower than long cells. *Stomata*: no abaxial stomata (Figs 11–18). *Papillae*: absent. *Prickles*: absent. *Micro-hairs*: none seen. *Macrohairs*: absent. *Costal zones*: usually indistinguishable from intercostal zones in surface view (Fig. 11); sometimes evident due to underlying fibres and slightly narrower long cells (Figs 12 & 14). Composition identical to intercostal zones.

Specimens examined:

CAPE. — 3219 (Wuppertal): Algeria State Forest, Cedarberg Mountains (-AC), *Ellis 2508*; Sneeuberg, *Taylor 5131*; Buffelshoek Pass, Koue Bokkeveld Mountains (–CA), *Ellis 2499, 2500*. 3318 (Cape Town): Jonkershoek, Stellenbosch (–DD), *Adamson 3980*. 3319 (Worcester): Franschhoek Pass, Franschhoek (–CC), *Ellis 2348*. 3321 (Ladismith): Garcia's Pass, Langeberg (–CC), *Ellis 2540*. 3322 (Oudtshoorn): top of Swartberg Pass (–AC), *Ellis 2557, 2582*: Robinsons Pass, Outeniqua Mountains (–CC), *Ellis 2548*. 3323 (Willowmore): Potjiesrivierhoogte Pass (–CA), *Acocks 21589*. 3324 (Steytlerville): Cockscomb Peak, Great Winterhoek Mountains (–DB), *Esterhuysen 28012*. 3418 (Simonstown): (–AB), *Ellis 2313, 2314, 2315*: Sugarloaf Peak, Hottentots Holland Mountains (–BB), *Ellis 2275, 2280, 2292, 2293*.

ANATOMICAL DESCRIPTION OF *PENTAMERIS OBTUSIFOLIA*

Leaf in transverse section

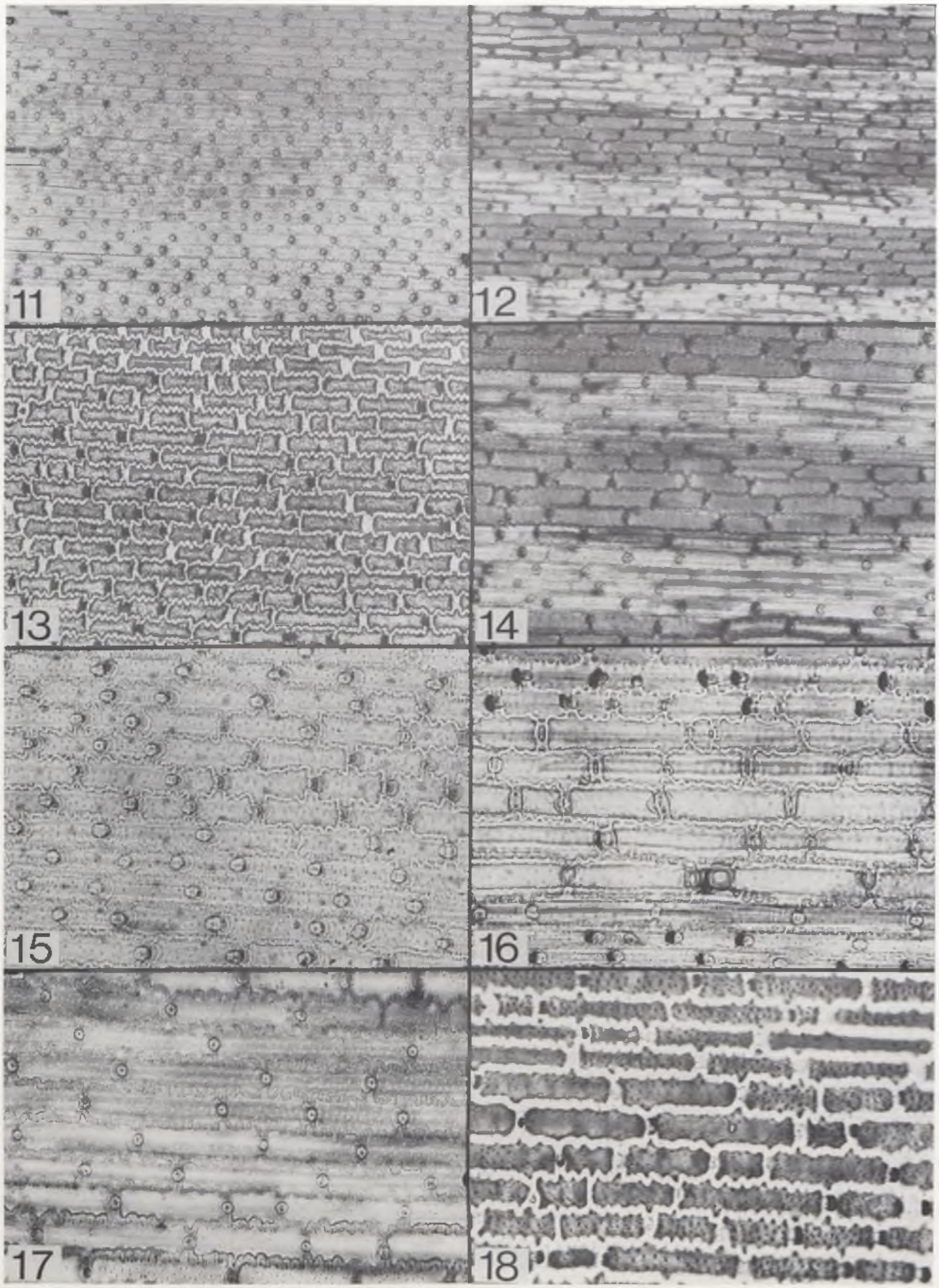
Two different types of leaf anatomy can be recognized in this species. These different anatomical types are based entirely on differences in the leaf outline but the remaining anatomical characteristics of the leaf blade are very similar to those described for *P. macrocalycina*. The detailed anatomical description given for *P. macrocalycina* can, therefore, serve adequately to describe *P. obtusifolia* and here only differences will be accentuated.

