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Studies in the Hypoxidaceae. II. Floral morphology and anatomy*

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ABSTRACT

The inflorescence and flowers of representatives of *Spiloxene*, *Pauridia* and *Empodium* were studied. The inflorescence shows a reduction from a several-flowered umbel to a single flower. The anthers are non-versatile in all three genera, unlike those of *Hypoxis* and *Rhodohypoxis*. In *Spiloxene* and *Pauridia* the ovary is 3-locular with axile placentation, while in *Empodium* it is unilocular with three parietal placentas. The floral vascular anatomy of the three genera is described and the generic differences pointed out. The close relationship between *Spiloxene* and *Pauridia* is demonstrated and the inclusion of *Pauridia* in the Hypoxidaceae is supported. *Spiloxene* is regarded as generically distinct from *Hypoxis*.

RÉSUMÉ

ÉTUDES SUR LES HYPOXIDACÉES: II. MORPHOLOGIE ET ANATOMIE FLORALES

On a étudié l'inflorescence et les fleurs de représentants de Spiloxene, Pauridia *et* Empodium. *L'inflorescence montre une réduction d'une ombelle multiflorale à une fleur unique. Dans les trois genres, à la différence d'*Hypoxis *et* Rhodohypoxis, *les anthéres sont non-versatiles. Chez* Spiloxene *et* Pauridia *l'ovaire est tri-loculaire avec une placentation axile, tandis que chez* Empodium *il est uniloculaire avec trois placentas pariétaux. L'anatomie vasculaire florale des trois genres est décrite et on signale les différences génériques. La forte affinité entre* Spiloxene *et* Pauridia *est démontrée et l'inclusion de* Pauridia *dans les Hypoxidacées est confirmée.* Spiloxene *est regardé comme un genre distinct d'*Hypoxis.

1. INTRODUCTION

It was pointed out in the first part of this work (Thompson, 1976) that the genera of the Hypoxidaceae are in need of taxonomic revision. The aim of these contributions is to compare anatomical and morphogical features of the genera *Spiloxene*, *Empodium* and *Pauridia* with special reference to characters that could be of taxonomic value. While the first paper dealt with corm and leaf, the present contribution discusses inflorescence and flower.

No previous work has been done on the floral anatomy of South African Hypoxidaceae. Scharf (1892) and Arber (1925) have remarked that the vascular bundles of the peduncle lie in a ring, not scattered as in the stems of most monocotyledons. This observation can be explained by the fact that the peduncle is not the main stem or axis, but an axillary structure. Nel (1914) studied the morphology of the inflorescence, flower and bracts of *Spiloxene* (as *Janthe*) and determined which parts are peduncle and which are pedicel.

2. MATERIAL AND METHODS

The following species were studied: *Spiloxene alba* (Thunb.) Fourc., *S. aquatica* (L.f.) Fourc., *S. capensis* (L.) Garside, *S. flaccida* (Nel) Garside, *S. minuta* (L.) Fourc., *S. ovata* (L.f.) Garside, *S. schlechteri* (Bol.) Garside, *S. serrata* (Thunb.) Garside; *Pauridia minuta* (L.f.) Dur. & Schinz, *P. longituba* M. F. Thompson; *Empodium plicatum* (Thunb.) Garside, *E. veratrifolium* (Willd.) M. F. Thompson.

Flowers of *Pauridia minuta* were fixed in FAA and embedded in paraffin wax. Serial microtome cross sections were made. They were stained with safranin and fast green and mounted in Depex. The larger flowers of *Spiloxene* and *Empodium* were fixed in FAA and stored in 70 % alcohol before hand sectioning or clearing.

The structure of the perianth segments, anthers and stigmas was studied using hand sections of fresh material stained with anilin chloride or safranin and fast green.

The vascular anatomy was studied using clearing techniques. The flowers were cleared by heating in pure lactic acid (Sporne, 1948), or boiling in 60% lactic acid. The tracheary and parenchymatous tissues were contrasted by condenser-iris-diaphragm regulation on a compound microscope. Fresh or preserved material was used. In addition to cleared material, cross sections were studied—either hand sections or, in *Pauridia*, serial microtome sections.

3. MORPHOLOGY

(1) *The Inflorescence*

Spiloxene

In *Spiloxene* the flowers are pedicellate and are borne on peduncles, which arise from the corm in the axils of the leaves. Nel (1914) maintained that in the species with two bracts and those with many flowers e.g. *S. aquatica* the peduncles arise terminally. In all the species studied, including *S. aquatica*, I found the peduncles to be axillary.

