

Anatomy of the leaves of the Velloziaceae in South Africa and South West Africa and a key based on leaf anatomy

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INTRODUCTION

According to the external morphology of the stem the Velloziaceae of South Africa and South West Africa can be divided into two groups, viz. the shrubs, which include *Xerophyta retinervis* Baker var. *retinervis*, *X. retinervis* Baker var. *equisetoides* (Baker) Coetsee, *X. retinervis* Baker var. *wentzeliana* (Harms) Coetsee, *X. clavata* Baker, *X. villosa* (Baker) Dur. & Schinz and *X. squarrosa* Baker, and the herbs, viz. *X. viscosa* Baker, *X. humilis* (Baker) Dur. & Schinz and *Talbotia elegans* Balfour.

The shrublike species have leaves borne in clusters near the stem apex and on small lateral branches among the leaf bases. The herbaceous species have terminal leaves (Coetsee, Van der Schijff and Steyn, 1973). In both groups the leaves occur along three orthostichies which, according to Weber (1954) alternate with three rhizostichies.

The leaves are linear, but *Xerophyta humilis*, *Talbotia elegans* and some representatives of *X. squarrosa* have linearlanceolate-shaped leaves. A keel is formed abaxially of the median vein where the leaf folds towards the adaxial side. In *X. viscosa*, however, the leaf halves roll up abaxially.

All the species, except *T. elegans*, have leaves with longitudinal furrows. In *X. retinervis* var. *retinervis*, *X. villosa* and *X. clavata* furrows occur on both surfaces. The leaves of *X. squarrosa* may also be furrowed on both sides or the adaxial surface may be sinuated while the abaxial surface may have shallow furrows.

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MATERIAL

Fresh material was collected from several localities, fixed in formalin-acetic-acid-alcohol and dehydrated in an ethanol series. Paraffin wax with a melting point of 55°C was used for embedding. Transverse sections, varying in thickness between 8 μm and 10 μm , were made with a rotary microtome and stained with fast green, safranin and haematoxylin or toluidine blue. Herbarium material used for anatomical studies was soaked in water at 60°C for twelve hours, rinsed and boiled for three minutes before fixation.

INVESTIGATION AND RESULTS

Epidermis

The epidermal cells are brick-like, elongated longitudinally and thin-walled with thickened inner or outer tangential walls. In surface view longitudinal rows of regularly-shaped cells cover the ridges, but irregular cells with concentrated pitfields occur in the furrows. In *Talbotia elegans*, where furrows are lacking, the epidermal cells have wavy anticlinal walls in the vicinity of the stomata. These cells occur in longitudinal strips between adjacent vascular bundles and alternate with strips of regular cells opposite the vascular bundles where stomata are lacking.

The adaxial epidermal cells opposite the median vein are always larger than elsewhere (fig. 1) and appear papillate in transverse section. According to Diogo (1926) these cells have, together with the underlying water-containing cells, the same function as the motor cells in the leaves of the Gramineae and enable the leaf to fold towards the adaxial side during water loss. The cuticle of the cells is extremely thin and this may be connected with the absorption of water, which gathers here.

The epidermal cells in the furrows are thin-walled with a thick, spiny cuticle and appear papillate in transverse section (fig. 2). As the stomata are restricted to the furrows, they are protected when the latter become narrower so that stomatal transpiration is minimal. Diogo (1926) maintains that the papillate epidermal cells absorb water, but the thick cuticle of the investigated species would probably prevent this.

The guard-cells are large and kidney-shaped with their long axis parallel to the long axis of the leaf (fig. 3). The large lateral subsidiary cells have striated transverse walls and partly overlap the guard cells. Ayensu (1969) maintains that the transverse striations protect the guard cells against tension during contraction of the leaves. The striations may therefore play an important physiological role and were found in all the investigated species.

The cell walls of the guard cells are thickened on the sides bordering the

stomatal pore and outer and inner ledges, covered by cuticle, occur. The stomatal chambers are usually small, but may be large in some cases with the abaxial chambers as big as or bigger than the adaxial chambers.

The cuticle may be smooth or may have regular, longitudinal grooves. The cuticle of the leaf margin is always thicker than elsewhere. In *Xerophyta villosa* and *X. squarrosa* the thickness of the cuticle varies in plants of the same species but different localities. The cuticle of *Talbotia elegans* is usually thinner than that of the other species.

When a difference in cuticle thickness occurs between the two leaf surfaces, the adaxial cuticle is thinner (eg. *X. retinervis*, *X. humilis*, *X. villosa* and *X. squarrosa*) except in *X. viscosa* where some plants have a better developed adaxial cuticle. *Xerophyta viscosa* is the only species with sunken glands in the adaxial epidermis (fig. 4) and also the only species where the leaves roll up abaxially, so that the leaf margins lie alongside the median vein.

