Bothalia 11, 3: 235–241 (1974)

Comparative Leaf Anatomy of *Paspalum paspalodes* and *P. vaginatum*

R. P. ELLIS*

ABSTRACT

The leaf blade and epidermal anatomy of *Paspalum paspalodes* (Michx.) Scribn. (syn. *P. distichum* L.) and *P. vaginatum* Swartz is compared and discussed. Numerous anatomical differences are evident and the species can be separated on the basis of the distribution of sclerenchyma and the shape and thickness of the leaf margin. Another distinct diagnostic difference is the shape of the adaxial ribs and furrows and their associated papillae. *P. paspalodes* has two distinct types of abaxial epidermis: cuticular and papillate.

INTRODUCTION

The need for a detailed investigation of the relationship between *Paspalum paspalodes* (Michx.) Scribn. (syn. *P. distichum* L.) and *P. vaginatum* Swartz arose because of the conflicting opinions in the literature as to the nomenclature and status of these two related species. These historical, morphological and taxonomic aspects are discussed by Loxton (1974). The present anatomical investigation was conducted in conjunction with the above taxonomic study and here the leaf and epidermal anatomy are compared and differences and similarities discussed.

Leaf material was collected and fixed in FAA in the field from a number of localities in South Africa. Transverse sections of the leaf were prepared by use of wax embedding techniques, and double-stained in safranin and fast green. The method of Metcalfe (1960) was used for preparing epidermal material for microscopic study. To minimize the possibility of intraspecific variation and to facilitate and standardize comparison, tissue from a point midway between the apex and the ligule of the leaf blade was examined.

* Botanical Research Institute, Department of Agricultural Technical Services, Private Bag X101, Pretoria.

TABLE 1.—The differences between *Paspalum paspalodes* and *P. vaginatum* as seen in transverse sections of the leaf blade.

Character	Paspalum paspalodes	Paspalum vaginatum
1. Width of blade at a point halfway between apex and ligule	1. More than 3,00 mm wide; usually wider than 7,20 mm	1. Less than 3,00 mm wide
2. Adaxial furrows	2a. Shallow furrows only; usually with distinct furrows less than ¼ of the leaf thickness deep, or leaf may be undulating with no regular furrows associated with the vascular bundles	2a. Furrows of medium depth; depth between ¼ and ½ of the leaf thickness (Fig. 10)
	2b. Furrows always wide and open; obtuse angle formed by the furrow sides at the base	2b. Furrows in the form of a narrow cleft
3. Second-order vascular bundles	3. Tall and narrow with vertical, parallel sides; rarely some bundles may be elliptical in shape	3. Elliptical, vertically elongated in shape
4. First-order vascular bundle	4a. Lysigenous cavity and protoxylem vessel always present (Fig. 15, 16)	4a. Lysigenous cavity and protoxylem rarely present together; usually only a protoxylem vessel is present but both may be absent (Fig. 10)
	4b. Vessels wider than the cells of the parenchyma sheath and always angular in section	4b. Vessels not as wide as the cells of the parenchyma sheath and rounded or curcular in section
5. Parenchyma sheath of third-order vascular bundles	5. Sheath rounded or circular in shape	5. Sheath usually elliptical, vertically elongated; some bundles may possess round sheaths
6. Parenchyma sheath of first-order vascular bundles	6a. Commonly round or circular in shape; some bundles may have elliptical, vertically-elongated sheaths	6a. Sheaths elliptical or egg-shaped with broadest side adaxial
	6b. Parenchyma cells of sheath often rounded in shape; elongated, elliptical cells or cells with straight radial and inflated tangential walls uncommon	6b. Cells of sheath usually with straight radial and inflated tangential walls; rounded cells do occur infrequently
7. Sclerenchyma of leaf margin in transverse section	7. Relatively small to well-developed sclerenchyma caps present; rounded in shape, rarely narrow and pointed (Fig. 22, 23, 24)	7. Very small sclerenchyma cap consisting of a few fibres; pointed in shape (Fig. 20, 21)
8. Colourless cells	8 No colourless cells present.	8. Irregular abaxial groups of colourless cells associated with the sclerenchyma strands present (Fig. 10)
9. Adaxial epidermal cells	9 No macro-hair bases found	9. Sunken constricted bases of short, thick macro-hairs relatively common
10. Abaxial epidermal cells	10 Two distinct types of epidermis occur: (i) Epidermis may be composed of small, inflated, bulliform cells with a very thin cuticle and papillae (ii) Epidermis may be composed of relatively small cells with no papillae and the outer tangential wall with a distinct, continuous cuticle	10 Epidermis composed of relatively large inflated bulliform cells with a distinct thick cuticle; no papillae

ANATOMY OF THE LEAF

Leaf Blade

Sections of the leaf blade of *P. paspalodes* and *P. vaginatum*, taken at a point midway between the leaf apex and the ligule, exhibit the following common anatomical features.