The peduncles may be one-flowered (e.g. *S. capensis*) to several-flowered (e.g. *S. aquatica*). In the latter case, the inflorescence is an umbel-like raceme. At the junction of the peduncle and the pedicel(s) one or two bracts occur. These may be small and setaceous (as in *S. serrata*) or linear-lanceolate foliaceous bracts as in *S. capensis*.

A many-flowered inflorescence is, in general, considered to be more primitive than the single flower which arises by reduction (Eames, 1961). The umbel-like inflorescence of the many-flowered forms of *Spiloxene* may be taken to be the most primitive condition from which there are grades of reduction. *S. aquatica* has two to seven flowers in an umbel with two foliaceous bracts. *S. flaccida* has two or three flowers, also with two foliaceous bracts. *S. schlechteri*, *S. serrata* and *S. minuta* have one or two flowers, while *S. capensis* and *S. ovata* have a single flower. The single-flowered forms of *S. schlechteri*, *S. minuta* and *S. capensis* have one foliaceous bract, while *S. ovata* and *S. serrata* have two setaceous bracts. Thus there is a reduction in number or in size of the bracts, as well as in the number of flowers.

Pauridia

The genus has an axillary inflorescence, like the single-flowered species of *Spiloxene*, with two setaceous bracts at the junction between peduncle and pedicel. In *P. longituba* the pedicel is very short (1–2 mm) and exceded by the bracts (2–10 mm), while in *P. minuta* it is longer than the bracts.

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TABLE 1.—Reduction in the inflorescence in *Spiloxene*

Species	Number of flowers in inflorescence	Number of bracts	Nature of bracts F. foliaceous S. setaceous	Filaments E. equal U. unequal
S. aquatica...	2–7	2	F	E
S. flaccida....	2–3	2	F	U
S. alba.....	1–2	2	F	U
S. schlechteri.	1–2	1–2	F	U
S. serrata....	1–2	2	S	E
S. minuta....	1–2	1	F	E
S. ovata.....	1	2	S	E
S. capensis...	1	1	F	E

Empodium

The flowers are axillary and borne singly. As there is no division into peduncle and pedicel, there are no bracts. The pedicels may be long as in *E. veratrifolium* or short and hidden within the sheathing leaves as in *E. plicatum*. In the latter case, the pedicel elongates during the fruiting stage thus the fruits are exserted from the sheath.

(2) *Perianth*

Spiloxene

The flowers are regular with two whorls of three free, subequal more or less lanceolate perianth segments spreading from the top of an inferior ovary. The segments of the inner whorl are generally smaller than those of the outer whorl. The adaxial surface is white or yellow with or without a dark spot at the base and the abaxial surface is often striped or tinged with green or maroon. In *S. capensis* there may be an irridescent spot at the base of the perianth segments. Some attempts have been made to define varieties based on the variation in size and colour of these spots; however, as Garside (1924) concluded, these variations are of a 'continuous' kind and varieties are better based on vegetative characters. A single population (e.g. *Thompson* 2939) may have flowers without spots, with dark spots of various sizes or iridescent "peacock" spots.

Pauridia

Pauridia has a regular perianth with a distinct tube. Geerinck (1969) incorrectly describes *Pauridia* as having free tepals. In *P. minuta* the tube is short (up to 5 mm) and equal to or less than the length of the lobes. In *P. longituba* it is up to 20 mm long and approximately three times the length of the lobes.

The lobes are subequal, narrowly ovate. The outer lobes have a small hooded tip with papillae on the inside. The reverse sides (abaxial) of the segments are green at the tip fading downwards, with the outer segments being darker.

Empodium

The perianth has six free lanceolate equal segments, which spread from the top of the ovary beak. In a flower opening for the third and fourth day the segments may become reflexed.

(3) *Androecium*

Spiloxene

There are two whorls of three free stamens attached to the base of the perianth segments. The filaments may be equal, e.g. *S. capensis*, or unequal in length, e.g. *S. flaccida*. (Table 1).

The anthers are linear 2-thecous, basifixed and non-versatile, i.e. the filaments are continuous with the connectives between the thecae without a joint or articulation. In *Hypoxis* and *Rhodohypoxis* the anthers are distinctly versatile. The terminology applied to the anther attachment has caused some confusion (Geerinck, 1969). However, the presence or absence of an articulation, a character very clearly seen in fresh material, is the distinguishing feature. The thecae open by longitudinal slits.

Pauridia

Pauridia has three stamens inserted on the perianth tube opposite the inner perianth segments. The anthers are 2-thecous, split longitudinally and are basifixed. The thecae separate from the connective at the top and bottom, thus the anther appears lobed.