In the specimens of *X. squarrosa* without obvious furrows, the epidermis in the vicinity of the stomata has fine cuticular outgrowths. Similar protuberances were seen in the furrows of *X. viscosa*.

Multicellular structures of epidermal and hypodermal origin occur on the leaves of all the shrubs (fig. 2). Greves (1921) regard similar structures on the ovary wall as hairs of taxonomic importance. In *X. retinervis* var. *retinervis* and *X. clavata* these structures may either occur on the adaxial leaf surface or may be lacking. In *X. retinervis* var. *wentzeliana* they are found adaxially or on both surfaces and in *X. retinervis* var. *equisetoides* they are present on both surfaces, as is the case in *X. villosa* which has an extremely thick covering of hairs. The epidermal cells of the hairy protuberances are elongated whilst elongated hypodermal sclerenchymatous cells form the remaining part of the structure.

Sunken, cup-shaped glands of epidermal and hypodermal origin are present in the adaxial leaf surface of *X. viscosa*. The cells are big and regular with dark contents and probably excrete the sticky substances found on the leaves of this plant (fig. 4).

A s s i m i l a t i o n t i s s u e

The leaves are isobilateral, except in *Xerophyta squarrosa*, *X. humilis* and *X. viscosa*. In the shrubs with isobilateral leaves the mesophyll consists of six (in the furrows) to twenty layers of chlorenchyma cells with minute intercellular spaces (fig. 8) which according to Haberlandt (1914) suggest xerophytic characteristics. *X. retinervis* var. *retinervis* plants growing under more moderate conditions have bigger intercellular spaces than those collected in drier areas. *Talbotia elegans*, however, which grows in a very wet habitat, also has minute intercellular spaces. This probably corresponds to the fact that *T. elegans* is periodically subjected to desiccation. Water-containing cells were found in the mesophyll of the latter species.

The adaxial hypodermal cells opposite the median vein of the leaves of all the species (fig. 1) as well as the first two hypodermal layers in the adaxial and abaxial furrows of the shrubs (fig. 5) consist of large, colourless, thin-walled palisade-like or rounded cells. In *X. squarrosa* these cells are less obvious adaxially between adjacent vascular bundles (fig. 6). Warming (1893) describes similar cells in *Barbacenia* and maintains that they do not occur in the leaves of *Vellozia*. Goedhart (according to Lotsy, 1911) agrees with Warming. Esau (1965) and Warming and Graebner (1933) describe similar cells as water tissue, while Warming (1893) regards them as water-supplying cells. According to Diogo (1926) these cells cause the closing of the furrows during loss of water and subsequent decrease in volume.

In a transverse section of the leaf the elongated chlorenchyma cells in most cases radiate from the water cells, with their long axis parallel to the leaf surface (fig. 5). In some examples of *Xerophyta retinervis* var. *retinervis*, *X. villosa* and *X. clavata* (fig. 8) the water cells are isodiametric and the chlorenchyma cells are not arranged in this characteristic way.

In *X. viscosa* a single, colourless hypodermal cell layer is present on both sides of the leaf (fig. 13). The cells are smaller and more regular than the mesophyll cells with fewer, if any, chloroplasts. Diogo (1926) regards them as watery parenchyma cells which provide protection against light or heat extremes.

The parenchyma on the adaxial side of the vascular bundles corresponds in transverse sections of the leaves of *X. squarrosa* to that found in the furrows of the leaves of the other shrublike species. These cells, which interrupt the bundle sheath adaxially, are separated from the epidermis by one to three layers of small parenchyma cells or, in some cases, by one to four layers of sclerenchyma cells (fig. 8). Warming (1893) regards similar cells in the leaves of *Vellozia candida* and *V. variabilis* as water-supplying cells.

The leaves of *Xerophyta humilis*, *X. viscosa* and *X. squarrosa* are dorsiventral. In the latter the palisade tissue consists of three to five cell layers with small intercellular spaces, but large spaces were found in the leaves of some plants where the palisade tissue is arranged in strands. The latter type of leaf lacks deep furrows, but has an irregularly sinuated adaxial surface and shallow furrows in the abaxial epidermis (fig. 6). The spongy parenchyma of *X. squarrosa* consists of six to twelve cell layers with small intercellular spaces in the vicinity of the vascular bundles and larger spaces opposite the furrows.

In *X. humilis* a gradual transition occurs between the three to four layers of palisade cells and the underlying three to five layers of spongy parenchyma cells. The mesophyll tissue contains small intercellular spaces. Towards the leaf margin the palisade cells gradually change into spongy parenchyma, so that the leaf becomes isobilateral in this area.

In *X. viscosa* the palisade tissue varies between three to eight, while the spongy parenchyma consists of two to ten cell layers. The size of the intercellular spaces varies, being the smallest near the vascular bundles (fig. 12).