1. Adaxial ribs, wherever present, are rounded and present only over the first- and second-order vascular bundles. Adaxial furrows are situated over the third-order vascular bundles.

2. Abaxial ribs are absent in both species. Specimens of *P. paspalodes* with inflated, abaxial epidermal cells may possess an irregular, undulating, abaxial surface, but the undulations are not regularly associated with any order of vascular bundle to form ribs (Fig. 1).

3. One, rarely two, third-order vascular bundle is located between consecutive first- and second-order vascular bundles.

4. The first- and second-order vascular bundles are centrally positioned in the leaf section, whereas the third-order bundles are abaxially situated.

5. The bundle sheath of all vascular bundles is single, entire and without parenchymatous projections. The sheath cells contain specialized chloroplasts, which are larger than those of the chlorenchyma and are often grouped near the outer tangential walls of the sheath cells.

6. No adaxial or abaxial sclerenchyma strands or girders are associated with the third-order vascular bundles.

7. No sclerenchyma is developed between the bundles.

8. Adaxial papillae are developed on all, or most, epidermal cells in both species. They are always wider than half the width of the epidermal cells and are either thin-walled or have the distal wall thickened.

Notwithstanding the above structural similarities between the two species, they can, nevertheless, be readily separated and distinguished by the diagnostic characters of the leaf blade set out in Table 1.

Fig. 1–9.—Leaf blade outline in transverse section. All ×6,25 bright field. Figs. 1–6, **Paspalum paspalodes.** Fig. 1, *Ellis* 1106. Fig. 2, *Ellis* 254. Fig. 3, *Ellis* 146. Fig. 4, *Ellis* 432. Fig. 5, *Ellis* 767. Fig. 6, *Ellis* 726. Figs. 7–9, **Paspalum vaginatum.** Fig. 7, *Ellis* 1114. Fig. 8, *Ellis* 276. Fig. 9, *Werger* 1622.

Although these diagnostic characters exhibit variation, there are distinct discontinuities between the two species. Numerous other differences occur, but the variation shown by these characters is relatively great and may overlap with the extreme of the same character in the other species. These cannot be used alone as diagnostic characters but, when used in combination with other differences, are nevertheless important.

