

Studies in the Hypoxidaceae. I. Vegetative morphology and anatomy†

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ABSTRACT

The leaf and corm morphology and anatomy of representatives of the genera *Spiloxene*, *Pauridia* and *Empodium* were studied. The corms are annual and tunicated, except in the group *Aquaticae* of *Spiloxene*. They are swollen stems consisting of a number of internodes. In *Spiloxene* and *Pauridia* the roots grow from the base of the corm, while in *Empodium* they develop from the sides. The epidermis of the older corms is replaced by several layers of thin-walled cork. Characters of the corm coverings are used to divide *Spiloxene* into six groups. Four leaf forms are recognised namely carinate, terete, canaliculate and plicate. Multicellular processes and unicellular hairs occur occasionally.

The leaf stomata are paracytic. Most species have mucilage canals containing pectic compounds of mucopolysaccharides. The vascular bundles have complete or incomplete bundle sheaths and larger bundles have sclerenchyma caps.

Résumé

ETUDES SUR LES HYPOXIDACEAE. I. MORPHOLOGIE VEGETATIVE ET ANATOMIE

La morphologie et l'anatomie de la feuille et du bulbe des représentants des genres *Spiloxene*, *Pauridia* et *Empodium* ont été étudiées. Les bulbes sont annuels et tuniqueés sauf dans le groupe *Aquaticae* de *Spiloxene*. Ils ont des tiges gonflées constituées de nombreux internoeuds. Chez *Spiloxene* et *Pauridia* les racines sortent de la base du bulbe, tandis que chez *Empodium* elles se développent sur les côtés. L'épiderme des bulbes plus âgés est remplacé par plusieurs fines couches de liège. Les caractères de la couverture du bulbe sont utilisés pour diviser les *Spiloxene* en six groupes. Quatre formes de feuilles sont reconnues, à savoir: carinate, terete, canaliculée et plicate. Des processus multicellulaires et des poils unicellulaires se rencontrent occasionnellement. Les stomates de la feuille sont paracytiques. La plupart des espèces ont des canaux mucilagineux contenant des composés pectiques de mucopolysaccharides. Les faisceaux vasculaires ont des étuis de faisceaux complets ou incomplets et les faisceaux les plus grands ont des coiffes de sclérenchyme.

1. INTRODUCTION

The Hypoxidaceae is represented in South Africa by five genera, namely: *Hypoxis* L., *Rhodohypoxis* Nel, *Spiloxene* Salisb., *Empodium* Salisb. and *Pauridia* Harv. *Empodium* is sometimes included in the tropical genus *Curculigo* Gaertn. and *Spiloxene* in *Hypoxis*. *Hypoxis* and *Rhodohypoxis* occur mainly in the summer rainfall areas. *Spiloxene* and *Pauridia* are confined to the winter rainfall region while *Empodium* is widespread from the south-west Cape to the Transvaal Drakensberg.

The genera are in need of taxonomic revision and the aim of this study is to compare anatomical and morphological features of the genera *Spiloxene*, *Empodium* and *Pauridia* with special reference to characters that could be of taxonomic value. This paper covers the corm and leaf, while a second will deal with the floral anatomy.

Previous anatomical work in the family was largely confined to *Hypoxis* and *Curculigo* (Scharf, 1892; Schulze, 1893; Arber, 1925; Nel, 1914a; Geerinck, 1968).

2. MATERIAL AND METHODS

Fresh material was collected in the field and voucher specimens are housed in the Government Herbarium, Stellenbosch (STE).

Fresh corms of *Spiloxene capensis* (L.) Garside, *S. aquatica* (L.f.) Fourc., *Empodium plicatum* (Thunb.) Garside and *Pauridia minuta* (L.f.) Dur. & Schinz were cut longitudinally at different seasons to show the development of the successive corms and the position of the roots. The corms were cut at the beginning and end of the growing season and during the dormant period. Corms fixed in FAA were embedded in paraffin wax, sectioned at 20-25 µm, stained with safranin and fast green and mounted in Depex.

The leaves of the following species were studied: *Spiloxene aquatica*, *S. capensis*, *S. flaccida* (Nel) Garside, *S. minuta* (L.) Fourc., *S. ovata* (L.f.) Garside, *S. schlechteri* (Bol.) Garside, *S. serrata* (Thunb.) Garside, *Empodium plicatum*, *Pauridia longituba* M. F. Thompson and *P. minuta*. The *Spiloxene* species were chosen to represent the groups defined by Nel (1914a). The material used for the cross-sections of the leaves was taken from the middle of the first two or three foliage leaves (i.e. excluding the completely sheathing leaves). Karpechenko's modification of Navashin's fluid was found to be the best fixative. The fixed material was embedded in paraffin wax, sectioned at 15-20 µm, stained with safranin and fast green and mounted in Depex.

3. THE CORM

(1) Morphology

(i) General

Two main types of underground storage organs are found in the Hypoxidaceae of Southern Africa: an erect, tuberous perennial rhizome in *Hypoxis* and *Rhodohypoxis* and an annual corm in *Spiloxene*, *Empodium* and *Pauridia*.