Hypodermal sclerenchyma

The distribution of hypodermal sclerenchyma is a constant characteristic of the species and this tissue is present in the leaves of all the shrubs. The sclerenchyma occurs in the ridges and on the margins of the furrows (figs. 2 and 7). The abaxial sclerenchymatous zones may contain fewer cell layers than the adaxial zones or may even be represented by a single layer or a number of isolated cell groups. In *X. villosa* two to five sub-epidermal sclerenchyma layers occur opposite the veins on the side where the girders associated with the vascular bundles are lacking (fig. 7).

Therefore, the presence of hypodermal sclerenchyma distinguishes the shrublike representatives of the genus from the herbaceous species.

On the abaxial side of the median vein hypodermal fibres may be present in *X. clavata* and *X. squarrosa* (fig. 8). These cells are probably responsible for the ribs or spines found on the keel of the leaf.

On the leaf margin of *X. clavata* and the varieties of *X. retinervis* a separate, local hypodermal sclerenchyma bundle occurs, separated from the sclerenchyma strand of the marginal vascular bundle by the bundle sheath (fig. 9). The epidermal cells overlying this sclerenchyma have a thick, grooved cuticle. A series of transverse sections shows that this structure originates as a small sclerenchyma group which enlarges to become the externally discernable spiny outgrowth of the leaf margin.

Vascular bundles

The lateral vascular bundles of the leaf are of approximately equal size and vary in number from leaf to leaf. They are collateral and are bordered ab- and adaxially by sclerenchyma girders (fig. 12).

The primary phloem consists of a continuous strand or two lateral strands separated by sclerenchyma (figs. 10 and 11). Ayensu (1969) maintains that this separation occurs by an intrusion of the abaxial sclerenchyma girder. This theory is not accepted in the present study since, in the investigated species, the sclerenchyma intrusion starts differentiating at the adaxial and median part of the phloem (fig. 10). Cheadle and Uhl (1948) maintain that such fibres should be regarded as part of the phloem. The lateral bundles nearer to the median vein usually have better developed sclerenchyma fibres than those nearer to the leaf margin.

The protoxylem lies on the adaxial side of the vascular bundle and is partly separated from the metaxylem by xylem parenchyma (fig. 10).

The metaxylem elements of the shrubs occur in the form of a V with the arms of the V facing the protoxylem (fig. 11). In the centre of the V a number of thickened metaxylem elements occur, with a single large element at the base.

The arms consist of relatively small elements (figs. 6, 7, 8 and 9). In the herbs, however, a number of large elements lies at the base of the metaxylem (fig. 10). According to Fahn (1954) the xylem of the leaves of *Talbotia elegans* contains tracheids only and Ayensu (1969) confirms this.

Among members of the Velloziaceae, the sclerenchyma associated with the lateral bundles varies in distribution. Ayensu (1967) regards this characteristic as being taxonomically so important that it justifies the grouping of the Velloziaceae species into members having a *Barbacenia*, a *Vellozia* and a *Xerophyta* type of vascular bundle.

During this study this grouping proved to be confusing. In the leaves of *X. viscosa*, for example, both the *Vellozia* type and *Barbacenia* type of vascular bundles occur, as well as transitions between the two types. Deviations from the basic *Vellozia* type were also found, eg. in *Talbotia elegans*. None of the plants examined exhibited a *Xerophyta* type of vascular bundle. Unless Ayensu's types are extended to include the South African and South West African species, this classification cannot be used taxonomically. It does, however, give a good idea of the main types of vascular bundles with associated parenchyma which occur in the Velloziaceae.

In the shrubs the abaxial sclerenchyma girder is Y-shaped (fig. 5), broadly U-shaped (fig. 6), or even semi-circular without a sclerenchyma extension to the epidermis (fig. 7). The adaxial girder is an inverted Y and prominent. In *X. squarrosa*, however, the adaxial girder is much smaller than the abaxial girder (fig. 6) while *X. villosa* has a small semi-circular girder (fig. 7). The arms of the abaxial and adaxial girders do not meet, but are separated by small, thin-walled (fig. 10) or thick-walled cells (fig. 11).

The girders are usually separated from the epidermis by the thin-walled bundle sheath only. In *X. squarrosa*, however, one to three layers of hypodermal parenchyma or sclerenchyma occur opposite the lateral vascular bundles (fig. 6).

The bundle sheath consists of thin-walled cells (fig. 11) with concentrated pit-fields or may contain a number of thick-walled cells lateral to the vascular tissue. In *X. clavata* these cells have pronounced thick walls. In *X. squarrosa* the bundle sheath is interrupted adaxially by one or more layers of palisade-shaped cells, regarded by Warming (1893) as water-supplying cells. The cells of the bundle sheath usually lack visible contents, but exceptions do occur (figs. 5 and 7).

