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, canalicate 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.

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 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, canalicate 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 tunicés sauf dans le groupe Aquaticae de Spiloxene. Ils ont des tiges gonflées constituées de nombreux internodes. 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, canaliculate 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 coffets de sclérenchyme.

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. 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 (1914). 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

(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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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* Nel: 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’”)

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. *Aquaticae* 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
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 subdiscoid 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 "Vorlaufterspitze" 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 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).

![Fig. 4.—Cross section of the leaf keel of *S. capensis*. mc, mucilage canal; ph, phloem; sc, sclerenchyma; xy, xylem.](image)

**Table 1. Comparison of leaf characters**

(X) indicates partial or occasional presence. MC, mucilage canal; VB, vascular bundle.

| Species              | Epiderm. wall thickened | Trichomes unicellular | Trichomes multicellular | Bulliform cell | Stomata scattered | Aerenchyma | MC assoc. with VB | MC scattered | MC absent | Bolea complete | Bolea incomplete | Sclerenchyma cap | Carinate | Canalicular | Terete | Plicate |
|----------------------|-------------------------|-----------------------|------------------------|----------------|------------------|------------|------------------|-------------|-----------|----------------|------------------|-----------------|-----------|-------------|--------|---------|
| *Spiloxene aquatica* | X                       | X                     |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             | X      |         |
| *Spiloxene capensis* |                        |                       |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             |        |         |
| *Spiloxene flaccida* |                        | X                     |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             | X      |         |
| *Spiloxene minuta*   | X                       |                       |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             |        |         |
| *Spiloxene ovata*    |                        |                       |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             | X      |         |
| *Spiloxene schlechieri* |                        |                       |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             |        |         |
| *Spiloxene serrata*  | (X)                     | X                     |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             | (X)    | (X)    |
| *Pauridia longituba* |                        |                       |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             |        |         |
| *Pauridia minuta*    | X                       |                       |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             |        |         |
| *Empodium plicatum*  | (X)                     | X                     |                        |                |                  |            |                  | X           | X         |                |                  |                 |           |             |        |         |
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 μm) 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*.
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 μm) than the abaxial (about 30 μm). 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 centrifugally 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.
large bundle in an abaxial ridge. The adaxial ridges all have large bundles. Arber (1922) said that the folds in Curculigo recurtata 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 form like the group Flaccideae 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 form, 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). On the other hand, in the group Pauridia of Spiloxene and there are no major differences in the leaf structure of the two genera.

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 verteenwoordigers 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 stengel 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 uitgroei. In die ou knol word die epidermis deur dunwandige kurk vervang. Kenmerke van die knolumhulsel word gebruik om Spiloxene in ses groepe te verdeel.

Vier blaarvorme word erkenn: gekiel, tereken, gekanaliseer en geplooи. Multisellulêre uitsteeksels en unisellulêre hare kom soms voor. Die huidmondjies by die blare is paracrytis. Slymkanale, met slym wat uit spektrumverbonds van positiewe steriele bestaan, word by die meeste soorte aangetref. Die vaatbundels het volledige of onvolledige bundelskedes en die groter bundels het sklerenchiemusse.

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