The annual corm is a swollen stem consisting of a number of internodes formed by the apical meristem of the shoot. There is no normal elongated stem and the cataphylls, foliage leaves and axillary inflorescences arise directly from the upper half of the corm. The branching is, therefore, monopodial and the growth is usually orthotropic. In *S. aquatica* the growth is usually somewhat plagiotropic i.e. horizontal (Fig. 1A), a condition brought about by the horizontal growth of the apical bud. This differs from the plagiotropic growth of the Iridaceae where the branching is sympodial and a new corm is formed from the uppermost axillary bud, the terminal bud having produced a flowering shoot in the previous season (Troll, 1937).

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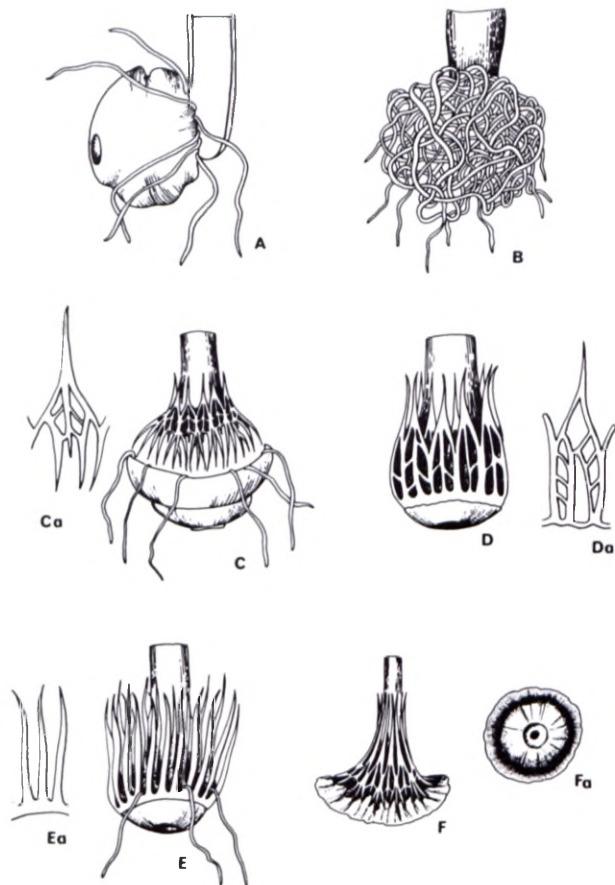


FIG. 1.—Corm coverings in *Spiloxene*: A, *S. aquatica* (Aquatitae); B, *S. ovata* (Ovatae); C, *S. capensis* (Stellatae); Ca, detail of fibres of C; D, *S. flaccida* (Flaccidae); Da, detail of fibres of D; E, *S. schlechteri* (Pectinatae); Ea, detail of fibres of E; F, *S. minuta* (Minutae); Fa, F seen from below.

A new corm is formed annually on top of the old one, the old shrunken storage organs of previous seasons remaining at the base as discs (Fig. 2B). The corm is either naked (in which case it is referred to as a tuber) or it has a fibrous covering of tunics formed from the remains of the sheathing foliage leaf bases and cataphylls.

(ii) *Spiloxene*

As Nel (1914a, b) has shown, *Spiloxene* (= *Ianthe*) can be divided into groups on the basis of the fibrous tunics of the corms. He recognized seven groups of which six have tunicated corms and one a naked fleshy tuber.

The groups of Nel (1914a, b) are given here with modified diagnoses:

(1) *Aquatitae* Nel: Tuber fleshy, without basal discs, never covered with fibres (Fig. 1A), e.g. *S. aquatica*.

(2) *Ovatae* Nel: Corm with discs, entirely covered with branching fibres and twisting roots (Fig. 1B), e.g. *S. ovata*.

(3) *Serratae* Nel: Differs from the *Ovatae* in having serrated leaves, e.g. *S. serrata*.

(4) *Stellatae* Nel: Corms with basal discs, fibres easily separable from the old corm, much branched below the middle or in the lower third and ending in numerous pungent ribs pointing upwards (Fig. 1C & 1Ca), e.g. *S. capensis*.

(5) *Flaccidae* Nel: Corm subovate with basal discs, the upper (inner) fibres adnate to the corm, the lower (outer) fibres easily separable but adpressed to the body of the corm, spreading above, joined

together below by a ridge (Fig. 1Da) and remaining attached to the basal disc, branched or evenly latticed at the base of the corm or reticulate, ending in a point above (Fig. 1D & 1Da), e.g. *S. flaccida*.

(6) *Pectinatae* Ne': Corm subovate, with basal discs, fibres pectinate, not branched, apiculate, spreading at the neck of the corm, normally adhering to the discs, if separated from the disc then tending to remain joined together at the base (Fig. 1E), e.g. *S. schlechteri*.

(7) *Minutae* Nel: Corm basally flattened, without basal disc, obconical, fibres adnate to the body of the corm, not easily separable, producing a raised disc or wide denticulate corona at the base (Fig. 1F, 1Fa), e.g. *S. minuta*.