In *X. humilis* the girders are rod-shaped and the phloem connects the adaxial girder with the abaxial laterally. The adaxial girder may form an inverted Y and border the protoxylem laterally. A single layer of parenchyma cells may be present between the bundle sheath and the epidermis.

In *X. viscosa* the vascular bundles of the lamina differ from those of the leaf base. The former have cup-shaped adaxial and abaxial girders and the bundle sheath is separated from both epidermal layers by three to four layers of mesophyll cells. The sub-epidermal layers consist of water tissue (fig. 12). In the leaf base the dorsal girder is Y-shaped while the ventral layer is either Y-shaped or V-shaped. The bundle sheath borders the epidermis ab- and adaxially.

In *T. elegans* the abaxial girder is cup-shaped and more extensive than the adaxial girder. The bundle sheath is generally separated from the epidermis by a parenchyma layer.

The sclerenchyma strand of the leaf margin is prominent in some cases (fig. 9) and is surrounded by the bundle sheath of the marginal vascular bundle. In *X. humilis* the strand, enclosed by a parenchyma layer, lies apart. The bundle sheath may be adjacent to the epidermis or separated from the latter by several parenchyma cells, eg. in *T. elegans*, *X. humilis* and *X. viscosa*. Where the bundle sheath encloses both the marginal vascular bundle and the sclerenchyma strand, the phloem consists of either one or two strands which partly surround the xylem. The bundle sheath cells adjacent to the vascular bundle may be thick-walled.

The median vascular bundle of the leaf is bordered abaxially by a large sclerenchyma strand (fig. 8), which partly surrounds the adjacent phloem. The latter may consist of a continuous semi-circular strand or two lateral strands. The primary xylem tissue consists of a few metaxylem elements arranged in a V and a small group of protoxylem elements. The vascular bundle and associated parenchyma are surrounded by a common thin-walled bundle sheath. In *X. squarrosa* this bundle sheath consists adaxially of elongated water cells (fig. 1). The cell walls of the bundle sheath may have reticulate thickenings.

DISCUSSION

Ayensu (1967) showed that the distribution of the sclerenchyma of the Velloziaceae leaf is of taxonomic importance. Hypodermal sclerenchyma is found only in the shrubs and this characteristic is clearly seen in transverse sections of the leaf.

Furrows in the leaf surface are lacking only in *Talbotia elegans*, while the depth of the furrows varies in the other species. Plants with sinuated leaf surfaces were also found.

Multicellular spines or hairy outgrowths are of little taxonomic importance, except in *Xerophyta villosa*, where the leaves have a thick covering of long, fine hairs. The differentiation of the mesophyll can be used successfully to distinguish between certain species. *X. squarrosa* is the only shrub-like species with palisade and spongy parenchyma. Differentiated mesophyll also occurs in the leaves of the herbs *X. viscosa* and *X. humilis*. In the latter, however, the difference between palisade and spongy parenchyma is not very obvious. The most distinctive characteristic of *X. viscosa*, however, is the presence of numerous sunken, cup-shaped glands in the adaxial epidermis, an anatomical feature not present in any other species.

The distribution of sclerenchyma associated with the vascular bundles, can also be of taxonomic importance, eg. in *T. elegans* and *X. humilis*, where the sclerenchyma is totally different from that of the other species. This character-

istic was, however, disregarded in the key, since other anatomically more obvious leaf characteristics were found in the species investigated. The presence of hypodermal water tissue in the leaves of *X. squarrosa* and *X. viscosa* and water cells in the mesophyll of *T. elegans* was also disregarded.

With regard to leaf anatomy, no distinction could be made between the leaves of *X. clavata* and the three varieties of *X. retinervis*.

The following key was compiled taking into account the above-mentioned taxonomically important characteristics.

- | | | |
|----|--|---|
| 1. | Hypodermal sclerenchyma present in ribs | 4 |
| | Hypodermal sclerenchyma not present in ribs | 2 |
| 2. | Leaves without abaxial furrows | <i>Talbotia elegans</i> |
| | Leaves with abaxial furrows | 3 |
| 3. | Leaves with sunken adaxial glands | <i>Xerophyta viscosa</i> |
| | Leaves without sunken adaxial glands | <i>Xerophyta humilis</i> |
| 4. | Mesophyll differentiated into palisade and
spongy parenchyma | <i>Xerophyta squarrosa</i> |
| | Mesophyll not differentiated into palisade
and spongy parenchyma | 5 |
| 5. | Leaves with numerous multi-cellular "hairs"
on both surfaces | <i>Xerophyta villosa</i> |
| | Leaves without multi-cellular "hairs",
except on margins of furrows where
spines may occur | <i>Xerophyta retinervis</i>
(3 varieties)
and
<i>Xerophyta clavata</i> |

A b s t r a c t

The anatomy of the leaves of seven species and two varieties of the South African and South West African Velloziaceae was investigated.

