

Leaf anatomy of the South African Danthonieae (Poaceae). XII. *Pentameris thuarii*

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ABSTRACT

The leaf blade anatomy of *Pentameris thuarii* Beauv. is described and illustrated. It is shown that the leaf anatomy of *P. thuarii* bears little resemblance to the anatomy of *P. macrocalycina* (Steud.) Schweick., *P. obtusifolia* (Hochst.) Schweick., *P. longiglumis* (Nees) Stapf or *P. dregeana* Stapf. The leaf anatomy of *P. thuarii* was found to correspond closely with that of some specimens of *Pentaschistis pallescens* (Schrad.) Stapf, *P. silvatica* Adamson and *P. tortuosa* (Trin.) Stapf. The morphology of these *Pentaschistis* specimens needs to be compared with that of *P. thuarii* in order to establish whether the true relationships of *P. thuarii* lie with these taxa. Anatomically, *P. thuarii* does not appear to be closely related to any species presently classified in *Pentameris*.

INTRODUCTION

Pentameris thuarii Beauv. is a robust perennial with stout woody culms. It is restricted to the mountains of the southern Cape Province from Stellenbosch as far eastward as the Outeniqua Mountains. This species prefers mesic habitats, often occurring on streambanks or on seepages.

No detailed accounts of the anatomy of *P. thuarii* have been published. De Wet (1956) notes that this species has the festucoid type of epidermis and anatomy. This implies that micro-hairs are absent and that the outer parenchyma sheath is poorly differentiated and that the chlorenchyma is uniformly distributed between the bundles. Renvoize (1981) places *Pentameris* in his core group of the arundinoid grasses — a group which possesses finger-like micro-hairs. In this respect, he differs from De Wet (1956).

It is the purpose of this paper to describe and illustrate the leaf anatomy of *P. thuarii* and to compare and contrast this structure with that of the other South African danthonoid grasses. In the anatomical descriptions which follow, the terminology of Ellis (1976, 1979) will be followed and the following abbreviations used:

- 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

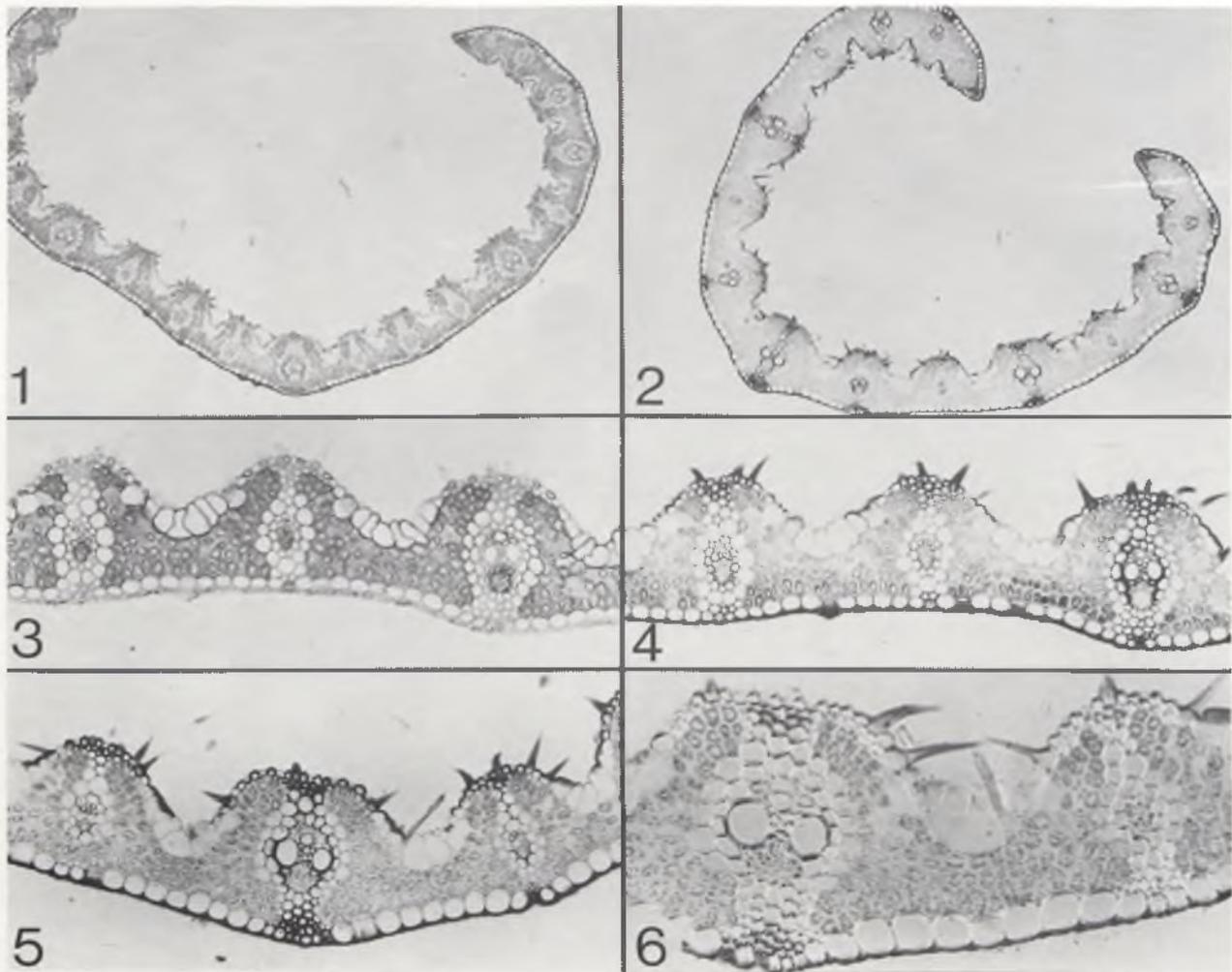
ANATOMICAL DESCRIPTION OF *PENTAMERIS THUARI* BEAUV.