With the exception of the *Serratae*, I regard these groups as well-defined. The group *Serratae*, which Nel separates from the *Ovatae* mainly because of its serrate leaves, is not considered worthwhile upholding as this character is variable in several of the groups. In the *Stellatae*, for example, *S. capensis* has serrated leaves while the leaves of all the other representatives are entire. The *Serratae* should thus be placed under the *Ovatae*.

The description by Nel (1914a) of the structure of the corm contains certain anomalies. He uses the term Zwiebelknolle or bulbous corm and states that this organ consists of leaf sheaths (p. 244 "besteht aus Blattscheiden"). The corm is, in fact, a swollen stem usually covered with the vascular remains of old leaf sheaths. Nel also makes the erroneous statement that the bases of the leaves may remain as discs ("Scheibe")

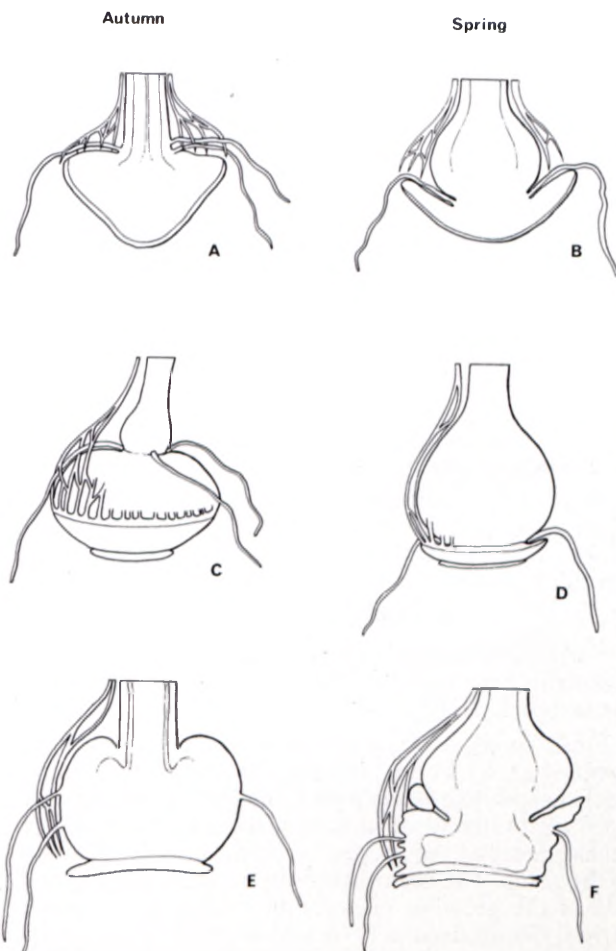


FIG. 2.—Corms: showing the position of the roots in autumn (A, C, E) and spring (B, D, F), after development of the new corm. A–B, *Spiloxene capensis* (approx. $\times 1,3$); C–D, *Pauridia minuta* (approx. $\times 2,3$); E–F, *Empodium plicatum* (approx. $\times 1,3$).

but this could possibly be a misprint for "Scheide"-sheath. In his key and description of the groups Nel describes all the corms except those of the *Aquaticae*, as "discoideus". This presumably refers to the old corms which remain as discs at the base of the functional corm. His description of the discs as two lamellae with a nutrient rich space in between fits this concept. In his description of the groups (1914b) he does use the terms subdiscoïd and subovate in addition to discoid.

In autumn the new roots grow from the top of the swollen corm, run under the tunics (where present) to the widest part of the corm and pass through the reticulations (Fig. 2A). After further development during the winter growing season, it becomes clear that these roots arise from the base of the present season's new corm. By spring the young corm has become the main storage corm with the roots growing from its base (Fig. 2B). The old corm remains as a disc. In most Iridaceae, by contrast, the roots arise from the base of a swollen storage corm and remain functional the year after this corm has acted as a storage corm (Troll, 1937; De Vos, 1970).

The position of the roots is the same in the autumn/winter-flowering *S. schlechteri* and the spring-flowering *S. aquatica* and *S. capensis*.

The old storage corm provides the nutrients for leaf formation and, in the autumn flowering species, for flowering.

An observation by Markötter (1936) that *S. schlechteri* frequently reproduces vegetatively was confirmed. In this species new corms appear to develop from axillary buds on the base of corms, a phenomenon seldom observed in other members of the genus.

(iii) *Empodium*

E. plicatum has a corm with coverings resembling those of the *Stellatae* group in *Spiloxene*, i.e. the reticulate vascular fibres of the tunic are free at the base. The dried-up intercostal tissue of the leaf bases tends to remain longer than in *Spiloxene*, resulting in a more scale-like covering, the reticulations being less obvious.

The roots do not arise at the top of the summer storage corm, but on its sides in the lower half and pass immediately through the meshes of the tunics (Fig. 2E). The roots develop after the first good autumn rains and then the flowers appear before the leaves.

The new corm is formed by the apical meristem above the old one in a monopodial orthotropic fashion. Cormlets may be formed in axillary positions at the base of the developing corm towards the end of the growing season (Fig. 2F).