The shrubs can easily be distinguished from the herbs by the presence of hypodermal sclerenchyma in the former. The sclerenchyma associated with the vascular tissue, however, varies within a species and this characteristic cannot be used to distinguish between the species of South Africa and South West Africa.

Hairy outgrowths of epidermal origin occur on the leaves of several species, but may also vary within the species.

Other anatomical characteristics regarded as taxonomically important, eg. glands,

water cells, hypodermal water tissue and longitudinal furrows on the leaf surface, were also investigated.

A key based on taxonomically important characteristics is given.

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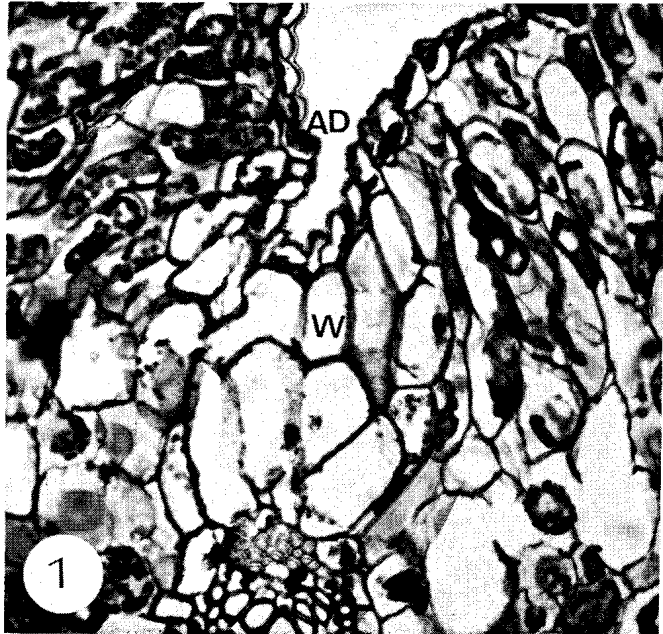


Fig. 1. Transection of a part of the leaf of *Xerophyta squarrosa* illustrating the tissues on the adaxial side of the median vascular bundle.
AD, adaxial epidermis; W, water-containing cells after loss of water.

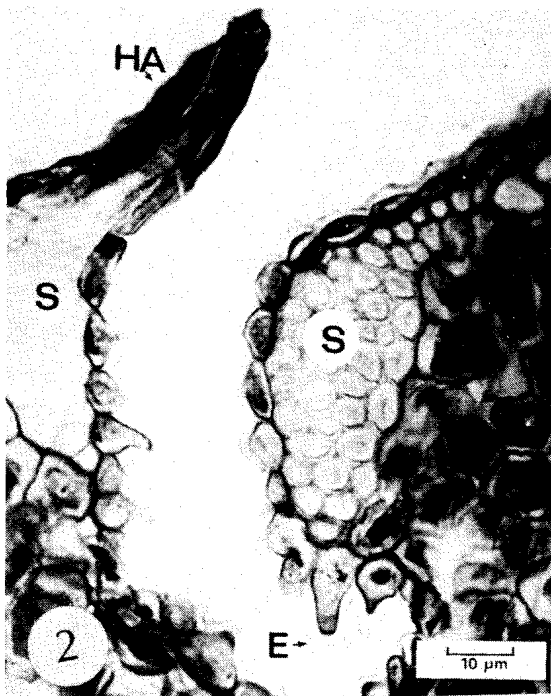


Fig. 2. Transection of a part of leaf of *Xerophyta retinervis* var. *retinervis* illustrating an adaxial furrow.
E, papillate epidermal cells with thickened cuticle; HA, multicellular hairy structure; S, hypodermal sclerenchyma of the ridge.

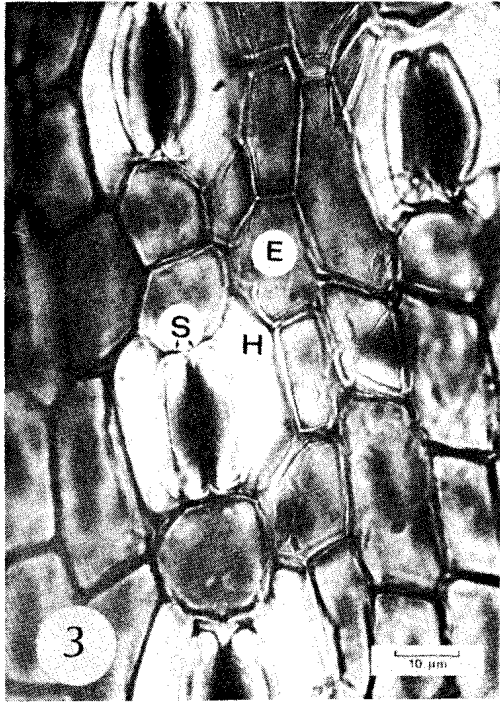


Fig. 3. Surface view of the epidermis of a part of the leaf of *Xerophyta retinervis* var. *wentzeliana*. E, epidermal cell; H, subsidiary cell; S, guard cells.