Empodium

Here there are six free stamens with short equal filaments attached to the base of the perianth segments. The anthers are linear, 2-thecous, opening by longitudinal slits, basifixed, non-versatile. Some species of *Empodium* have caudate appendages on the anthers.

(4) *Gynoecium*

Spiloxene

There are three free or fused, commissural stigmas borne on a very short style. The ovary is normally three-locular with axile placentation and numerous ovules. Sometimes the septa do not extend to the top of the ovary, leaving the top part unilocular, as in *S. aquatica*. The ovary is usually slightly constricted below the perianth (most noticeable in the fruiting stage). In *S. alba* this constriction forms a neck, from the top of which the perianth segments and stamens arise. The fruit is a capsule with circumcissile dehiscence or irregular fragmentation.

Pauridia

In *Pauridia* the stigma is 6-lobed with three long, erect, commissural lobes and three short recurved lobes or appendages over the ovary chambers. Some or all of the lobes occasionally abort. A freak flower (in *Thompson* 278) tended to form anthers on the short lobes, one almost complete. The style is short in *P. minuta* and long in *P. longituba* in direct relationship to the length of the perianth tube.

The ovary is 3-locular with numerous ovules and axile placentation. The fruit may be a capsule with circumcissile dehiscence (*P. minuta*) or be thin walled with irregular fragmentation (*P. longituba*). Two similar forms of fruit have been recorded within the genus *Rhodohypoxis* (Hilliard & Burtt, 1973).

Empodium

This genus has three subulate stigmatic lobes on a short style, except in *E. gloriosum* (Nel) B. L. Burtt. The ovary is unilocular with parietal placentation and develops into a slightly succulent, indehiscent fruit. In some species, e.g. *E. plicatum*, the pedicel being short the ovary is enclosed within the leaf sheath. The pedicel elongates exposing the fruit. In others, e.g. *E. veratrifolium*, the pedicel being long the ovary and fruit are exposed. Many of the species have a long ovary beak or neck. This is a solid prolongation of the ovary or, possibly, the receptacle, which bears perianth and androecium. The length of the beak is inversely related to the length of the pedicel.

(5) *Comparison*

Of the three genera *Spiloxene* has the simplest basic flower structure. *Empodium* differs from *Spiloxene* in having no bracts on the peduncle, a one-chambered ovary, an indehiscent fruit and in the development of

TABLE 2.—Comparison of morphological characters

Organ	*Spiloxene*	*Pauridia*	*Empodium*	*Hypoxis*	*Rhodohypoxis*
Rootstock	Corm	Corm	Corm	Tuberous rhizome	Tuberous rhizome.
Pubescence	Glabrous or few simple hairs	Glabrous	Glabrous or simple hairs	Pubescent with comound hairs	Pubescent with compound hairs.
Inflorescence	1–7-flowered umbellate	1(or2)-flowered	1-flowered	1- several-flowered raceme	1–2-flowered.
Bracts	1 or 2	2	0	1 per flower	1 or 2.
Perianth segments	Free	Tube	Free	Free	Tube and "blind look".
No. stamens	6	3	6	6	6
Anthers	Non-versatile	Non-versatile	Non-versatile	Versatile	Versatile.
Stigma	3-lobed	6-lobed	3-lobed	3-grooved	3-lobed.
Ovary	3-locular	3-locular	1-locular	3-locular	3-locular.
Placentation	Axile	Axile	Parietal	Axile	Axile.

an ovary beak in many species. *Pauridia* differs from *Spiloxene* in having a perianth tube, only 3 stamens and a six-lobed stigma.

The differences are summarized in Table 2.

4. ANATOMY

(1) *Soft tissues*

The three genera show little difference in the anatomy of the soft tissues of the perianth, stamens and gynoecium. The following description applies to all three unless otherwise stated.

Perianth

The upper (adaxial) epidermal cells of all three genera have strongly convex or dome-shaped outer walls. The cells are from 30 μm high in *P. minuta* to 70 μm in *Empodium plicatum*. The cuticle is rough with striations radiating from the highest point of the cell. In surface view the cells are isodiametric over the greater part of the perianth segment and become elongated towards the base of the segment. The outer cell walls also flatten out towards the base and on the tube in *Pauridia*.

The abaxial epidermal cells do not have markedly convex outer walls. The cells are elongated along the long axis of the segment. The anticlinal walls are undulate in *Empodium*, but smooth in *Spiloxene* and *Pauridia*. The cuticle is smooth and scattered stomata occur.