(iv) *Pauridia*

Pauridia has a corm similar to that of the *Flaccidae* group in *Spiloxene*, i.e. it is covered with reticulating fibres which remain attached to the basal discs formed by the previous seasons' corms. As in *Spiloxene* the roots arise at the base of the developing corm (Fig. 2C).

(2) *Anatomy*

Anatomically the corms of the three genera, including all the groups of *Spiloxene*, are very similar.

In the young corm the epidermis consists of a single layer of thin-walled cells. Immediately interior to this is a layer of parenchyma three to four cells deep which lacks starch. The epidermis of the mature corm is replaced by several layers of thin-walled cork cells arising from a phellogen situated in the sub-epidermal parenchyma (Fig. 3).

The main body of the corm is made up of a densely packed ground tissue of parenchyma cells rich in starch. Throughout the ground tissue there are mucilage canals, which are not associated with the vascular bundles. Canals are more numerous in the mature corm than in the younger one. As in the leaf, the canals are surrounded by radially flattened cells. Scharf (1892) found that in *Hypoxis* the canals arise schizogenously near the growing point and that they have no membrane but are embedded in a ring of smaller cells.

Numerous vascular bundles run irregularly through the ground tissue and supply the roots and leaves. The bundles normally have three to four tracheal elements with ring or spiral thickenings.

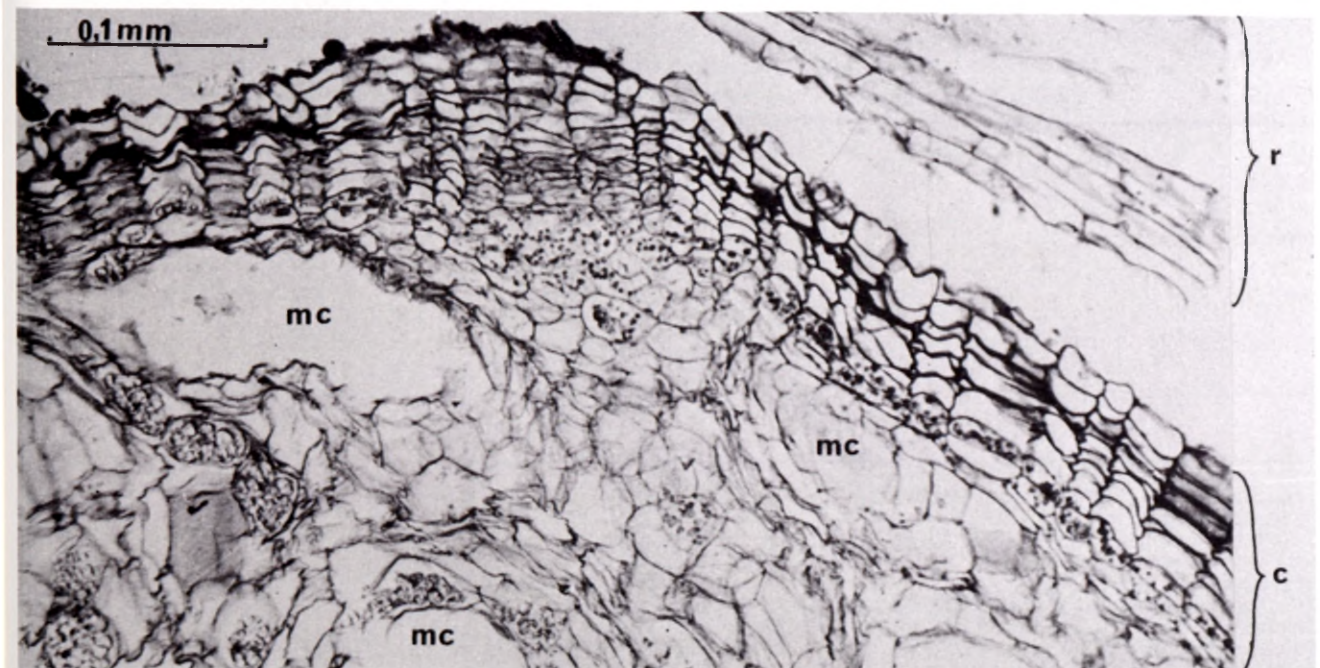


FIG. 3.—Longitudinal section of the outer zone of the corm of *S. capensis*. c, cork; mc, mucilage canal; r, root.

4. THE LEAF
(1) General

The leaves in the Hypoxidaceae are radical with a more or less sheathing base. The outermost leaves of each year are reduced to bifacial leaves or cataphylls. The foliage leaves are generally bifacial, but may be unifacial and terete. In the bifacial forms the lip is usually unifacial and represents the "Vorläuferspitze" of Troll (1939).

The following description relates to the species listed under Material and Methods and the main features are summarized in Table 1.

(2) Anatomy

(i) Epidermis

The leaf epidermis of all the species studied consists of a single layer of largely thin-walled cells, covered by a smooth thin cuticle. In surface view the cells are rectangular, elongated in the direction of the long axis of the leaf, and have straight walls. The walls of the epidermal cells along the leaf margin and keel are sometimes thickened as in *S. capensis* (Fig. 4). Some epidermal cells may be enlarged to form bulliform cells as in the angle of the V of many of the carinate leaf forms e.g. in *S. serrata* and *P. minuta* and in the folds in *Empodium*. In most of the bifacial leaves the cells on the adaxial surface are larger than those on the abaxial side, but are not enlarged to form bulliform cells (e.g. *S. ovata*).