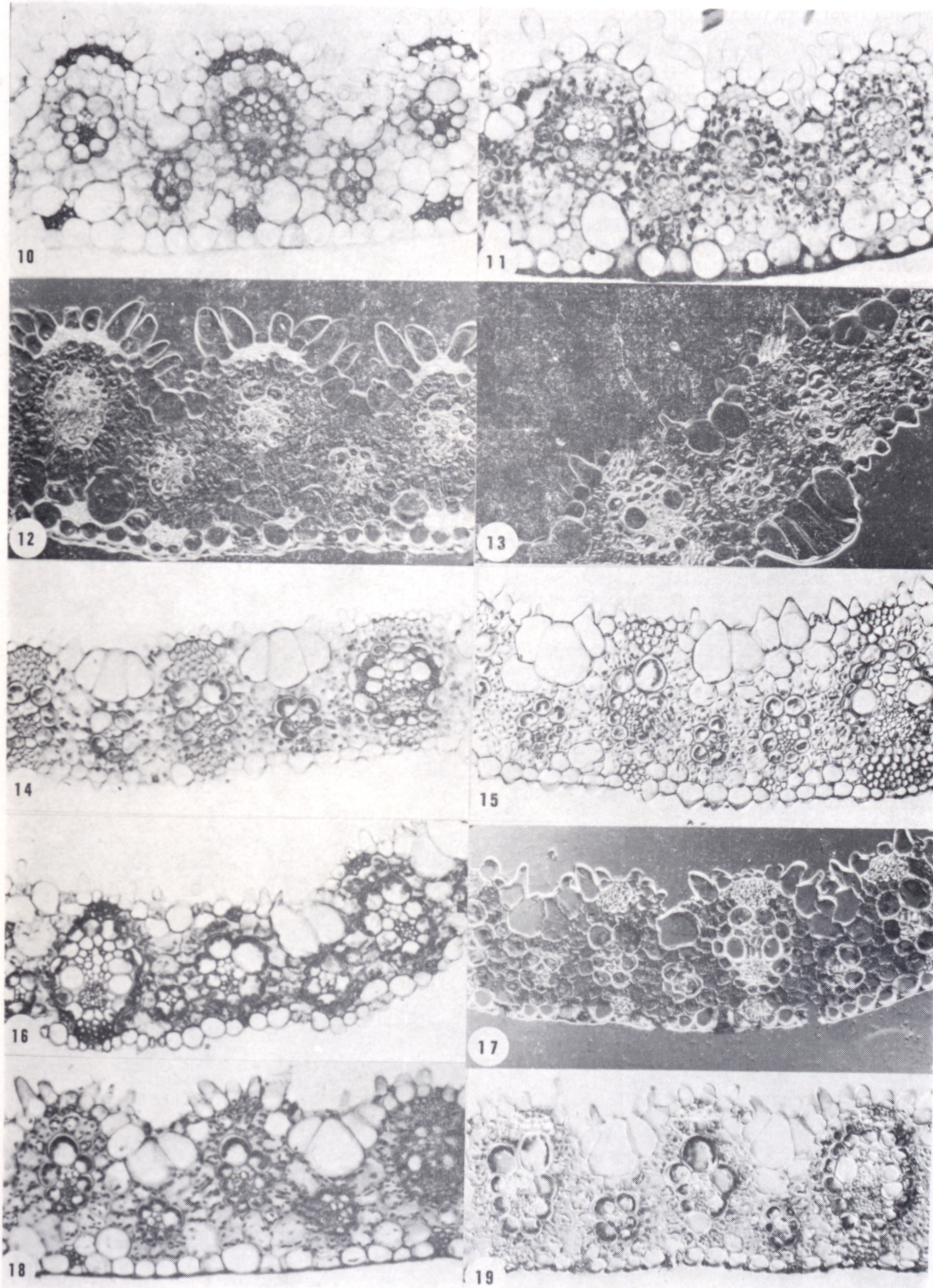

FIG. 10–19.—Transverse sections of leaf blade. All ×40. Figs. 10–12, **Paspalum vaginatum.** Fig. 10, *Ellis* 276 bright field. Fig. 11, *Werger* 1622 bright field. Fig. 12, *Ellis* 276 interference contrast. Figs. 13–19, **Paspalum paspalodes.** Fig. 13, *Ellis* 1106 interference contrast. Fig. 14, *Ellis* 146 lateral region of leaf, bright field. Fig. 15, *Ellis* 146 central region of leaf, interference contrast. Fig. 16, *Ellis* 254 bright field. Fig. 17, *Ellis* 432 interference contrast. Fig. 18, *Ellis* 762 interference contrast. Fig. 19, *Ellis* 767 interference contrast.

The outline of the blade of *P. paspalodes*, as seen in transverse section, is expanded and gently undulating (Fig. 2) or broadly V-shaped with the arms of the "V" outwardly bowed (Fig. 5, 6) or irregularly wavy or bent (Fig. 2). Many leaves exhibit various degrees of inrolling from both margins (Fig. 3, 4, 6) and this loosely involute condition appears to be basic. Under adverse moisture conditions probably all leaves assume the involute shape of Fig. 4. Leaves of *P. vaginatum* are either V- (Fig. 7) or U-shaped (Fig. 8, 9), with the lamina arms either straight or concave, respectively. The angle formed by the arms of the lamina at the median vascular bundle is usually small, but may be 90° in certain cases.

In *P. vaginatum* the median vascular bundle is distinguishable only by the central position in the leaf section and is structurally identical to the other first-order bundles of the leaf. Some specimens of *P. paspalodes* possess only a median vascular bundle (Fig. 2, 3, 4, 6), but in others a keel comprising 7–9 bundles is developed (Fig. 1, 5). Only a single first-order bundle is present in the keel. Keel shape is often not distinct from the leaf outline, the keel merely being thicker than the rest of the lamina. Well-developed keels may be semicircular or rounded with a raised, flattened adaxial side.