In the yellow-flowered species the adaxial epidermal cells contain chromoplasts which are lacking in the white flowers. In most species the abaxial subepidermal cells contain numerous chloroplasts. These may be restricted to the cells near the veins, e.g. in *P. minuta* which as a green stripe down the centre of the abaxial side of each segment. In species with maroon backs to the segments e.g. *S. schlechteri*, the chloroplasts are present in the subepidermal layer and the cell-sap of the abaxial epidermal cells is coloured red (presumably with anthocyanin).

The mesophyll is generally about ten cells deep and consists of irregularly shaped cells with intercellular spaces. Scattered raphide-containing cells occur.

Stamens

The single trace of the filament continues into the connective which, like the filament, consists of parenchymatous tissue covered with a smooth epidermis.

The anthers dehisce by means of longitudinal slits. The endothecial cells have secondary wall thickenings in the form of strips on the anticlinal and inner periclinal walls. Cells with similar thickenings extend into the ground tissue of the connective near the junction of the two pollen sacs on each side of the anther.

Stigma

The three lobes of the stigma in *Spiloxene* and *Empodium* have papillose edges which form the receptive surfaces. The pollen frequently germinates on the papillae and the pollen tube grows down the outside of a papilla and into the stigmatic tissue at the base of the papilla.

In *Pauridia* the long lobes of the stigma are similar to those in *Spiloxene*. The short lobes do not have papillae, but pollen is received in the small adaxial groove and has been observed to germinate there.

(2) *Vascular anatomy*

Spiloxene (Fig. 1)

The vascular anatomy of the flowers of *S. aquatica*, *S. capensis*, *S. schlechteri* and *S. serrata* differs only slightly in small details such as the actual position of branching. The following description applies to *S. aquatica*.

The hollow pedicel has six vascular bundles. Well below the ovary the outer three bundles give off two subopposite side branches (lp: Fig. 1.2), and then continue free up the ovary to become the median bundles (op: Fig. 1.3) of the outer Perianth segments. The side branches (lp) run free to the bases of the perianth segments where each divides to form the lateral veins (lpb: Fig. 1.9) of adjacent segments. In the outer segments they branch again to give a total of five to nine veins in a segment. According to Fraenkel (1903) members of the Hypoxidaceae have a vascular arrangement in the perianth segments belonging to his group III, i.e. with one median nerve and two equal independent free ending side nerves.

The inner three pedicel bundles form a bundle complex just below the ovary (comp: Fig. 1.3). From this complex run: (i) the ventral carpel bundles (vc: Fig. 1.4) which run up the median axis and supply the ovules (vcb: Fig. 1.5); (ii) the lateral carpel bundles (lc: Fig. 1.4–1.7) which lie in the ovary wall opposite the septa and which comprise the fused lateral carpel bundles, inner perianth segment median traces (ip: Fig. 1.8) and inner stamen traces (ia: Fig. 1.8) (iii) the dorsal carpel bundles (dc: Fig. 1.4 and 1.5) which lie close to the outer perianth trace (op) on the same radius. The dorsal carpel bundle includes the outer staminal trace (oa: Fig. 1.6–1.9) which branches off near the top of the ovary. The dorsal carpel bundle continues into the style (g: Fig. 1.6–1.9) where it divides to supply two adjacent stigmatic lobes (g_1 & g_2). This supply is normal in commissural stigmas (Eames, 1961), since the stigma lobes are formed from two halves of adjacent carpels and lie opposite the inner perianth segments and over the ovary septa.