In *Spiloxene* and *Pauridia* the stomata are scattered on both surfaces, while in *Empodium* they are confined to the intercostal zone. In all three genera they are paracytic, i.e. with a single subsidiary cell parallel to and flanking each of the guard cells (Fig. 5E). This agrees with the observations of Stebbins & Kush (1961), but Shah & Gopal (1970) found that in *Curculigo orchioides* Gaertn. sixty per cent of the stomata were tetracytic (i.e. with four to six subsidiary cells). Shah & Gopal report further that in this species the epidermal cells are not rectangular, as in the hypoxid leaves which I have studied, but have an irregular shape and arrangement.

The structure of the guard cells varies only slightly in the species studied. The anterior cavity is well-developed due to an outer ledge formed by the cell wall and cuticle. The posterior cavity is poorly

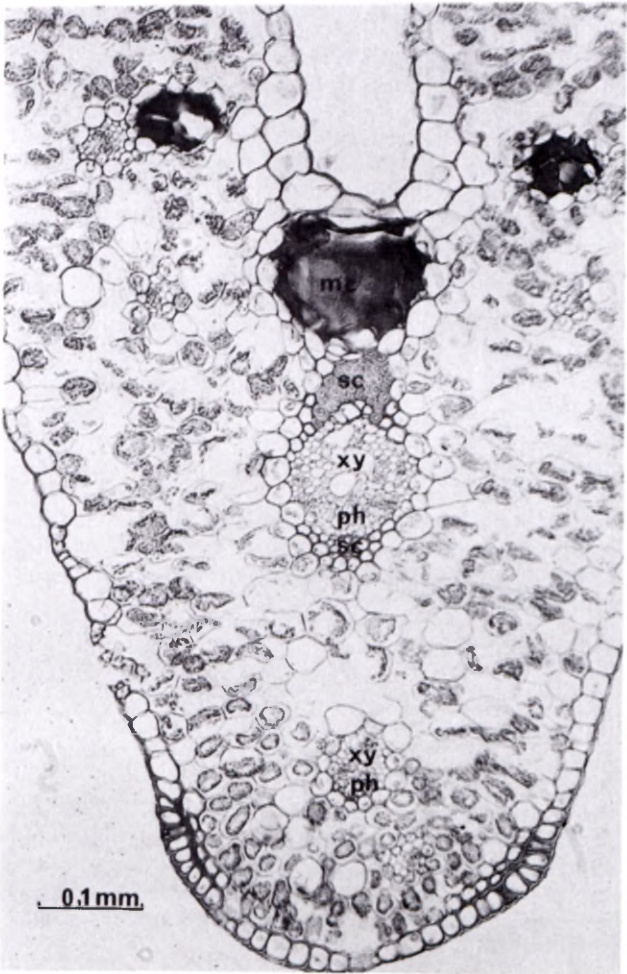


FIG. 4.—Cross section of the leaf keel of *S. capensis*. mc, mucilage canal; ph, phloem; sc, sclerenchyma; xy, xylem.

developed (e.g. *S. aquatica*) or undeveloped (e.g. *S. flaccida* and *S. capensis*). The guard cell walls are unevenly thickened, as shown in cross-section (Fig. 5D). The median region of the wall bounding the aperture and the entire opposite wall are thin and elastic and together they constitute the hinges (vide Eames & MacDaniels, 1947).

TABLE 1. Comparison of leaf characters
(X) indicates partial or occasional presence. MC, mucilage canal; VB, vascular bundle.

	Epid. wall thickened	Trichomes unicellular	Trichomes multicellular	Bulliform cells	Stomata scattered	Stomata intercostal	Aerenchyma	MC assoc. with VB	MC scattered	MC absent	B/sheath complete	B/sheath incomplete	Sclerenchyma cap	Carinate	Canaliculate	Terete	Plicate
<i>Spiloxene aquatica</i>			X		X		X	X		X	X		(X)			X	
<i>Spiloxene capensis</i>	X				X			X			X		X				
<i>Spiloxene flaccida</i>					X			X				X	(X)				
<i>Spiloxene minuta</i>	X			X	X			X		X	X		(X)				
<i>Spiloxene ovata</i>					X			X			X		X				
<i>Spiloxene schlechteri</i>					X			X			X		X			X	
<i>Spiloxene serrata</i>			X	X	X			X			X	X	X				
<i>Pauridia longituba</i>					X			X			X		X				
<i>Pauridia minuta</i>					X			X			X		X				
<i>Empodium plicatum</i>	(X)	X		X		X			X			X	X				X