The arrangement of the different orders of vascular bundle along the leaf differs in the two species. In *P. paspalodes* there are 3 or 4 second-order vascular bundles between successive first-order bundles. There is no regular arrangement in *P. vaginatum* and the number of second-order bundles between successive first-order bundles decreases rapidly from centre to margin. There is only one second-order bundle between the lateral pair of first-order bundles.

The bundle sheath of the first-order bundles of both species is composed of smaller parenchyma sheath cells than second- and third-order bundles. These sheath cells are normally thin-walled with large chloroplasts situated near the outer tangential wall. In a few specimens of *P. paspalodes*, however, the sheath cells are distinctly thickened on their inner tangential and radial walls thus resembling a mestome sheath. In these instances the chloroplasts are concentrated near this thicker, inner tangential wall (Fig. 14).

Sclerenchyma development associated with the first- and second-order vascular bundles in *P. vaginatum* is scant and in the form of a shallow, sub-epidermal strip adaxially and a small strand abaxially (Fig. 10, 11, 12). Girders were never found. In *P. paspalodes* both the adaxial and abaxial sclerenchyma is in the form of small strands (Fig. 18), but girders are sometimes developed when these strands are in contact with the bundle sheath (Fig. 15, 19).

The chlorenchyma of both species is irregular or sometimes indistinctly radiate with the adaxial cells tabular. It is continuous between the vascular bundles. The indistinctly radiate condition is more commonly found in *P. vaginatum*.

In both species the adaxial bulliform cells are either extensive groups present throughout the epidermis and only reduced opposite the first- and second-order vascular bundles, or they are in fan-shaped groups at the base of furrows.

The adaxial papillae of *P. vaginatum* are inflated, thin-walled and as wide as the epidermal cell on which the papillus is located (Fig. 12). They are longer than those of *P. paspalodes* and almost every cell is papillate. Those of *P. paspalodes* are narrower and often thickened distally (Fig. 13, 19).

Thus there are numerous anatomical differences between *P. paspalodes* and *P. vaginatum* and they can easily be separated on anatomical criteria of the leaf blade as seen in transverse section. The most outstanding and obvious difference is that of the sclerenchyma distribution and shape, as seen in cross-section, of the leaf margin. Figs. 20–24 illustrate this clearly, together with the distinct difference in leaf thickness at the margin. The shape of the adaxial ribs and furrows and their associated papillae is another distinct diagnostic difference between the two species.