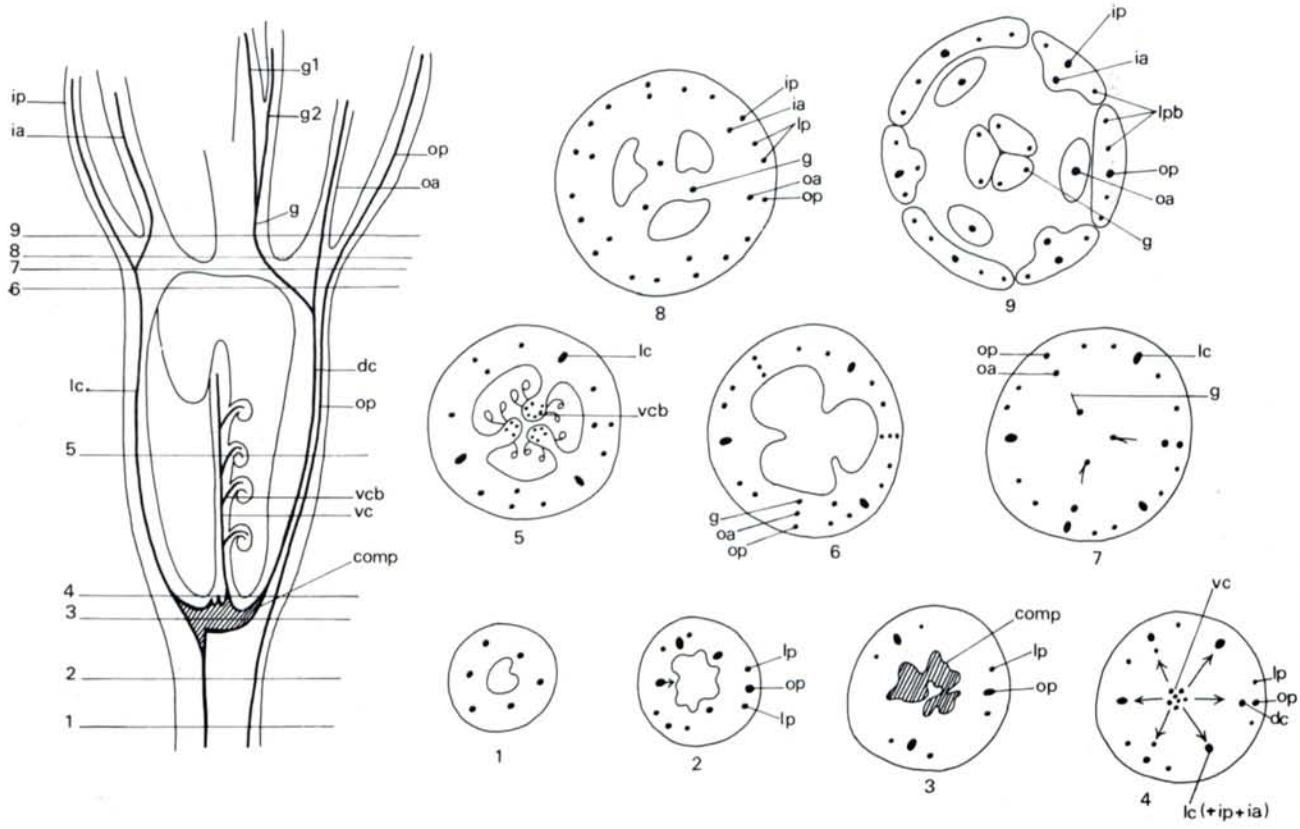

FIG. 1.—Vascular anatomy of the flower of *Spiloxene aquatica* showing one diagrammatic longitudinal section and nine sections taken at the levels indicated on the longitudinal section. comp, bundle complex; dc, dorsal carpel bundle; g, style bundle; g_1 and g_2 branches of the style bundle; ia, inner stamen trace/bundle; ip, inner perianth bundle; lc, lateral carpel bundle; lp, lateral perianth bundle; lpb, branch of lp; oa, outer stamen bundle; op, outer perianth median bundle; vc, ventral carpel bundle; vcb, branches of the ventral carpel bundle.