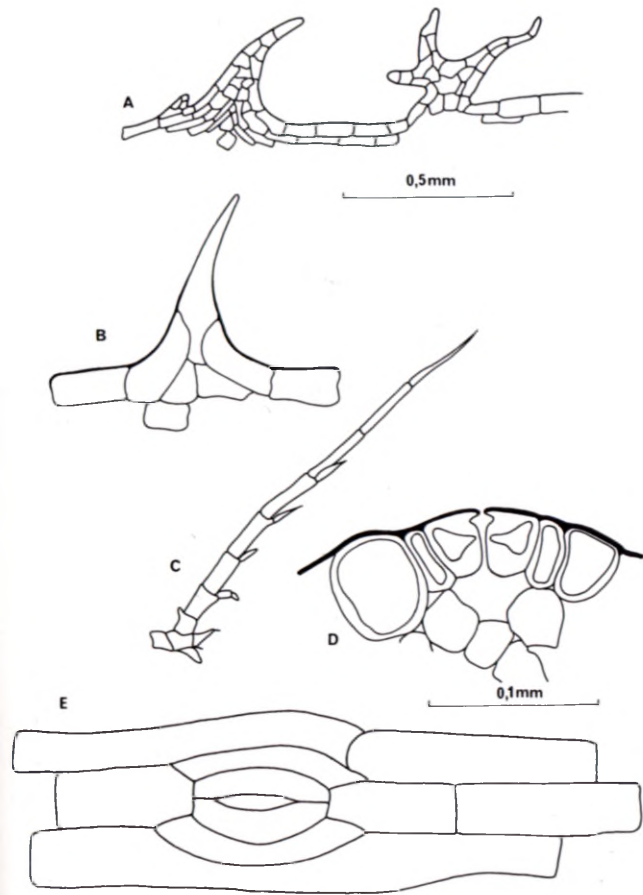


FIG. 5.—Leaf epidermis. A, epidermal processes on the keel of *S. capensis*; B, unicellular hair of *E. plicatum*; C, multicellular hair of *S. capensis*; D, cross section of stoma of *S. flaccida*; E, surface view of stoma of *S. aquatica*.

The serrations that occur along the margins of the lower part of the leaf in *S. serrata*, and sometimes on the margins and keel towards the tip of the leaf in *S. capensis*, are multicellular epidermal processes.

In *S. serrata* the epidermis produces regular incurved serrations two cells thick at the base. The processes in *S. capensis* are very irregular. They include the sub-epidermal thick-walled cells of the margin and keel. They are often branched and may extend into long pointed multicellular hairs (Fig. 5A & C). Nel (1914a) reports that the teeth sometimes contain chlorophyll but I found no chloroplasts in the serrations.

On the ridges of the folds of *Empodium plicatum* are unicellular hairs surrounded at their bases by slightly raised epidermal cells (Fig. 5B) which do not form part of the hair. These hairs resemble the cushion macro-hairs of the Gramineae (Metcalf, 1960). The cuticle, thin throughout, continues over the trichomes.

(ii) Mesophyll

The cells of the mesophyll are mostly irregular, rounded to oval in shape, rich in chloroplasts and with large inter-cellular spaces. Scattered cells contain raphides and lack chlorophyll. The bifacial leaf forms of *Spiloxene* and *Pauridia* show a tendency to form palisade tissue towards the adaxial side. There is no palisade in the plicate leaf of *Empodium*. The cells on either side of the midrib in the carinate leaves may be enlarged and without chlorophyll as in *S. minuta* and *S. serrata*. In the terete leaf of *S. aquatica* the mesophyll has an aerenchymatous central part.

The mucilage in *Spiloxene* and *Pauridia* is confined to mucilage canals which lie adaxially to, or, in terete leaves centripetally to, the larger vascular bundles (Figs. 4 & 6). The canals are bounded by radially flattened cells. In *Empodium* the canals are scattered in the mesophyll independently of the vascular bundles. Mucilage canals are lacking in the leaves of *S. aquatica*, although they are present in the corm.

In sections of fresh leaves the mucilage showed no reaction with Schultze's solution and gave a reddish colour with ruthenium red, indicating that the mucilage is a pectic and not a cellulosic substance. Tests with Alcian blue indicated the presence of mucopolysaccharides. Scharf (1892) records that the "colourless slime turns hard and brown when treated with alcohol". I found that the mucilage was dispersed by fixatives containing alcohol and that it is soluble in alcohol and not precipitated by it. Karpechenko's fluid (without alcohol) did not effect the position of the mucilage.

(iii) Vascular bundles and sheaths

Cheadle & Uhl (1948) described five different types of vascular bundles found in monocotyledons. The larger vascular bundles of the species studied fall into their Type IV which possesses one or two large central metaxylem elements. These elements are tracheids with ring or spiral thickenings. Cheadle (1968) recorded primitive vessels with scalariform perforation plates in the roots of Hypoxidaceae but not in the rest of the plant. The phloem consists of sieve tubes, companion cells and phloem parenchyma, irregularly arranged. The bundles often have sclerenchyma caps at one or both poles (Fig. 4).

The smaller bundles generally lack sclerenchyma and resemble Type I of Cheadle & Uhl (1948) which has no larger metaxylem elements.