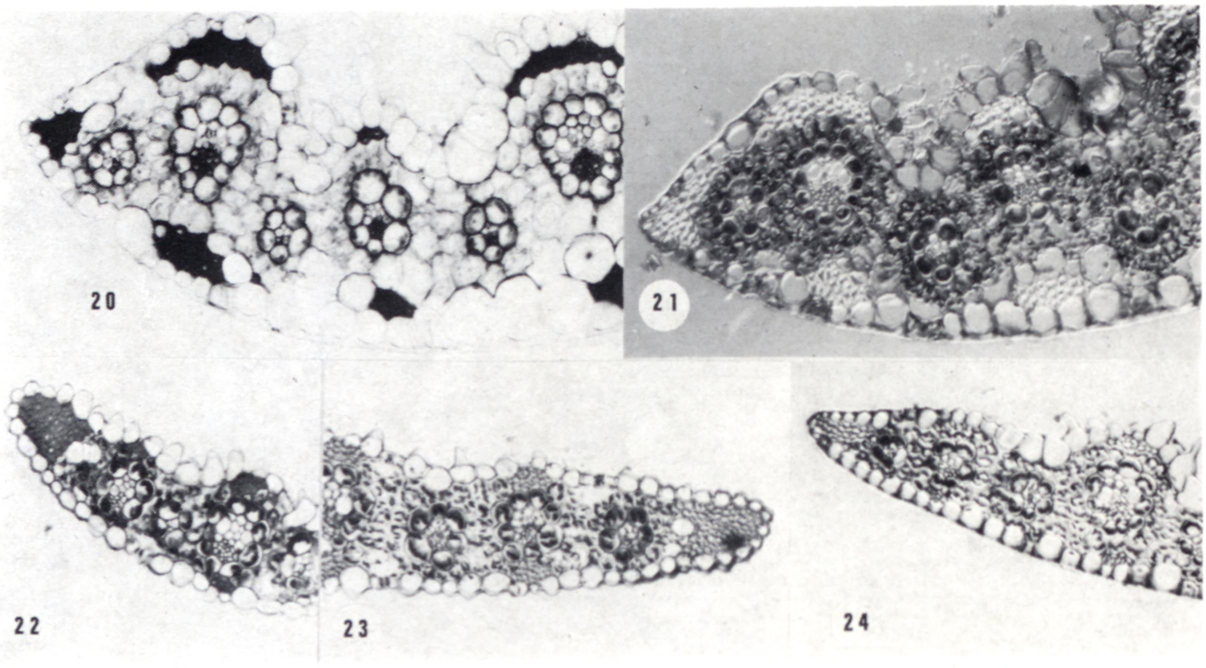

FIG. 20–24.—Transverse sections of the leaf margins. All ×40. Figs. 20–21. **Paspalum vaginatum.** Fig. 20, *Ellis* 276 bright field. Fig. 21, *Werger* 1622 interference contrast. Figs. 22–24. **Paspalum paspalodes.** Fig. 22, *Ellis* 254 bright field. Fig. 23, *Ellis* 1106 interference contrast. Fig. 24, *Ellis* 726 interference contrast.

Epidermis

Epidermal scrapes of both the abaxial and adaxial epidermides were prepared for microscopical examination. The description of the epidermis of these two species is complicated by the fact that in *P. paspalodes* two distinct types of abaxial epidermis are present: those with a distinct, continuous cuticle and having no papillae (Fig. 27, 28), and those with a thin, indistinct cuticle and papillate epidermal cells (Fig. 29, 30).

Correlated with this difference are numerous others in the abaxial as well as the adaxial epidermides. For the sake of convenience these two forms of *P. paspalodes* will be termed cuticular and papillate respectively.

In *P. vaginatum* and cuticular *P. paspalodes* the abaxial intercostal long cells are elongated, with parallel side walls and vertical, anticlinal end walls. These walls are moderately undulating (Fig. 26, 28). In *P. vaginatum* cell shape and size are remarkably constant, but in cuticular *P. paspalodes*, cell-length is variable within a single file of long cells. Adjacent long cells are frequently separated by silico-suberose couples or solitary cork cells. In *P. vaginatum* and cuticular *P. paspalodes* there are no bulliform cells on the abaxial surface. In papillate *P. paspalodes* (Fig. 29, 30), however, the intercostal long cells are shortly rectangular or hexagonal in shape and resemble bulliform cells. They are not interspersed with intercostal short cells.

Two rows of stomata, separated by more than one file of intercostal long cells, are found in each intercostal zone in both species. Their shape, as determined by the shape of both subsidiary cells, is low triangular in *P. vaginatum* and cuticular *P. paspalodes*. In papillate *P. paspalodes* the stomata are low dome-shaped, with the subsidiary cells ovoid in shape.

The interstomatal long cells of both species are very similar in shape and size to the intercostal long cells. A single interstomatal cell is most commonly present between successive stomata in *P. vaginatum* and cuticular *P. paspalodes*, but in papillate *P. paspalodes* three or more interstomatal cells are found.

No prickle hairs were observed on the epidermal surface of either of the two species examined.

Macro-hairs were occasionally observed on the abaxial surface of papillate. *P. paspalodes*. These are typical cushion hairs with raised epidermal cells surrounding the sunken base of the hair (Fig. 13).