The first anatomical type of *P. obtusifolia* (Figs 19–22) has a tightly acicular, permanently infolded leaf lamina which is round in section and has a narrow, cleft-like adaxial channel. The second type (Figs 23–26) differs in having an inrolled leaf which cannot be regarded as being of the permanently infolded type and which lacks a cleft-like adaxial channel with vertical sides.

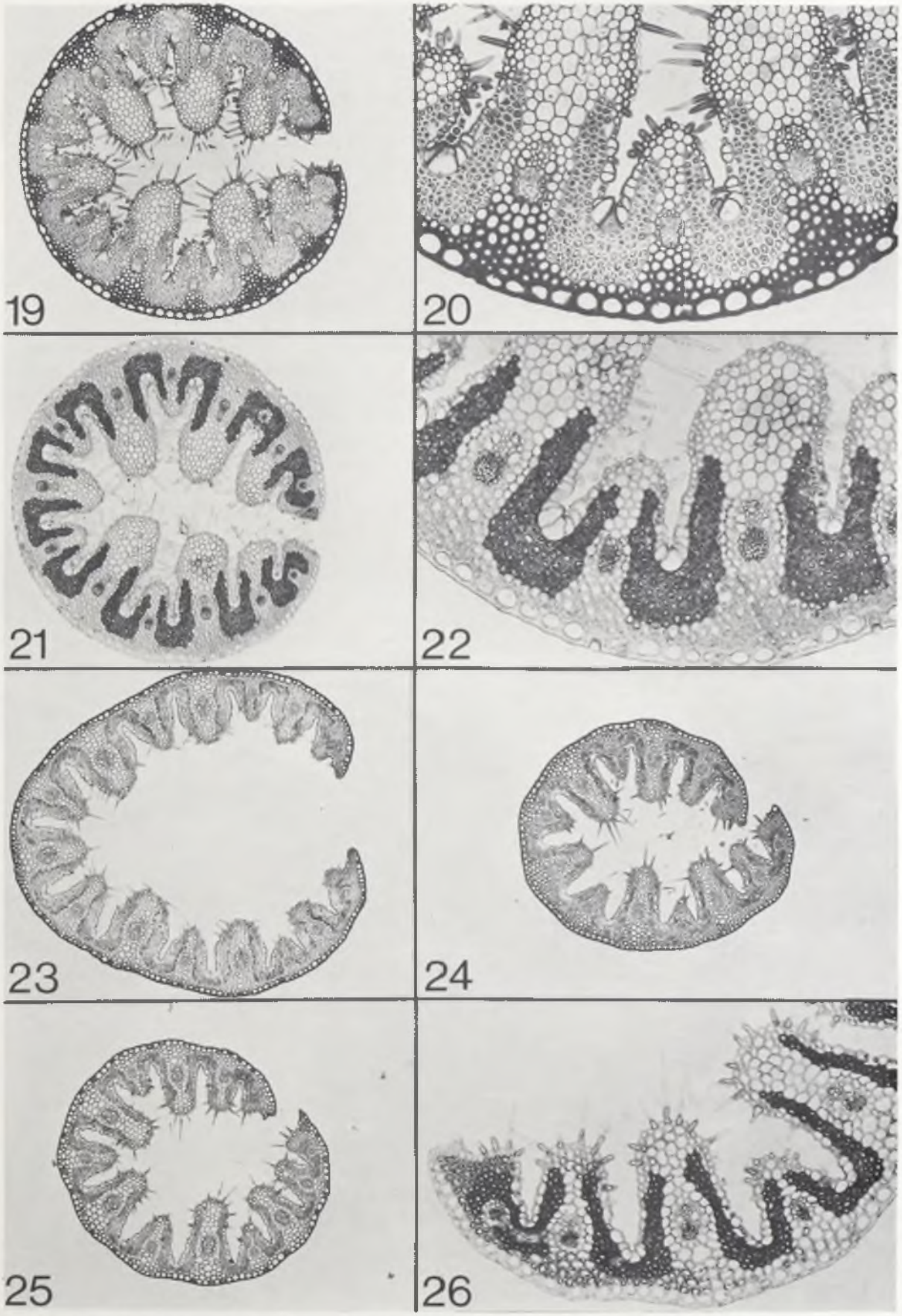
The first type is virtually identical to *P. macrocalycina* (Figs 1–10) in all details of leaf anatomy. The only differences are quantitative and *P. obtusifolia* has a leaf diameter of 7,5 mm as opposed to 3,0–4,0 mm in *P. macrocalycina*. For comparative purposes Figs 1–4 and Figs 19 & 21 are of identical magnification and clearly show the larger size of the *P. obtusifolia* leaf sections.

This type of leaf anatomy was only observed in one specimen — *Ellis* 2478. It may, or may not, be significant that this was the only freshly fixed specimen of *P. obtusifolia* collected for this study and is, therefore, not completely comparable with the other specimens examined. It appears unlikely, however, that the differences between this type and the other are due to a lack of fixation and consequent dehydration and shrinkage of tissue. The first type of *P. obtusifolia* has a maximum leaf thickness of 3,0 mm (Figs 20 & 22), whereas the second type is only 1,7 mm thick (Fig. 26). A shrinkage of almost 50% is very difficult to imagine and it appears as if this difference does in fact represent a structural difference. In addition, in the *P. macrocalycina* sections prepared from herbarium material the degree of shrinkage was insignificant, an observation which also indicates that these different anatomical types in *P. obtusifolia* may be structurally meaningful.