Leaf in transverse section

Leaf outline: broadly V-shaped with slightly involuted margins (Figs 1 & 2). **Ribs and furrows:** rounded adaxial ribs located over all vbs; furrows of medium depth, wide (Figs 3 & 4). No abaxial ribs. **Median bundle:** no structurally distinct midrib

present. **Vascular bundle arrangement:** 5, sometimes 7, 1'vbs in entire blade (Figs 1 & 2). Laterally 1 3'vb occurs between consecutive 1'vbs but this arrangement is variable on either side of the median vb where 2 (Fig. 2) or 3 (Fig. 1) 3'vbs may be present between successive 1'vbs; sometimes a 2'vb occurs immediately adjacent to the median bundle (Fig. 2). All bundles situated in the centre of the blade (Figs 3 & 4). **Vascular bundle structure:** 3'vbs elliptical with xylem & phloem clearly visible. 1'vbs elliptical with phloem adjoining ibs and metaxylem vessels with vessel width slightly greater than that of obs cells (Figs 5 & 6). **Vascular bundle sheaths:** double; outer sheath elliptical, with slight abaxial and adaxial interruptions; extensions grade into fibres of girders (Figs 5 & 6); obs cells inflated to elliptical, regular in size; not very conspicuous; walls slightly thicker than mesophyll cell walls; chloroplasts absent (Figs 5 & 6). Ibs complete; cells relatively large with inner tangential and radial walls thickened. **Sclerenchyma:** adaxial strands rounded, following shape of rib and tapering toward junction with bundle sheath extensions (Figs 4 & 5); abaxial strands minute in association with 3'vbs (Figs 4 & 5) but more conspicuous opposite 1'vbs where they grade into the bundle sheath extensions. Strands comprised of lignified fibres; walls not markedly thickened. Minute sclerenchyma caps present in margin (Fig. 2) which is often very pointed. **Mesophyll:** indistinctly radiate especially in adaxial ribs (Fig 3); continuous between bundles with abaxial layer of cells almost palisade-like being tightly packed and regularly arranged; remainder of chlorenchyma less regular with many air spaces; intermediate between isodiametric and truly irregular types. **Colourless cells:** absent (Fig. 3). **Adaxial epidermis:** fan-shaped groups of bulliform cells located at bases of furrows (Fig. 3); not very restricted and up to 8 cells wide. Epidermal cells much smaller than abaxial epidermal cells. Prickles common on ribs (Figs 4, 5 & 6). No papillae. Micro-hairs visible near bases of furrows (Figs 5 & 6); basal cell very elongate with short distal cell. **Abaxial epidermis:** no bulliform cells. Cells large and inflated (larger than obs cells) with continuous cuticle (Figs 3 & 6). No macro-hairs, prickles, papillae or micro-hairs.