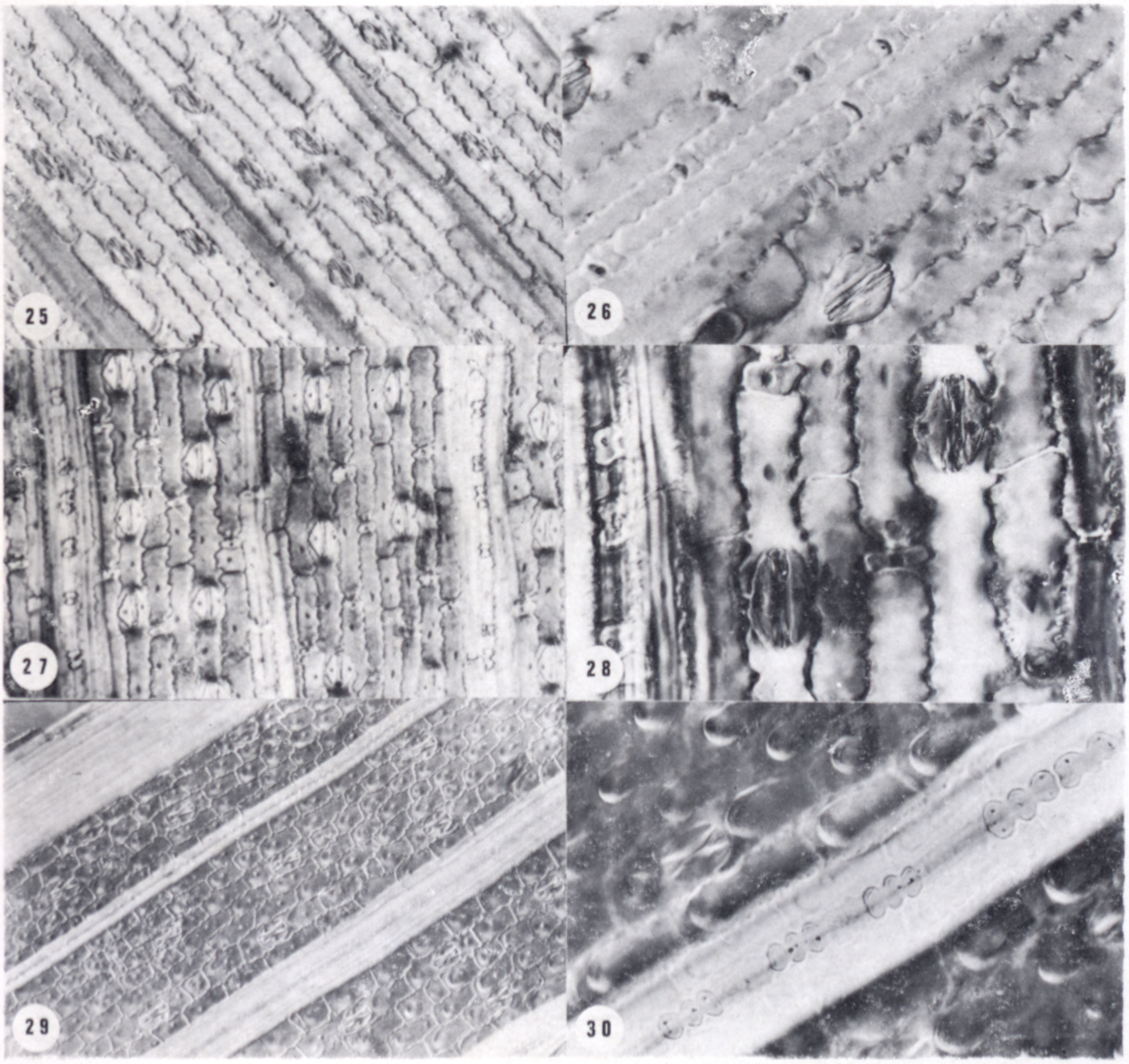

FIG. 25–30.—Abaxial epidermis, interference contrast. Figs. 25–26, **Paspalum vaginatum.** Fig. 25, *Ellis* 276 ×40. Fig. 26, *Ellis* 276 ×100. Figs. 27–30 **Paspalum paspalodes.** Fig. 27, *Ellis* 432 ×40. Fig. 28, *Ellis* 432 ×100. Fig. 29, *Ellis* 254 ×40. Fig. 30, *Ellis* 146 ×100.

No micro-hairs were seen on *P. vaginatum*. On *P. paspalodes* (both cuticular and papillate forms) micro-hairs are infrequently present on isolated parts of the leaf. These have thickened distal cells tapering to a point. The basal cell is exceptionally short and very difficult to see. This is in agreement with Metcalfe (1960), but Türpe (1966) illustrates micro-hairs with the basal cell up to one third the total length of the micro-hair.