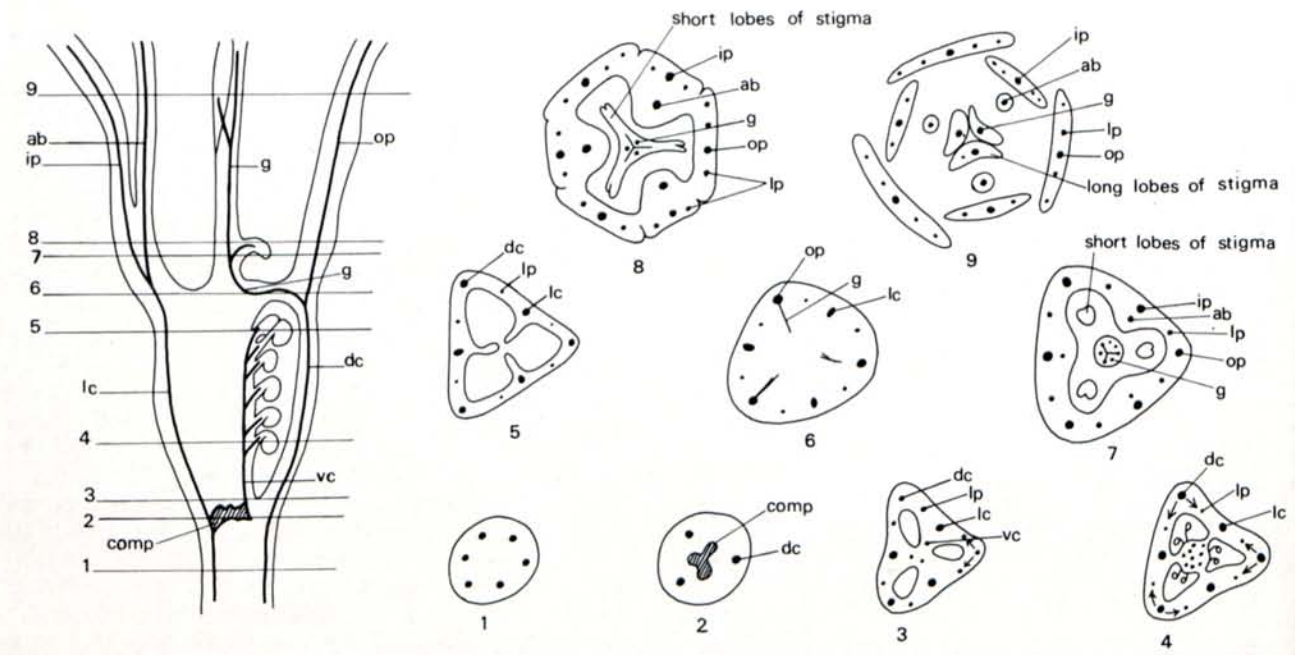

FIG. 2.—Vascular anatomy of the flower of *Pauridia minuta*. ab, stamen bundle; comp, bundle complex; dc, dorsal carpel bundle; g, style bundle; ip, inner perianth bundle; lc, lateral carpel bundle; lp, lateral perianth bundle; op, outer perianth bundle; vc, ventral carpel bundle.

Pauridia minuta (Figs 2 and 3A)

The peduncle has three vascular bundles. At the node between this and the pedicel a trace leads to each of the opposite bracts. The solid pedicel, i.e. above the bracts, has six bundles (Fig. 2.1).

Three of these bundles represent the dorsal carpel traces (dc) which at this level (Fig. 2.1 and 2.2) comprise the dorsal carpel bundles, the outer perianth segment median traces (op) and the lateral perianth traces (lp). Near the base of the ovary (Fig. 2.3) each dorsal bundle gives off two side branches, the lateral perianth bundles (lp) which dichotomise at the top of the perianth tube to form the lateral veins of two adjacent perianth segments—one outer and one inner (Fig. 2.8; 3A). The dorsal carpel bundles give off the median bundles (op) of the outer perianth segments (OP) at the top of the ovary (Fig. 2.6) and continue as the style bundles(g). These latter divide into three, the central branch supplying the appendages or short stigma lobes and the two side branches going to adjacent commissural long lobes. The two bundles in a long lobe (from different dorsal carpel bundles) may fuse to form one.

The remaining three pedicel bundles anastomose in the receptacle area to form a bundle complex (comp: Fig. 2.2). This gives rise to: (i) the ventral carpel bundles (vc) which run up the central axis and supply the ovules, but do not continue into the style; (ii) the lateral carpel bundles (lc) which later give rise to the inner perianth segment median traces (ip) and the staminal traces (ab). The division into these bundles occurs just above the top of the ovary (Fig. 2.2-2.6).

Pauridia differs from *Spiloxene* in that the dorsal carpel bundle (dc) and outer perianth trace (op) are fused and run from the pedicel to the top of the ovary without forming part of the bundle complex below the ovary chambers. The vascular supply of the short stigma lobes is basically the same as that of the outer stamens in *Spiloxene*. This, and their position, could indicate that the short lobes are reduced stamens.

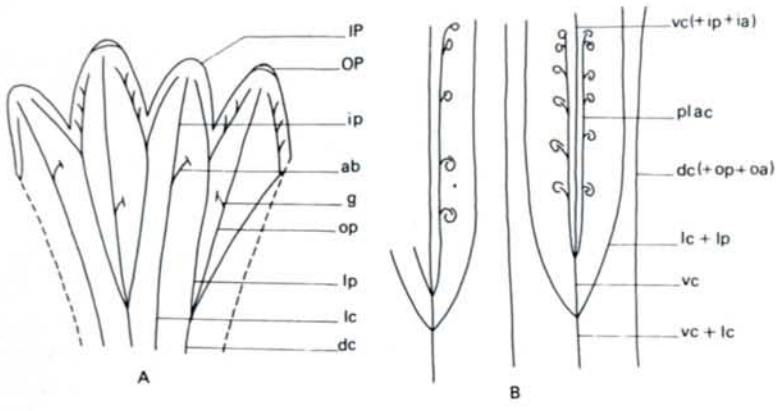

FIG. 3.—Vascular anatomy of the flower. A, *Pauridia minuta*—part of ovary wall and perianth slit longitudinally and spread out (central axis and ovules removed). B, *Empodium plicatum*—part of ovary wall slit longitudinally and spread out. ab, stamen bundle; dc, dorsal carpel bundle; g, style bundle; ia, inner stamen bundle; IP, inner perianth segment; ip, inner perianth bundle; lc, lateral carpel bundle; lp, lateral perianth bundle; oa, outer stamen bundle; OP, outer perianth segment; op, outer perianth bundle; plac, placental bundle; vc, ventral carpel bundle.