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FIGS 1 - 6. — Leaf blade anatomy of *Pentameris thuarii* as seen in transverse section. 1, Ellis 2221, $\times 100$; 2, Ellis 660, $\times 100$; 3-4, Ellis 2220, $\times 250$; 3, taken with red filter to enhance cellulose walls; 4, taken with a green filter to accentuate lignified tissue; 5, Ellis 660, $\times 250$, adaxial micro-hairs located at the bases of the furrows; 6, Ellis 660, $\times 400$, interference contrast showing micro-hair beneath adaxial prickles.

Abaxial epidermis in surface view

Intercostal long cells: elongated, with parallel side walls, vertical end walls and slight undulations (Figs 7-10). Cell shape and size noticeably constant throughout all intercostal zones. Long cells separated by hooks, cork cells or cork-silica cell pairs. No bulliform cells. **Stomata:** no abaxial stomata. **Intercostal short cells:** either solitary or paired; tall and narrow (Fig. 10). **Papillae:** absent. **Prickles:** medium prickles with barbs sometimes present on costal zones (Figs 7 & 8); barbs all orientated in same direction. **Hooks:** intercostal hooks common on some specimens (Figs 7 & 8); barb orientation variable. **Micro-hairs:** none observed; presumed absent. **Macro-hairs:** absent. **Silica bodies:** very reduced and indistinct; tall and narrow and solitary (Fig. 10) or irregularly rounded and associated with cork cell (Figs 8 & 9). **Costal zones:** very narrow; consist of only 1 or 3 files of cells; long cells narrower than intercostal long cells.

Specimens examined:

Pentameris thuarii

CAPE. — 3318 (Cape Town): Jonkershoek State Forest, Stellenbosch (-DD), Ellis 2220, 2221, Kruger 798. 3320 (Montagu): Tradouw's Pass, Barrydale (-DC), Ellis 660, 1202.

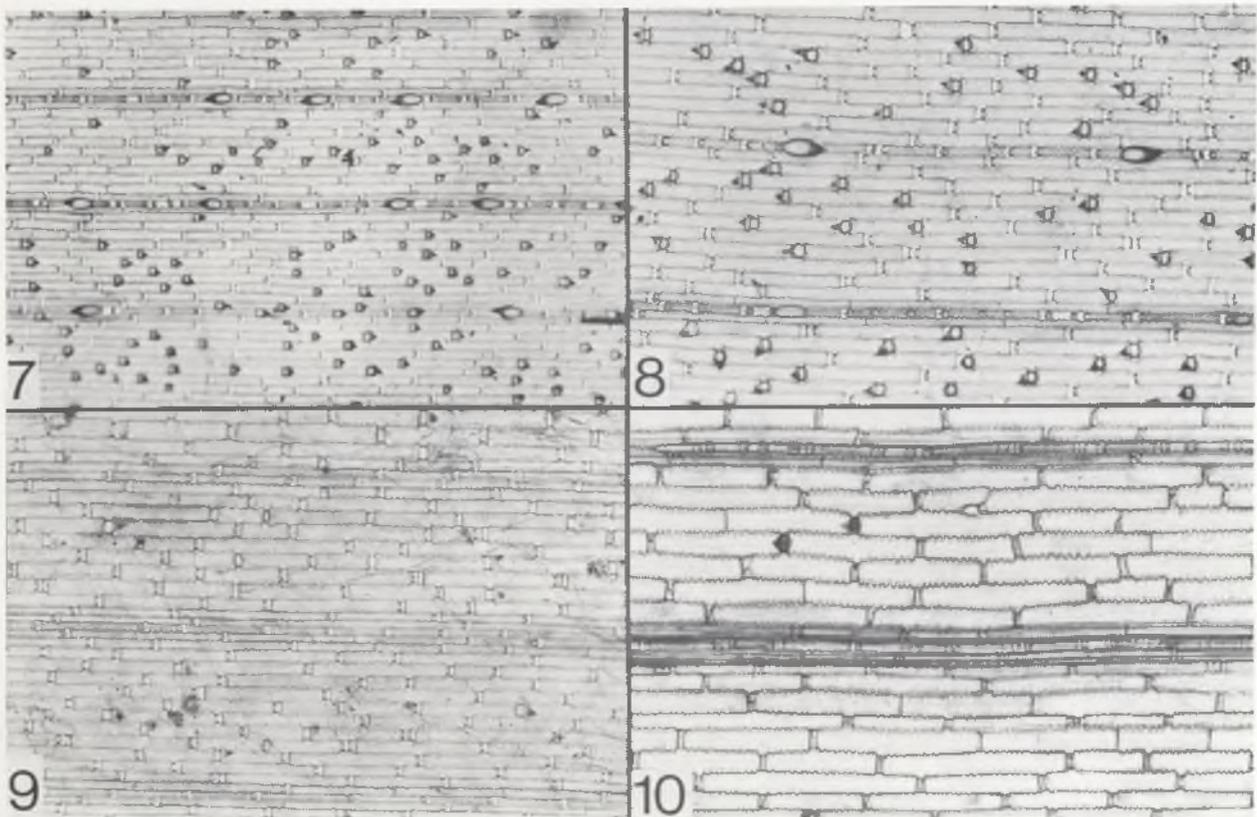
3322 (Oudtshoorn): Outeniqua Pass, George (-CD), Acocks 21743, Barker 7653.