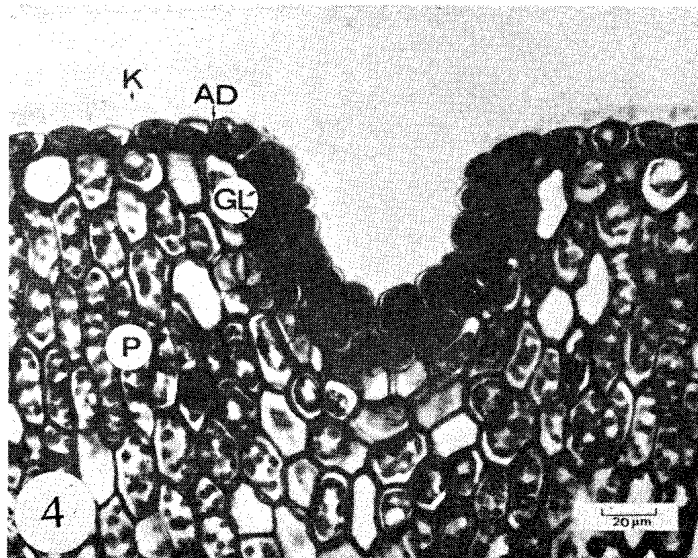


Fig. 4. Transection of a part of the leaf of *Xerophyta viscosa* illustrating a cup-shaped gland. AD, adaxial epidermis; GL, glandular cells; K, thickened cuticle; P, palisade parenchyma.

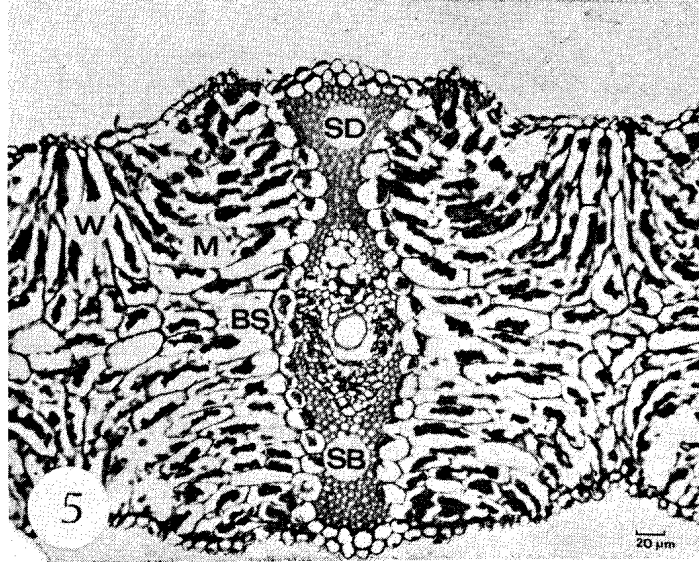


Fig. 5. Transection of a part of the leaf of *Xerophyta retinervis* var. *retinervis*. BS, bundlesheath; M, horizontal chlorenchyma cells; SB, abaxial sclerenchyma girder; SD, adaxial sclerenchyma girder; W, water-containing cells.

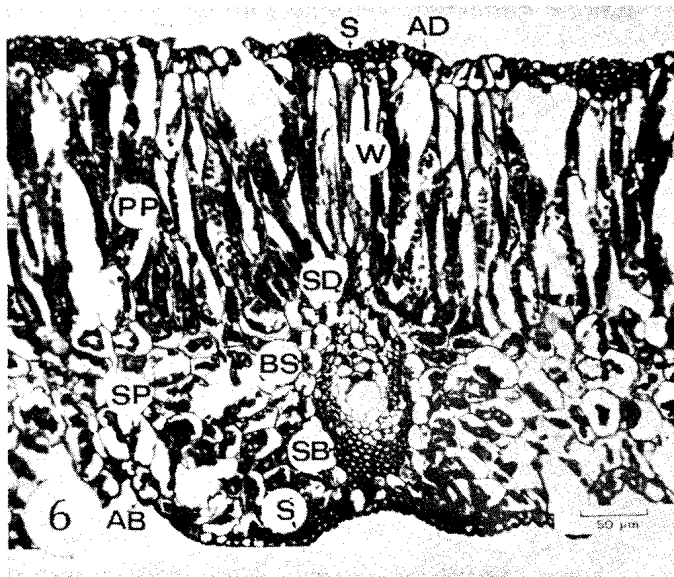


Fig. 6. Transection of a part of the leaf of *Xerophyta squarrosa* illustrating a lateral vascular bundle. AB, abaxial epidermis; AD, adaxial epidermis; BS, bundle sheath; PP, palisade parenchyma; S, hypodermal sclerenchyma; SB, abaxial sclerenchyma girder; SD, adaxial sclerenchyma girder; SP, spongy parenchyma; W, water-containing cells.