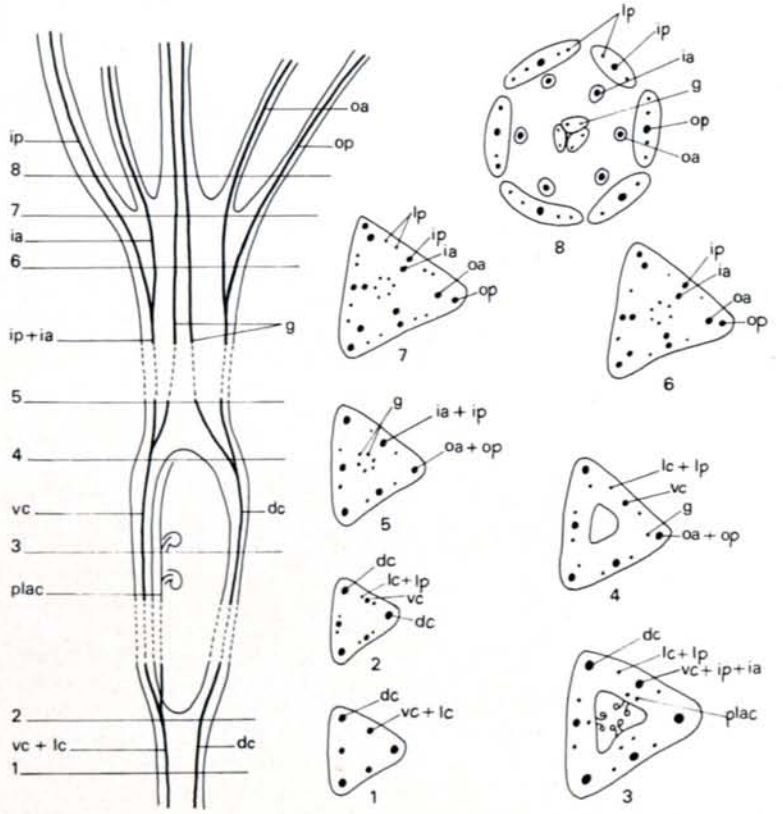

FIG. 4.—Vascular anatomy of the flower of *Empodium plicatum*. dc, dorsal carpel bundle; g, style bundles; ia, inner stamen bundle; ip, inner perianth bundle; lc, lateral carpel bundle; lp, lateral perianth bundle; oa, outer stamen bundle; op, outer perianth bundle; plac, placental supply; vc, ventral carpel bundle.

Empodium plicatum (Figs. 3B and 4)

The solid pedicel has six vascular bundles (Fig. 4.1) which become the three dorsal carpel traces (dc) and three ventral-lateral carpel traces (vc+lc). Just below the ovary the ventral-laterals give off two branches which run undivided up the ovary and beak, as the fused lateral carpel and lateral perianth traces (lc+lp Figs. 3B and 4.2–4.6). At the base of the perianth segments (Fig. 4.7) they divide to form the lateral bundles of adjacent perianth segments (lp). In the segments they divide again to form additional parallel veins.

The dorsal carpel bundles (dc) comprise the fused dorsal carpel, outer perianth median bundle and outer stamen traces (dc+op+oa). At the top of the ovary the dorsal carpel bundle continues as the style bundle (g). The outer perianth and outer stamen traces remain fused to about two-thirds of the way up the beak where the division into the outer stamen trace (oa) and median bundle of the outer perianth segment (op) occurs (Fig. 4.6).

At the base of the ovary the ventral-laterals (vc+lc) divide to give rise to: (i) the ventral carpel bundles (vc) which represent the fused ventral carpel, inner perianth and inner stamen traces (vc+ip+ia); almost immediately these bundles give off two branches to the placentas (plac) which supply the ovules and end at the top of the ovary. (ii) Two fused lateral carpel and lateral perianth traces (lc+lp: Figs 3B and 4.2).

Where the ovary grades into the beak (Fig. 4.4 and 4.5) the ventral-carpel bundles (vc) divide into the style traces (g) and the fused inner perianth and inner stamen bundle (ip+ia). The style traces (g), with the three traces from the dorsal carpel bundles, run up the centre of the beak into the style and stigma, two bundles going to each stigmatic lobe (Fig. 4.5–4.8). The inner perianth and inner stamen traces remain fused up to the same level as the outer perianth and stamen traces, where they divide to form the inner staminal bundle (ia) and the median bundle of the inner perianth segment (ip: Fig. 4.6).