DISCUSSION AND CONCLUSIONS

Five species comprise the genus *Pentameris* (Smook & Gibbs Russell, 1984). These are *P. thuarii*, *P. macrocalycina* (Steud.) Schweick., *P. obtusifolia* (Hochst.) Schweick., *P. longiglumis* (Nees) Stapf and *P. dregeana* Stapf. The leaf anatomy of *P. dregeana* differs considerably from the other species and will be described separately in a later paper. *P. dregeana* will, therefore, be excluded from the following discussion and must not be included in the concept of the genus *Pentameris*.

P. longiglumis (Ellis, 1985), *P. macrocalycina* and *P. obtusifolia* (Ellis, 1985a) share many anatomical features and form a recognizable, coherent anatomical group consistent with that of most genera. Each species has characteristic attributes of its own, yet all have the same basic anatomical ground plan.

A comparison of the leaf anatomy of *P. thuarii* with that of these three species (Table 1) reveals many obvious and striking differences. The



FIGS 7 - 10. — Abaxial epidermal structure of *Pentameris thuarii*. 7-8, Ellis 2220; 7, costal and intercostal zones, $\times 160$; 8, intercostal hooks and costal prickles, $\times 250$. 9, Ellis 2221, intercostal and costal short & silica cells; few hooks present, $\times 250$; 10, Ellis 660, shape and structure of long cells, $\times 250$.

illustrations of the anatomy of *P. longiglumis* (Ellis, 1985) and of *P. macrocalycina* and *P. obtusifolia* (Ellis, 1985a) should be compared with Figs 1-6 and Figs 7-10 to assess visually the magnitude of these structural differences.

The leaf anatomy of *P. thuarii* differs so much from that of the other three species that a generic difference appears to be indicated. The heavily lignified, thick, setaceous leaves of *P. macrocalycina*, *P. obtusifolia* and *P. longiglumis* are strongly reminiscent of members of the genus *Merxmuellera* and these species show a definite anatomical relationship with this genus. *P. thuarii*, on the other hand, shares little in common with *Merxmuellera* and its phylogenetic connections must be sought elsewhere in the Danthonieae.