The vascular bundles are surrounded by a single-layered bundle sheath of parenchymatous cells with few or no chloroplasts. The sheaths may be (i) complete, i.e. continuous round the bundle, e.g. *S. capensis* (Fig. 4), or (ii) incomplete, i.e. interrupted by sclerenchyma caps at one or both poles, e.g. in *S. flaccida* and *Empodium plicatum*.

When the bundle sheath continues round the mucilage canal to the adaxial epidermis, as in *S. capensis* (Fig. 4), it may be regarded as a bundle sheath extension.

(3) Leaf forms

On the basis of morphology and general anatomy the leaves of the species studied may be divided into four groups, namely, carinate, canaliculate, terete and plicate (See Table 1).

(i) The carinate leaf

Examples: *S. capensis*, *S. flaccida*, *S. minuta*, *S. serrata*, *Pauridia longituba* and *P. minuta*. (Fig. 6A, 6C).

The greater part of the length of the leaf is V-shaped in cross-section with a large vascular bundle in the angle of the V, forming a definite midrib and sometimes a marked keel as in *S. capensis* and *S. flaccida*. *S. serrata* and *S. minuta* do not show as definite a keel but the central bundle is still larger than the rest of the bundles. In *S. serrata* and sometimes in *S. minuta* the cells of the central adaxial mesophyll are enlarged (up to 50 μ m) and lack chlorophyll. The mucilage canals lie adaxially to the larger vascular bundles, except in *S. minuta* where they are lacking. The bundles may have sclerenchyma caps as in *S. capensis*.

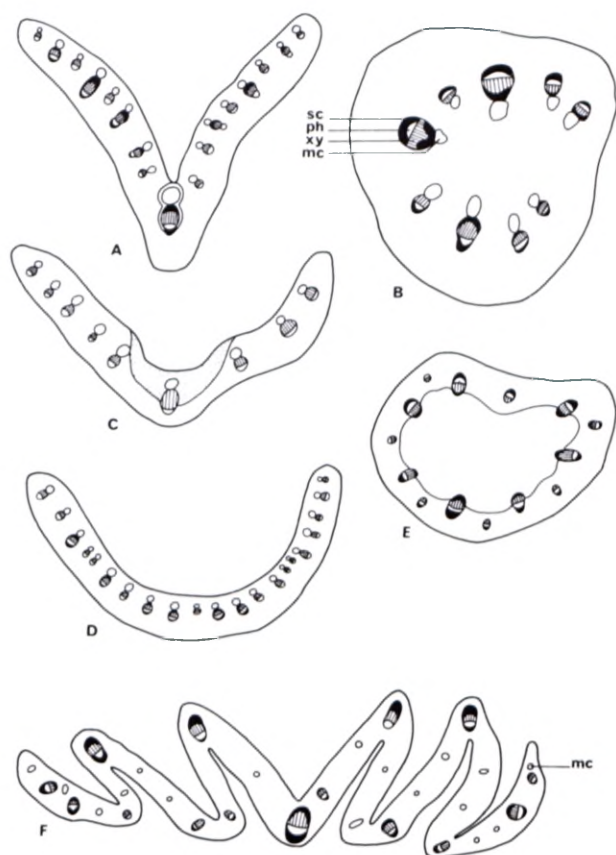


FIG. 6.—Diagrammatic cross-sections of leaves demonstrating leaf forms. A, Carinate: *S. capensis*, $\times 10$; B, Terete: *S. schlechteri* $\times 18$; C, Carinate: *S. serrata*, $\times 18$; D, Canaliculate: *S. ovata*, $\times 10$; E, Terete: *S. aquatica*, $\times 10$; F, Plicate: *E. plicatum*, $\times 10$; mc, mucilage canal; ph, phloem; sc, sclerenchyma; xy, xylem.

The sheathing part of the leaf does not have a marked midrib. The tip of the leaf is a unifacial “Vorläuferspitze” (Troll, 1939).

This is the most common type of leaf found in *Spiloxene*. Geerinck (1968), in comparing the leaves of Haemodoraceae and Hypoxidaceae, regards this as the typical hypoxidaceous leaf.

(ii) *The canaliculate leaf*

Example: *S. ovata*. (Fig. 6D).

The leaf is bifacial, U-shaped in cross-section and without a midrib.

The adaxial epidermal cells are larger (about $50\ \mu\text{m}$) than the abaxial (about $30\ \mu\text{m}$). The mesophyll consists of more or less even-sized irregular cells without the formation of a palisade. Mucilage canals bounded by radially flattened cells lie adaxially to the vascular bundles. The 15–30 bundles are more or less equal in size throughout the width of the leaf or the alternating ones are somewhat larger. There is little or no sclerenchyma associated with the vascular bundles.

This type of leaf is less common than the carinate leaf and, among the species studied, only occurs in *S. ovata*. Garside (1942) describes this type in *S. canaliculata* Garside and considers the leaf shape important in separating *S. canaliculata* from *S. capensis*.

(iii) *The terete leaf*

Examples: *S. aquatica* and *S. schlechteri* (Fig. 6B, 6E).

The leaf is unifacial with a ring of ectophloic bundles. The peripheral mesophyll is denser than the

central part which may be aerenchymatous (e.g. *S. aquatica*). Mucilage canals, when present, lie centripetally to the vascular bundles.