The silica bodies of papillate *P. paspalodes* are horizontally elongated and nodular in outline on both the abaxial (Fig. 30) and adaxial (Fig. 34) surfaces. *P. vaginatum* has horizontally elongated, but noticeably angular, silica bodies as well, but these are only present on the adaxial surface. Abaxial costal silica bodies are very rare (Fig. 25), but crescent-shaped intercostal silica bodies are common in *P. vaginatum* (Fig. 26). Cuticular *P. paspalodes* has rows of shortly dumb-bell-shaped silica bodies with wide central portions in the costal zones (Fig. 27, 28).

P. vaginatum and cuticular *P. paspalodes* bear no abaxial papillae. In papillate *P. paspalodes* the abaxial papillae are inflated, unthickened and dome-shaped, with a diameter greater than half the vertical width of the long cell on which it is located (Fig. 30). There are no papillae on the costal zones, but all intercostal and interstomatal long cells bear a single, centrally-positioned papillus. Adaxial papillae are found on *P. vaginatum* and both forms of *P. paspalodes*. They are extremely large, elongated, oblique and inflated on *P. vaginatum* (Fig. 31, 32). These papillae are the same width as the epidermal cell, which is thus protruded to form the papillus. Most epidermal cells on the adaxial ribs and furrows bear papillae. The adaxial bulliform cells of cuticular *P. paspalodes* bear papillae which taper to narrow, thickened distal ends (Fig. 33), whereas those of papillate *P. paspalodes* are more inflated and oblique, but are distally thickened as well (Fig. 34).

Specimens Examined

Paspalum paspalodes. TRANSVAAL.—2527 (Rustenburg): Schoemansville, Hartebeespoort Dam (–DD), *Ellis 432*. 2528 (Pretoria): National Botanical Gardens, Brummeria (–CA), *Ellis 767*. Constantia Park Extension (–CB), *Ellis 146*. O.F.S.–2926 (Bloemfontein): Botanical Gardens, Bloemfontein (–AA), *van Heerden 95*. NATAL.—3030 (Port Shepstone): Eureka Farm, Izothsa (–CB), *Ellis 726*. CAPE.—3028 (Matatiele): 16 Km S.W. of Matatiele (–BD), *Ellis 254*. 3228 (Butterworth): Fort Warden farm, Komga (–CC), *Ellis 1106*.

Paspalum vaginatum. TRANSVAAL.—2528 (Pretoria): Glasshouse in National Botanical Gardens, Brummeria (–CA), *Ellis 1235*. NATAL.—2930 (Pietermaritzburg): Isipingo beach mangrove fringes (–DD), *Werger 1622*. CAPE.—3228 (Butterworth): Mazeppa Bay (–BC), *Ellis 276*. Haga Haga (–CC), *Ellis 1114*. 3422 (Mossel Bay): Wilderness lagoon (–BB), *Ellis 1299*.

DISCUSSION

The material examined can be separated satisfactorily by a number of apparently unrelated diagnostic characters especially of the leaf blade as seen in transverse section. The most easily studied of these are the obvious differences of the leaf margin and of the shape and size of the adaxial ribs and furrows and their associated papillae. Distinct differences are not so readily evident in epidermal preparations, because of the complications caused by *P. paspalodes* having two distinct types of epidermis: papillate and cuticular.

Undoubtedly, when the abaxial epidermis is studied alone (Fig. 25–30), cuticular P. *paspalodes* resembles *P. vaginatum* more closely than it does papillate *P. paspalodes*. It can also be reasonably assumed that specimens of *P. paspalodes* will be found with shorter and relatively thicker and narrower leaves than typical *P. paspalodes*. Thus differences as seen in