The leaf anatomy of *P. thuarii* was compared with the anatomy of all the other 16 South African danthonoid genera and it is only with a few species of the genus *Pentaschistis* that similarities were found. Of the 49 South African species of this genus (Smook & Gibbs Russell, 1984), 40 were available for comparative purposes and, of these, only three had similar leaf anatomy to that of *P. thuarii*. These were *Pentaschistis tortuosa* (Trin.) Stapf, *P. silvatica* Adamson and *P. pallescens* (Schrad.) Stapf (Figs 11-19). Even in these three taxa only certain specimens showed anatomical resemblances to *Pentameris thuarii*. The following specimens of *Pentaschistis*, as they are presently identified, conform with the *Pentameris thuarii* type of anatomy:

Pentaschistis pallescens

CAPE. — 3318 (Cape Town): Stellenbosch, Jonkershoek (-DD), Ellis 2250, 2251. 3418 (Simonstown): Hottentots Holland Mountains, Sugarloaf Peak (-BB), Ellis 2271, 2272.

Pentaschistis silvatica

CAPE. — 3318 (Cape Town): Table Mountain, Kirstenbosch (-CD), Ellis 2309.

Pentaschistis tortuosa

CAPE. — 3418 (Simonstown): Hottentots Holland Mountains, Sugarloaf Peak (-BB), Ellis 2276, 2277.

These *Pentaschistis* specimens share the following characteristics with *Pentameris thuarii* but not with other *Pentameris* species.

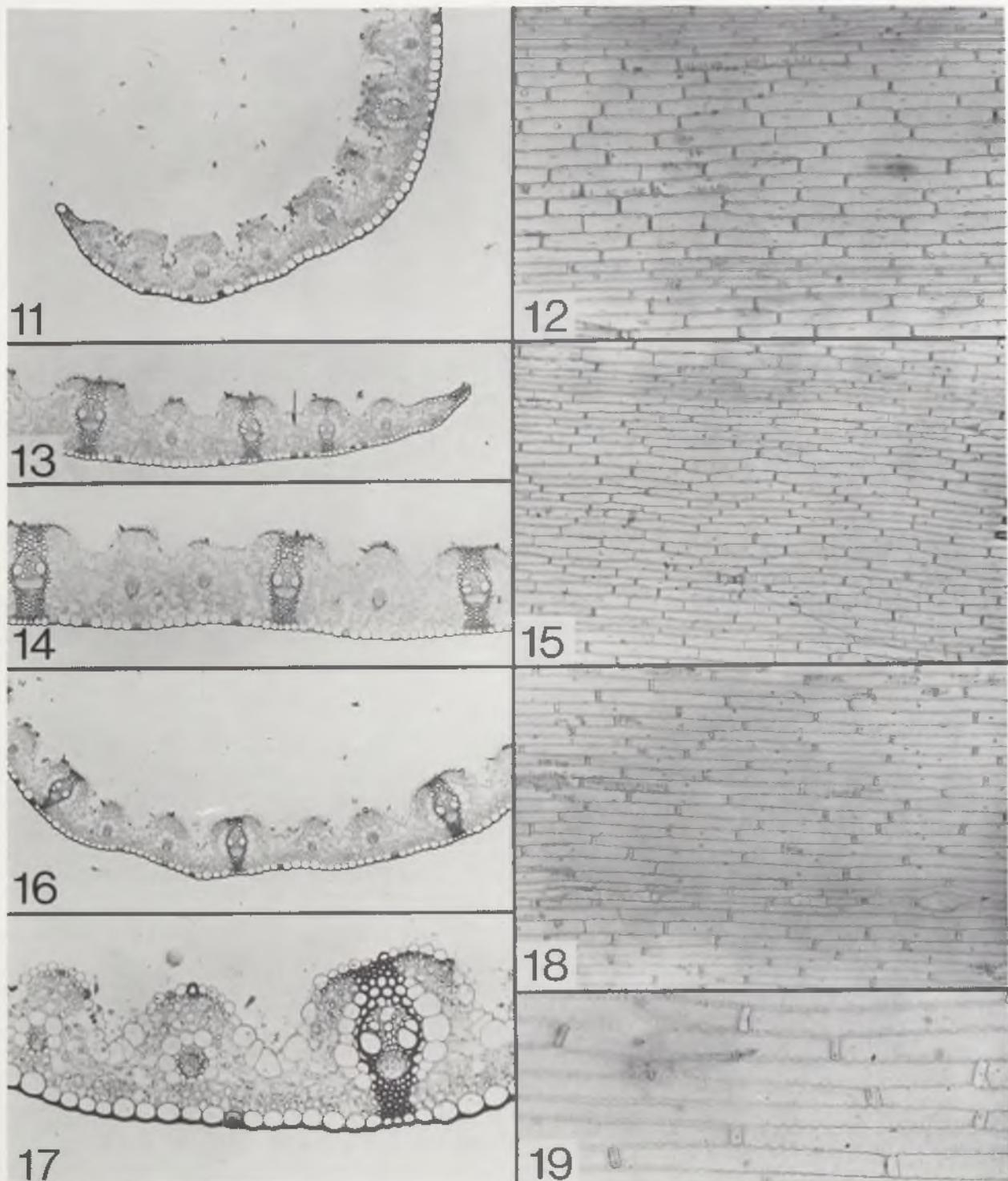
1. The leaf is thin and expanded and similar adaxial rib and furrows are associated with all the vascular bundles. In the *Pentaschistis* specimens the ribs over the first order bundles are slightly larger and may be flat-topped (Figs 11, 13, 14, 16 & 17).