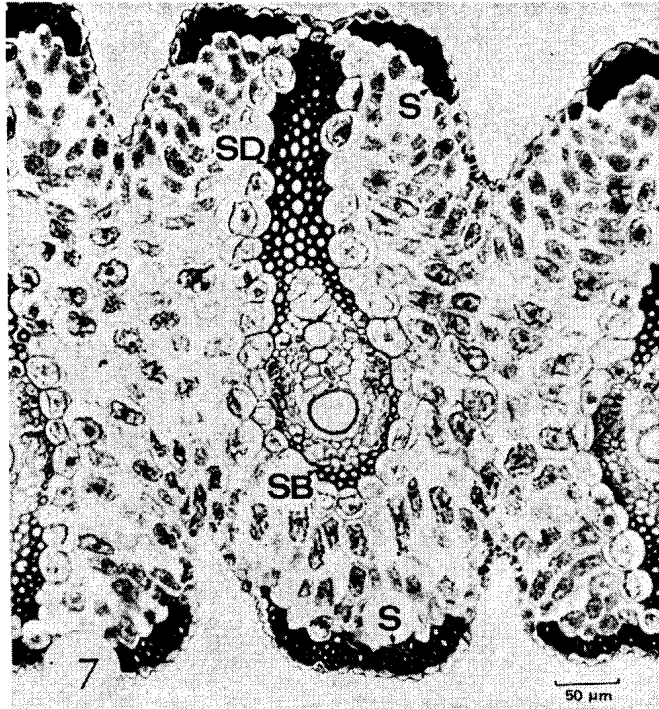


Fig. 7. Transection of a part of the leaf of *Xerophyta villosa*.
 S, hypodermal sclerenchyma; SB, abaxial sclerenchyma girder; SD, adaxial sclerenchyma girder.

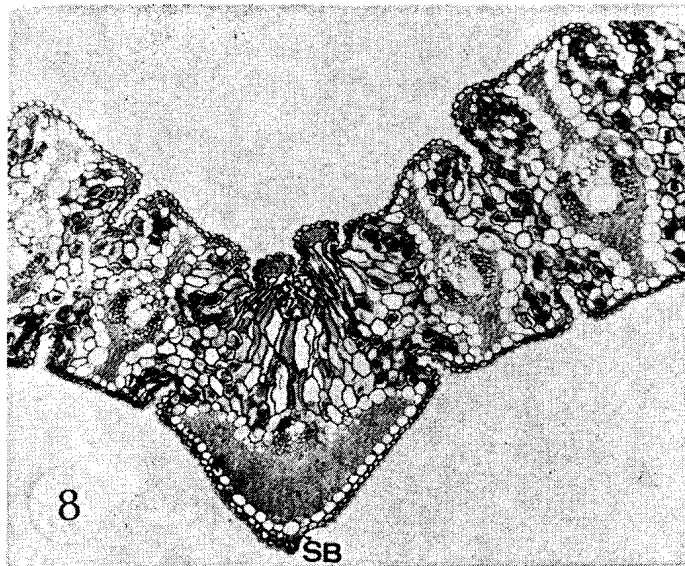


Fig. 8. Transection of a part of the leaf of *Xerophyta clavata*.
 SB, hypodermal sclerenchyma on the abaxial side of the median vein.

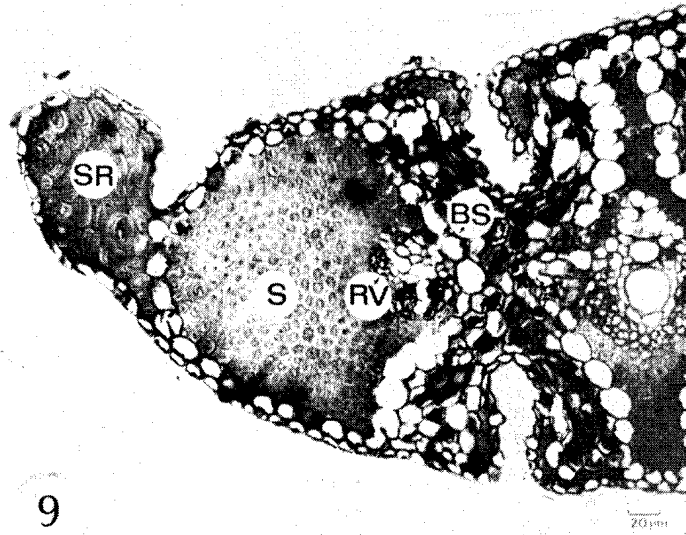


Fig. 9. Transection of the leaf margin of *Xerophyta clavata*.
BS, bundle sheath of marginal vascular bundle; RV, marginal vascular bundle;
S, sclerenchyma strand of marginal vascular bundle; SR, hypodermal scleren-
chyma of leaf margin.