The second type, with inrolled leaves lacking cleft-like abaxial channels, has a much thinner leaf blade than either the first type of *P. obtusifolia* or *P. macrocalycina*. Apart from this apparently significant difference in leaf outline, however, the remainder of the leaf structure is identical to that described for *P. macrocalycina* and the relevant descriptions will also suffice for this type. Vascular bundle number and arrangement, mesophyll and sclerenchyma structure and epidermal cell characteristics are all very similar in both species and it is only the leaf outline of these specimens of *P. obtusifolia* which differs at all from *P. macrocalycina*. The outline of the leaf,



FIGS 11 – 18. — Abaxial epidermal preparations of *Pentameris macrocalycina*. 11, *Ellis* 2293, × 160; 12 & 14, *Ellis* 2582: 12, × 160; 14, × 250. Note indistinct costal and intercostal zones: 13, *Ellis* 2292, × 250. Epidermal cells filled with air: 15, *Ellis* 2280, × 400; 16, *Ellis* 2548, × 400; 17–18, *Ellis* 2499, × 400. Fig. 18 with air-filled cell lumens.



FIGS 19 – 26. — Leaf blade anatomy of *Pentameris obtusifolia* as seen in transverse section. 19–22, *Ellis* 2478: 19–20, green filter used, 21–22, red filter used; 19, × 100; 20, × 250; 21, × 100; 22, × 250. 23, *Esterhuysen* 18210, × 100; 24, *Esterhuysen* 27442, × 100. 25–26, *Esterhuysen* 16531: 25, × 100; 26, × 250, red filter.

although visually very clear and distinct, may, therefore, represent only an insignificant anatomical difference.

Abaxial epidermis

Identical to *P. macrocalycina* and the reader is referred to the relevant description for structural details. No epidermal differences were noted between specimens exhibiting the two types of leaf outline as seen by comparing Figs 27 & 28 with Figs 29 & 30.

Specimens examined:

CAPE. — 3319 (Worcester): Leeuwfontein Peak, Gydoberg (–AB), *Ellis 2478*; Waaihoek Mountains, (–AD), *Esterhuysen 18210*; Buffelshoek Peak, Hex River Mountains (–BD), *Esterhuysen 27442*; Slanghoek Mountains, Wittenberg (–CA), *Esterhuysen 16531*; Sneeukop, upper Wellington, *Esterhuysen 26517*; Fonteintjiesberg, Hex River Mountains (–CB), *Esterhuysen 22209*, Stettynsberge (–CC), *Esterhuysen 11115*.