2. The leaf margin is projected into a prominent, narrow pointed cap (Figs 11 & 13). In *P. thuarii* this projection is not always so prominent but in some specimens (Fig. 1) there is a definite narrowing at the pointed cap of the margin.

3. Laterally only a single third order bundle occurs between adjacent first order bundles but in the region of the median bundle 2-3 smaller bundles may be present between successive first order bundles. Compare Figs 3 & 4 with Figs 14, 16 & 17. This condition is not found in any other *Pentameris* species (Table 1).

TABLE 1.—A comparison of the leaf anatomy of *Pentameris thuarii* with other representatives of the genus

	<i>Pentameris thuarii</i>	<i>Pentameris macrocalycina</i> , <i>P. obtusifolia</i> & <i>P. longiglumis</i>
Outline & furrows	Expanded, slightly involute; thin (maximum thickness 200 μ). Similar ribs over all vbs.	Permanently inrolled; thick (maximum thickness 500 μ –600 μ). Ribs over 1'vbs larger than 3'vb ribs.
vascular bundle arrangement	2–3 3'vbs separate 1'vbs from median vb; 2'vbs may be present.	1 3'vb between 1'vbs adjacent to the median vb; no 2'vbs.
mesophyll	Abaxial girders minute; slight adaxial bundle sheath extensions. Sclerenchyma not continuous between bundles.	Conspicuous abaxial girders and adaxial extensions. Abaxial sclerenchyma continuous between bundles as hypodermal layer.
bulliform cells	Well developed fan-shaped groups at bases of furrows; cells inflated and conspicuous.	Bulliform groups poorly developed and individual bulliform cells small.
epidermal micro-hairs	Common near bases of furrows.	None observed.
costal long cells	Narrow, elongated, thin-walled with slight undulations.	Short, wide, with pitted walls and deep undulations.
costal short cells	Same width as long cells.	Much narrower than long cells.
stomata	Present on costal zones.	Absent on all specimens.
epidermal papillae	Common in intercostal zones.	Absent on all specimens.
epidermal bodies	Reduced and inconspicuous, even in costal zones.	Very common and located between virtually all epidermal cells.



FIGS 11 - 19. — Anatomy of *Pentaschistis* species showing anatomical resemblances with *Pentameris thuarii*. 11-12, *Pentaschistis tortuosa*, Ellis 2277: 11, transverse section showing projecting margin, $\times 100$; 12, abaxial epidermis, $\times 160$. 13-15, *Pentaschistis pallescens*: 13 & 14, Ellis 2250, $\times 100$, transverse sections with projecting margin and two smaller bundles between adjacent large bundles; 15, Ellis 2272, $\times 160$, abaxial epidermis with stomata absent. 16-19, *Pentaschistis silvatica*, Ellis 2309: 16-17, leaf in transverse section; 16, $\times 100$; 17, $\times 250$; 18-19, abaxial epidermis, 18, $\times 160$; 19, $\times 400$ showing characteristic micro-hair.