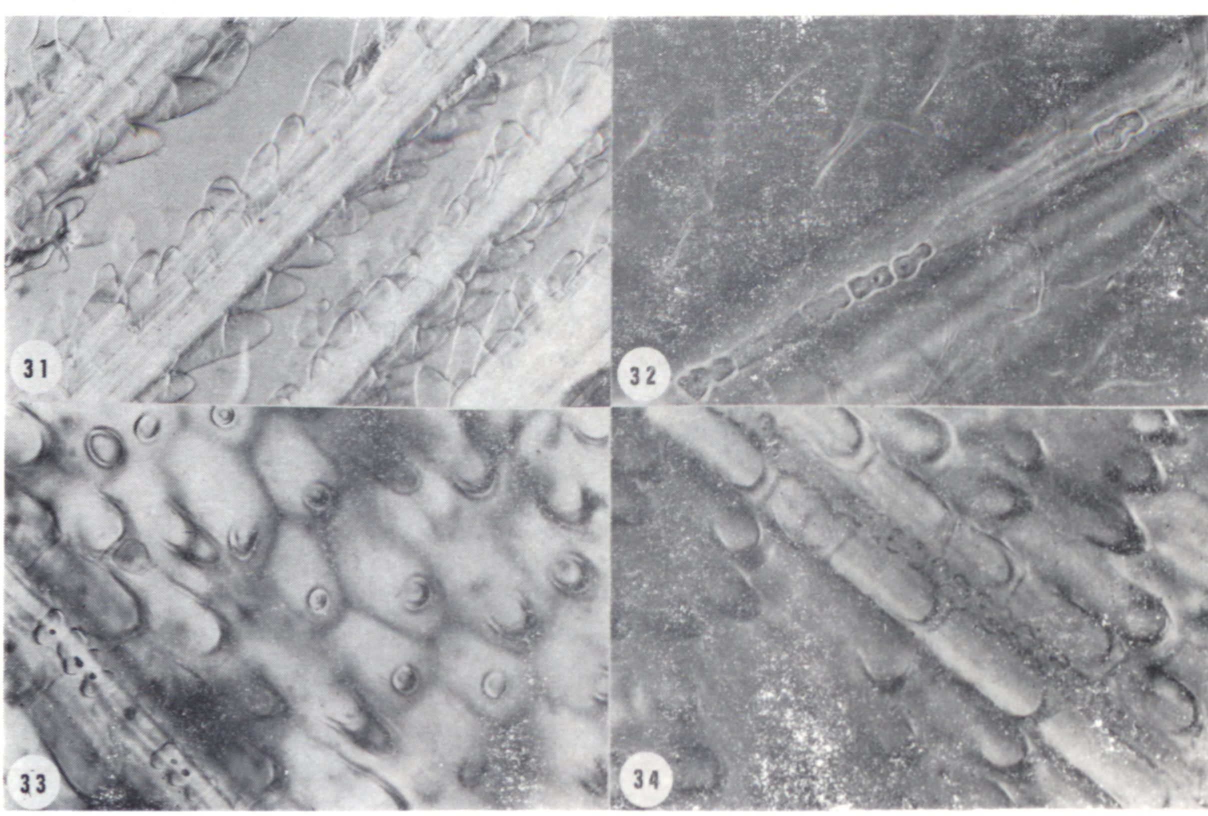

FIG. 31–34.—Adaxial epidermis, interference contrast. Figs. 31–32, **Paspalum vaginatum**. Fig. 31, *Ellis* 276 ×40. Fig. 32, *Ellis* 276 ×100. Fig. 33–34, **Paspalum paspalodes**. Fig. 33, *Ellis* 432 ×100. Fig. 34, *Ellis* 254 ×100.

transverse section might not be so distinct and a complete range of intermediates may be found from papillate *P. paspalodes*, through narrower and thicker cuticular *P. paspalodes* to typical *P. vaginatum*. This development of an abaxial cuticle, and other associated differences, on *P. paspalodes* is not correlated with a saline environment as was expected. *P. vaginatum* is a maritime species and always grows in a saline habitat, but the cuticular specimens of *P. paspalodes* were collected at Hartebeespoort Dam (*Ellis* 432), a pond in the National Botanical Gardens, Pretoria (*Ellis* 146) and at Port Shepstone (*Ellis* 726). The reason for this cuticular development in moist habitats is obscure.

The capable technical assistance of Miss E. V. C. Taylor and Miss L. Breytenbach is acknowledged. For the photographic enlargements the author is grateful to Mr S. R. van Jaarsveld.

REFERENCES

Loxton, A. E., 1974. The taxonomy of *Paspalum paspalodes* and *P. vaginatum* Swartz as represented in South Africa. *Bothalia* 11: 243–245.

Metcalfe, C. R., 1960. *Anatomy of the monocotyledons*. 1 *Gramineae*. Oxford: Clarendon Press.

Türpe, A. M., 1966. Histotaxonomia de las especies argentinas del genero *Paspalum*. *Lilloa* 32: 35–299.