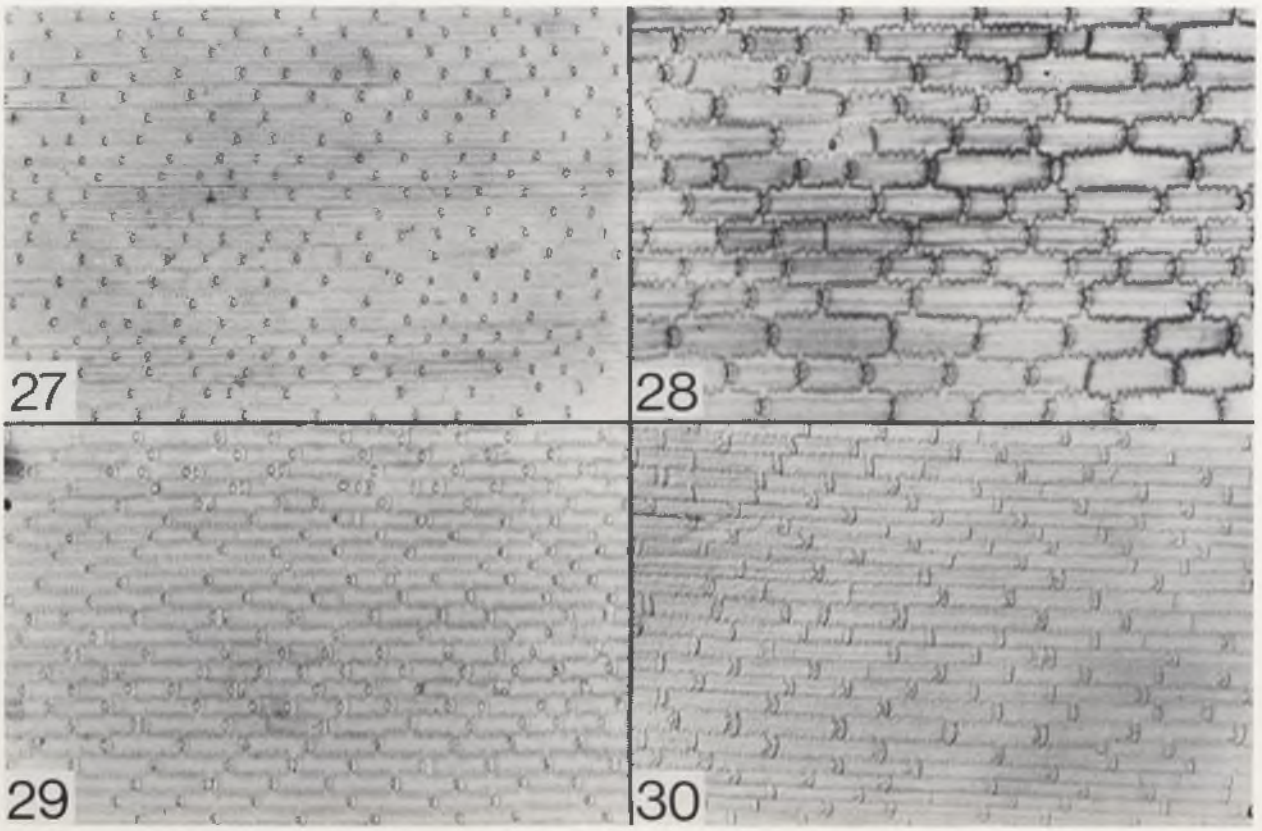
DISCUSSION AND CONCLUSIONS

The leaf anatomy of *P. macrocalycina* and *P. obtusifolia* is very similar indeed and it is only in the outline of the transections that significant anatomical differences can be detected. Metcalfe (1960) is of the opinion that in permanently infolded leaves structural criteria such as the shape of the blade as outlined by the abaxial surface, the number of vascular bundles present in the section, the adaxial channel and leaf width and thickness are of significant specific diagnostic value. If this is indeed so, then the virtually identical anatomy of all the *P. macrocalycina* specimens and the *Ellis* 2478 specimen of *P. obtusifolia*, suggests that *Ellis* 2478 actually should be reclassified as *P. macrocalycina*. If this single specimen were to be transferred to *P. macrocalycina*, then two distinct anatomical groups would result — *P. macrocalycina* with permanently infolded acicular leaves with cleft-like adaxial channels and *P. obtusifolia* with inrolled leaves lacking cleft-like adaxial channels. These two taxa would then be anatomically distinct and two separate, but very closely related, species could be distinguished.

The specimen of *P. obtusifolia* with anomalous leaf anatomy *(Ellis* 2478) has been verified by the staff of the National Herbarium (B. de Winter, pers. comm.) as being correctly identified as *P. obtusifolia*. Consequently the difference in leaf outline between *P. macrocalycina* and *P. obtusifolia* is not diagnostic and *Ellis* 2478 represents a clear intermediate. This suggests that *P. macrocalycina* and *P. obtusifolia* are exceedingly closely related and only an infraspecific separation appears justified.