4. Abaxial sclerenchyma girders are not extensively developed and no continuous hypodermal fibrous layer is present.

5. Well developed groups of bulliform cells occur at the bases of the adaxial furrows (Fig. 17) as is the case with *Pentameris thuarii* (Fig. 3).

6. Adaxial micro-hairs are visible in only one specimen (Ellis 2271), but these resemble those of

Pentameris thuarii with an elongated basal cell and a very short, tapering distal cell (Figs 5 & 6). Similar micro-hairs were also observed on the abaxial epidermis of some of these specimens (Fig. 19). The hair on the adaxial surface of Fig. 13 is not a micro-hair but a unicellular macro-hair. Similar macro-hairs occur on both adaxial and abaxial surfaces of all these *Pentaschistis* specimens but were not observed on *Pentameris thuarii*.

7. Narrow, elongated intercostal long cells with thin slightly undulating walls are common to *Pentameris thuarii* and all these *Pentaschistis* specimens (Figs 7–10 and Figs 12, 15, 18 & 19).

8. The intercostal short cells are the same width as the long cells (Figs 18 & 19) and not much narrower as in *Pentameris macrocalycina* and *P. obtusifolia*.

9. Prickles sometimes occur on the costal zones (Fig. 18) as is the case with *Pentameris thuarii*.

10. Costal silica bodies are inconspicuous.

These *Pentaschistis* specimens, therefore, bear a very strong anatomical resemblance to *Pentameris thuarii* and a morphological evaluation of this anatomical observation is necessary to interpret objectively the findings of this study. This is particularly important as many other specimens of *Pentaschistis pallescens*, in particular, have a totally different anatomical structure. These specimens are Ellis 649, 2226, 2227, 2228, 2260 and 2261. These specimens, together with Esterhuysen 27320 (*P. tortuosa*) are completely different from the specimens considered here and show close similarities to *Pentaschistis colorata* (Steud.) Stapf. It, therefore, seems as if the identification of the *Pentaschistis* specimens resembling *Pentameris thuarii* is very suspect and requires checking. This is unlikely at present as the taxonomy of *Pentaschistis* is very confused and more reliable identifications are not possible.

However, a morphological comparison, using the *Pentaschistis* herbarium vouchers of specimens resembling *Pentameris thuarii* in leaf anatomy, should be undertaken. Particular attention should be given to the structure of the ovary and of the ripe fruit as the structure of these in *P. thuarii* is diagnostic (Stapf, 1900; Chippindall, 1955; De Wet, 1956). In *Pentaschistis* the structure of the ovary and fruit differs considerably from that encountered in *Pentameris* (Stapf, 1900) and this comparison should quickly establish whether this group of specimens does show morphological relationships with *P. thuarii*. As *P. thuarii* is the type of the genus, this morphological comparison will enable a new circumscription of the genus to be formulated and compared with the condition in the other species currently recognized as belonging to the genus. The anatomical indications are that *P. thuarii* is closely related to the *Pentaschistis* specimens but not to *Pentameris macrocalycina*, *P. obtusifolia*, *P. longiglumis* or *P. dregeana*.

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UITTREKSEL

Die blaaranatomie van Pentameris thuarii Beauv. word beskryf en geïllustreer. Daar word bewys dat die anatomiese struktuur van die blaar van P. thuarii geen ooreenkomste met die anatomie van P. macrocalycina, (Steud.) Schweick., P. obtusifolia (Hochst.) Schweick., P. longiglumis (Nees) Stapf of P. dregeana Stapf toon nie. Die anatomie van P. thuarii vergelyk baie gunstig met dié van sekere monsters van Pentaschistis pallescens (Schrad.) Stapf, P. silvatica Adamson en P. tortuosa, (Trin.) Stapf. Die morfologie van hierdie Pentaschistis monsters behoort vergelyk te word met dié van P. thuarii om vas te stel of die natuurlike verwantskappe van P. thuarii wel met hierdie groep spesies lê. Anatomiese aanduidings is egter dat P. thuarii geen verwantskappe met enige van die spesies wat tans in Pentameris geklassifiseer word, toon nie.

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