Apart from the modification related to the elongation of the ovary into a beak and the parietal placentation, *Empodium* differs from *Spiloxene* and *Pauridia* in: (i) lacking a bundle complex below the ovary: (ii) the supply to the style and stigmas—here the six bundles are branches, alternately, of the dorsal and ventral carpel bundles, whereas in *Spiloxene* and *Pauridia* only the dorsal bundles supply the style, each bundle dividing again; (iii) the perianth supply. Here the traces to the perianth, stamens and carpels are fused in the ovary wall, whereas in *Spiloxene* the traces to the outer perianth segments are free. Here the lateral bundles of the perianth are fused to the ventral lateral carpel bundles at the base. In *Spiloxene* they arise from the outer perianth trace.

5. DISCUSSION AND CONCLUSIONS

This study of the floral morphology and anatomy, with that of the vegetative parts (Thompson, 1976) confirms the close relationship between *Spiloxene* and *Pauridia*. The inflorescence and bracts of *Pauridia* are similar to those of some species of *Spiloxene*. Both genera have a 3-locular ovary with axile placentation and similar fruits.

The anatomy of the soft tissues shows little difference, while in vascular anatomy *Pauridia* differs from *Spiloxene* in that the dorsal carpel bundle (dc) and outer perianth trace (op) are fused and run from the pedicel to the top of the ovary without forming part of the bundle complex below the ovary chambers.

Pauridia shows a reduction in the number of stamens from six (3+3) to three, lying opposite the inner perianth segments. It is possible that the three short lobes of the stigma represent reduced stamens which have become fused to the gynoecium. Their vascular supply is basically the same as that of the outer stamens of *Spiloxene*. A freak flower (in *Thompson* 278) tended to form anthers on the short lobes, one almost complete. An undescribed species of *Spiloxene* has four perianth segments and two stamens; the stamens fused to the style. The fusion (connation) of the perianth segments to form a perianth tube in *Pauridia* is an advanced feature.

Empodium shows more marked differences from *Spiloxene*. The inflorescence always consists of a single flower without bracts. There is no distinction into peduncle and pedicel. *Empodium* has a unilocular ovary with parietal placentation and forms an indehiscent fruit. The parietal condition is not generally regarded as having been derived from the axile but rather that both developed independently from the submarginal type (Eames 1961).

The prolongation of the ovary into a neck or beak, a common feature in *Empodium* is also found in *Spiloxene* (e.g. *S. alba* and an undescribed species). Hilliard & Burtt (1973) discuss the value of the ovary beak as a generic character in relation to *Empodium* and *Curculigo* and *Rhodohypoxis*.

The vascular anatomy of *Empodium* differs from the others in the lack of a bundle complex, the style being supplied by dorsal and ventral carpel bundles and in the fusion of the median perianth traces to the dorsal carpel bundle and the lateral perianth traces to the ventral-laterals.

Spiloxene has been included in *Hypoxis* by various authors such as Baker (1896) and Geerinck (1969). I disagree with this arrangement on grounds of differences in the rootstock, hairiness, leaf arrangement, inflorescence, manner in which the anthers are borne and geographical distribution.

The South African genera in the family fall into two groups, which do not warrant sub-family status. *Hypoxis* and *Rhodohypoxis* are closely related, while *Spiloxene*, *Pauridia* and *Empodium* form the other group with *Spiloxene* and *Pauridia* most closely related.

Of the characters found in the floral morphology and anatomy, the form of the ovary, number of locules and placentation, the number of stamens appear the most important taxonomically. The vascular anatomy has confirmed generic relationships and differences.

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UITTREKSEL

Die bloeiwyse en blomme van verteenwoordigers van Spiloxene, Pauridia *en* Empodium *is bestudeer. Die bloeiwyse toon 'n reduksie van 'n skerm met verskeie blomme tot 'n enkele blom. Die helmknoppe is onbeweeglik by al drie genera, anders as by* Hypoxis *en* Rhodohypoxis. *By* Spiloxene *en* Pauridia *is die vrugbeginsel 3-hokkig met asstandige plasentasie, terwyl by* Empodium *dit eenhokkig is met drie randstandige plasentas. Die anatomie van die vaatstelsel by die blomme van die drie genera is beskryf en die generiese verskille is demonstreer. Die nou verwantskap tussen* Spiloxene *en* Pauridia *is demonstreer en die insluiting van* Pauridia *in die Hypoxidaceae is ondersteun.* Spiloxene *word beskou as generies verskillend van* Hypoxis.

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