It is of interest to note that the anatomical sample of *P. obtusifolia* examined in this study actually comprises the entire collection of *P. obtusifolia* in the National Herbarium. Of these six specimens, three were originally identified as either *P. macrocalycina* or *P. dregeana* and were only renamed at the suggestion of the anatomical evidence reported here. Freshly fixed anatomical material is required to evaluate this apparently significant anatomical difference and until this is forthcoming it appears sensible to continue recognizing these two closely related taxa at the specific level.

Leaf anatomy, therefore, indicates that these two taxa are closely related. This observation disagrees



FIGS 27 – 30. — Abaxial epidermis of *Pentameris obtusifolia*. 27–28, *Ellis* 2478: 27, × 160; 28, × 250. 29, *Esterhuysen* 26517, × 250; 30, *Esterhuysen* 27442, × 250.

with Chippindall's (1955) statement that *P. obtusifolia* is allied to *P. dregeana*. However, due to nomenclatural confusion this apparent conflict may not actually exist and it appears as if the concept of *P. obtusifolia* differs between Chippindall (1955) and that used here. The leaf anatomy of *P. dregeana* differs considerably from that of *P. macrocalycina* and *P. obtusifolia* (Ellis, in press) and it appears unlikely that the morphology would indicate a close relationship. A more likely explanation is that *P. obtusifolia*, as used today, actually represents the undescribed species from the mountains of the Worcester District referred to by Chippindall (1955). *P. obtusifolia*, as defined here, is confined to the Worcester area in the higher peaks of the Hex River Mountains, the Wittenberg, the Gydoberg and the Waaihoek Mountains.