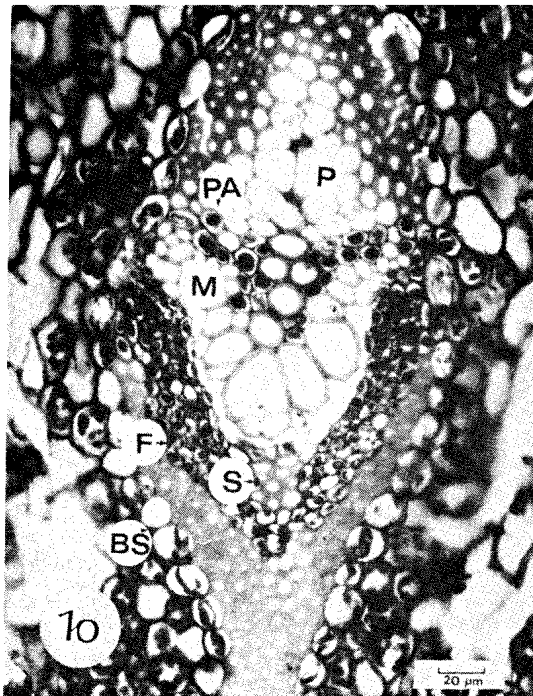


Fig. 10. Transection of a lateral vas-
cular bundle of *Xerophyta viscosa*.
BS, bundle sheath; F, phloem; M, metaxylem; P,
protoxylem; PA, xylem parenchyma; S, sclerenchy-
ma separating the phloem.

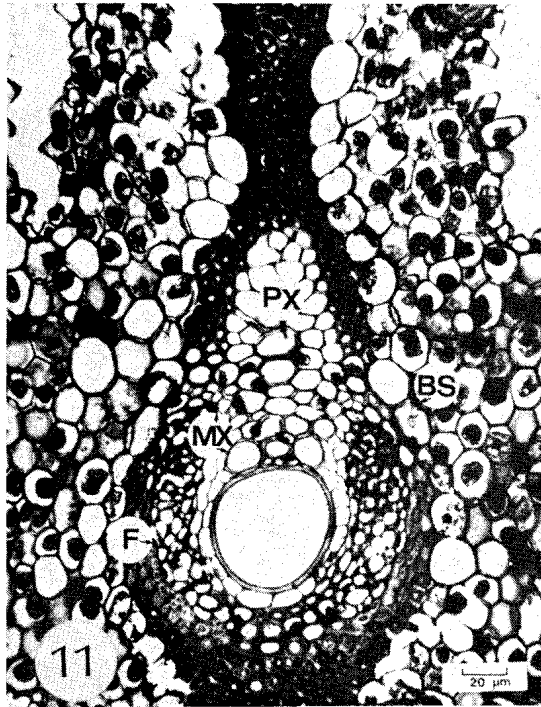


Fig. 11. Transection of a lateral vascular bundle of *Xerophyta retinervis* var. *retinervis*. BS, bundle sheath; F, phloem; MX, metaxylem; PX, protoxylem.

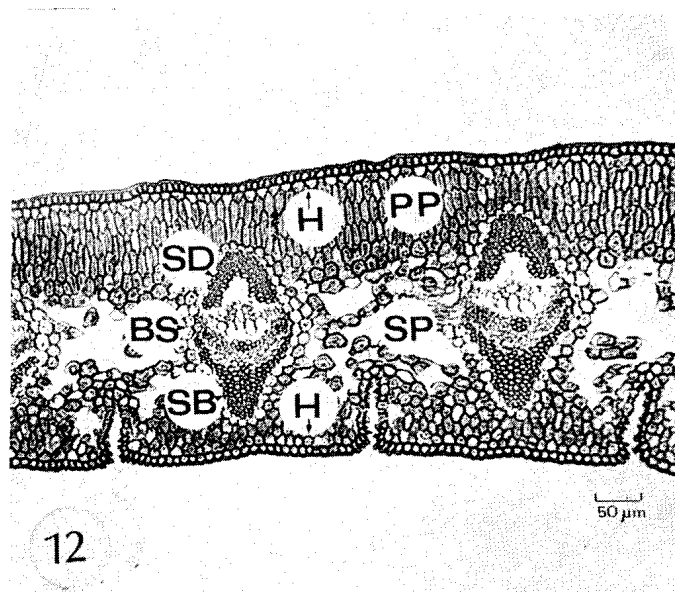


Fig. 12. Transection of a part of the leaf of *Xerophyta viscosa*. BS, bundle sheath; H, hypodermal water tissue; PP, palisade parenchyma; SB, abaxial sclerenchyma girder; SD, adaxial sclerenchyma girder; SP spongy parenchyma.