There is a gradual transition from the bifacial, canaliculate sheath to the unifacial terete part (Fig. 7a–d). The adaxial surface decreases gradually until the entire leaf surface consists of the abaxial epidermis.



FIG. 7.—Transition from the bifacial leaf sheath to the unifacial blade in *S. aquatica*. Cross-sections a–d taken at the points marked on plant on left.

In the species investigated the terete condition appears to develop differently from that in the Haemodoraceae as described by Geerinck (1968) where the leaves are “folded-welded”. Geerinck described the Haemodoraceae as having a folded (V-shaped in cross-section) basal part which fuses to form a vertically flattened part with vascular bundles alternating in direction, or a terete portion with bundles in a ring with a peripheral phloem.

(iv) *The plicate leaf*

Example: *Empodium plicatum*. (Fig. 6F).

The leaf is bifacial and is folded longitudinally with two or three folds on either side of the midrib.

Within the folds (ad- and abaxial) the epidermal cells are enlarged to form bulliform cells. On the ridges the cell walls, especially the outer, are thickened. Trichomes occur along the ridges and margins (Fig. 5B). Stomata are frequent in the inter-costal zones of both surfaces. The mesophyll is uniform without differentiation of a palisade. Mucilage canals occur irregularly in the mesophyll and are not associated with the vascular bundles as in *Spiloxene*.

Unlike the palm leaf, which has a prominent rib at each fold (Tomlinson, 1961), not every fold has a vascular bundle at the ridge. The midrib is the only

large bundle in an abaxial ridge. The adaxial ridges all have large bundles. Arber (1922) said that the folds in *Curculigo recurvata* develop by alternating dorsal (i.e. abaxial) and ventral (i.e. adaxial) invaginations of the petiole or leaf sheath. The ventral sinuses occur between the lateral bundles and opposite the midrib while the dorsal sinuses occur opposite the main lateral bundles (cf Fig. 6F).

5. CONCLUSIONS

The similarity in the vegetative anatomy and morphology of *Pauridia* and *Spiloxene* suggests that these genera are closely related. *Pauridia* has a corm like the group Flaccidae of *Spiloxene* and there are no major differences in the leaf structure of the two genera.

The differences between *Empodium* and the other two genera are greater. The corm, although superficially similar, differs in the position of the roots. The plicate leaf form is only found in *Empodium*. The mucilage canals of the leaves are scattered in the mesophyll in *Empodium*, while in *Spiloxene* and *Pauridia*, where present, they are associated with the vascular bundles (Table 1). The stomata are scattered on both leaf surfaces in *Spiloxene* and *Pauridia* while in *Empodium* they are confined to the intercostal zones. *Empodium* has unicellular hairs while the epidermal processes observed in *Spiloxene*, were all multicellular.

Within the genus *Spiloxene* the nature of the corm coverings can be used to define groups (Nel, 1914a, b). With the exception of the *Serratae*, which should be combined with the *Ovatae*, the groups of Nel are accepted.

The leaf form does not appear to be a good basis for grouping species in any of the three genera, as otherwise dissimilar species can have the same leaf form. On the other hand, in the group *Ovatae* of *Spiloxene* carinate [*S. cuspidata* (Nel) Garside, *S. gracilipes* (Schltr.) Garside], canaliculate [*S. ovata*, *S. linearis* (Andr.) Garside] and terete [*S. dielsiana* (Nel) Garside] forms occur. However, the type of leaf can be used to distinguish between some closely related species such as *S. capensis* and *S. canaliculata* (Garside 1942).

Apart from the fact that the internal structure reflects the outward morphology, the leaf anatomy was not found to provide characters of taxonomic value. The presence of aerenchyma in *S. aquatica* is probably a habitat response. Mucilage canals are absent from the leaves in species as different as *S. minuta* and *S. aquatica*. In *Empodium* however, their arrangement is characteristic and different from the other species investigated. The bundle sheaths are generally indistinct and the presence of sclerenchyma is not constant.

The morphology of the corm was found to provide the vegetative characters most useful to the taxonomist.

UITTREKSEL

Die blaar- en knolmorfologie en anatomie van veertienwoordigers van die genera Spiloxene, Pauridia en Empodium is bestudeer. Die knolle is gerok (uitsluitend die groep Aquaticae van Spiloxene), eenjarig en bestaan uit 'n verdikte stingel met meer as een lit. By Spiloxene en Pauridia groei die wortels uit die basis van die knol, terwyl hulle by Empodium by die kante van die knol uitgroe. In die ou knol word die epidermis deur dunwandige kurk vervang. Kenmerke van die knolomhulsel word gebruik om Spiloxene in ses groepe te verdeel. Vier blaarvorme word erken: gekiel, tereet, gekanaliseer en geplooi. Multisellulêre uitsteeksels en unisellulêre hare kom soms voor. Die huidmondjies by die blare is paracyties. Slymkanale, met slym wat uit pektienverbindinge van polisakkariede bestaan, word by die meeste soorte aangetref. Die vaatbundels het volledige of onvolledige bundelskedes en die groter bundels het sklerenchiemusse.

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