Chippindall (1955) referred the name *P. obtusifolia* to specimens collected in the Houw Hoek Mountains of the Caledon District. It appears as if the specimen actually alluded to is *Burchell 8076*, called *P. squarrosa* Stapf by Stapf (1900). *P. obtusifolia*, as it is known today, does not occur in the southern mountains and therefore, it appears highly likely that genuine nomenclatural confusion exists regarding the name of the entity discussed here. This has resulted in these apparently conflicting statements in the literature.

The specimens here referred to as *P. obtusifolia* form a coherent morphological, ecological and anatomical entity and the type must be examined in order to establish the correct name. Nevertheless, these specimens undoubtedly constitute a recognizable and distinct species. The uniformity of this taxon would be further increased with the removal of *Ellis* 2478 to *P. macrocalycina*. This specimen is much more robust than the remainder of the specimens assigned to *P. obtusifolia* and also has rigid, erect setaceous leaves whereas the other *P. obtusifolia* specimens have shorter, curly leaves.

There seems to be a good case, both morphologically and anatomically, for the transfer of this specimen to *P. macrocalycina*. This would enable the recognition of two distinct taxa which, together with *P. longiglumis* (Nees) Stapf *(Ellis,* 1985) appear to form a natural grouping best accorded generic status apart from *P. thuarii (Ellis,* 1985a) and *P. dregeana (Ellis,* in press).

ACKNOWLEDGEMENTS

The author is grateful to Mrs A. Romanowski for photographic assistance, Mrs S. Thiart for typing the manuscript and to the staff of the National Herbarium (PRE) for plant identifications.

UITTREKSEL

Die blaaranatomie van Pentameris macrocalycina *(Steud.) Schweick. en* P. obtusifolia *(Hochst.) Schweick. word beskryf en geïllustreer. Die anatomie van hierdie twee spesies toon noue ooreenkomste wat verwantskappe tussen hulle aandui. Die omgrensing van* P. obtusifolia, *skep sekere probleme en die taksonomiese regstelling hiervan behoort 'n klassifikasie te gee wat heeltemal ooreenstem met dié wat op anatomie gebaseer is. In hierdie geval sal sekere kenmerke van die blaar in deursnit vir die onderskeiding van hierdie twee taksa diagnostiek word. Daar bestaan ook onsekerheid oor die nomenklatuur van* P. obtusifolia *wat verwarring skep. Hierdie probleem behoort opgelos te word deur verwysing na die betrokke tipe monsters.* P. macrocalycina *en* P. obtusifolia, *saam met* P. longiglumis *(Nees) Stapf, vorm 'n duidelike genus en geen anatomiese verwantskappe met* P. thuarii *Beauv. en* P. dregeana *Stapf word aangedui nie.*

REFERENCES

CHIPPINDALL, L. K. A., 1955. In D. Meredith, *The grasses and pastures of South Africa*. Johannesburg: CNA.

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 Danthonieae (Poaceae). XI. *Pentameris longiglumis* and *Pentameris* sp. nov. *Bothalia* 15: 567–571.

ELLIS, R. P., 1985b. Leaf anatomy of the South African Danthonieae (Poaceae). XII. *Pentameris thuarii*. *Bothalia* 15: 573–578.

METCALFE, C. R., 1960. *Anatomy of the Monocotyledons*. I. *Gramineae*. Oxford: Clarendon Press.

STAPF, O., 1900. Gramineae. In R. Thiselton-Dyer, *Flora Capensis*, Vol. 7. London: Reeve.