MORPHOLOGICAL AND ANATOMICAL STUDIES IN HELOBIAE

V. Vascular Anatomy of the Flower of Lilaea scilloides (Poir) Hamm.*

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INTRODUCTION

The monotypic genus Lilaea has been retained in the family Scheuchzeriaceae (sometimes also known as Juncaginaceae) by most authors (Engler and Parantl, 1899; Hooker, 1894; etc.). Hieronymus (1892) and Schumann (1892; quoted from Campbell, 1898) were probably among the first to consider it as representing a separate family Lilaeaceae. Small (1909, quoted from Lawrence, 1951) segregated it as a separate unigeneric family Lilaeaceae. More recently the treatment of Lilaea in a separate family has been supported by Uhl (1947), Lawrence (1951), Hutchinson (1959), etc. Hutchinson (1959) proposed an alternative name Heterostylaceae for this family "for any one who may quite naturally object to the use of a family name so similar to that of Liliaceae".

Because of a need for a better understanding of the morphological nature of the flower of Lilaea scilloides, that has been a centre of some controversy, the present investigation has been initiated. This paper deals with the vascular anatomy of the flower of Lilaea scilloides.

MATERIAL AND METHODS

The inflorescences of different ages of Lilaea scilloides (Poir) Hamm. (syn. Lilaea subulata H.B.K.) were obtained from California (U.S.A.) through the courtesy of Dr. H. F. Copeland. The material was fixed in Bouin's fluid and then transferred to 70% ethyl alcohol. It was dehydrated with ethyl alcohol-xylol series and embedded in paraffin following customary methods. Serial transverse and longitudinal sections were cut at 10-12 microns. Two different stain combinations safranin-fastgreen and crystal

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Morphological and Anatomical Studies in Helobiae—V

violet-erythrosin were used, the latter gave better results. Entire cleared preparations stained with basic fuchsin were also studied.

Observations

Organography.—Lilaea scilloides is a small Isoetes-like marsh plant occurring in alkaline lakes or muddy vernal waters along the pacific coast. It is a stemless scapigerous herb with a very short rhizome, bearing fibrous roots and basal crowded leaves. The flowers are arranged in a spiral manner on axillary spikes. In the terminal part of the spike the flowers are densely crowded but in the lower region a few flowers lie separated from one another. In addition to the flowers borne on the spike, two flowers are frequently placed laterally at the base of each inflorescence axis. These basal flowers are quite conspicuous because of their very long styles. The styles are up to 10 cm. in length in the material available to the author but Hieronymus (1892) records that sometimes they reach up to 14 cm. in length.

Two types of spikes were observed in the material available for the present investigation. The basal spikes, which are completely hidden in the sheathing leaf-bases, bear perfect flowers and are terminated by a male flower, while the scapose spikes comprise only the pistillate flowers. Hieronymus (1892) reported the occurrence of spikes consisting of exclusively staminate or pistillate flowers. According to Jepson (1925, quoted from Hutchinson, 1959), the spikes are of two types, one exclusively consisting of unisexual flowers and the other mixed, with the pistillate flowers below, the perfect in the middle and the staminate above.

The single sessile stamen of the staminate flower lies within the base of a triangular perianth segment and has a 2-locular, extrorse anther, opening by longitudinal slits. Its connective is produced slightly beyond the locule. The pollen grains are globose.

The pistillate flower consists of a single sessile carpel and there is no perianth, although Campbell (1898) reports the occurrence of perianth in the basal pistillate flowers. The ovary is unilocular with a solitary, erect, anatropous ovule, that is more conspicuous in the flowers at the base of the scape. The style is short with a capitate, penicellate and papillose stigma. The perfect flowers are sessile and each has a perianth segment, a stamen and a closely appressed carpel (Fig. 1) placed at a slightly higher level in a concavity of the inflorescence axis. The fruit is compressed, winged and indehiscent. In the basal pistillate flowers it is 3-angled and has three unequal horns at top.
Anatomy of Inflorescence and Flower.—Usually, two vascular bundles enter the base of the scape from the rhizome and these divide immediately producing four to six (rarely more) bundles at the base of the spike (Fig. 2).

LILAEA SCILLOIDES

Figs. 1-11. Lilaea scilloides. Fig. 1. External view of a perfect flower. Figs. 2-11 Serial cross-sections of a spike from below upward.
(c., carpel; p., perianth; s., stamen).
These are arranged equidistantly in a circle. The cortex of the scape is aerenchymatous and is composed of a large number of lacunae which are separated by walls one cell in thickness.

The traces for the flowers arise in a spiral fashion from the scape bundles (Figs. 5–8). Each flower receives a single trace that splits up tangentially into two within the cortex of the receptacle. The outer of these further divides into two and supplies the stamen and its subtending perianth segment (Figs. 3, 4). The bundle in the perianth segment takes the median position and extends up to the tip unbranched. It is flanked on either side by a lacuna. The concentric staminal bundle extends unbranched up to the top of the connective.

The inner of the two bundles referred to above supplies the gynoecium (Fig. 13). At the base of the ovary it becomes somewhat tri-lobed, and two traces diverge from it simultaneously (Figs. 14, 15) and take lateral positions in two of the three angles of the ovary wall. The remaining bundle extends as such for a short distance and at the level of the locule it gives off one more trace that takes its position in the third angle of the ovary wall which faces the adaxial side (Fig. 16). This bundle is more prominent than the other two bundles which lie in the ovary wall. The remaining stelar tissue extends towards the centre of the ovary and enters into the base of the single anatropous ovule (Figs. 12, 17). It extends in the outer integument of the ovule for some distance (Fig. 18). All the three bundles in the ovary wall are normally oriented with their xylem facing towards the centre of the gynoecium. These bundles continue in the style as such and disappear at the base of the stigmá (Figs. 19–23). Of the three bundles in the ovary wall the one which lies on the adaxial angle extends for a slightly higher level than the other two (Figs. 21, 22).

The epidermal cells of the ovary wall are radially elongated with their outer walls thickened. In between the epidermal layers there are several layers of loosely arranged parenchymatous cells. In the young carpels there is a narrow stylar canal which is lined by a layer of glandular cells (Figs. 23, 24). Later on it becomes completely closed by the cohesion of the cells forming its wall. The stigma is papillose; the papillae arise from the superficial cells and in the mature carpel they form dense tufts of conspicuous hairs.

As pointed out earlier, a staminate flower terminates the spike of perfect flowers. The single bundle left at the top of the inflorescence axis constitutes the vascular supply of this male flower and behaves in a similar manner as the one for the perianth segment and the stamen of a perfect flower (Figs. 9–11).
Figs. 12–24. *Lilaea scilloides*. Fig. 12. Longitudinal section of pistillate flower showing course of vascular bundles. Figs. 13–23. Serial cross-sections of pistillate flower from below upward. Fig. 24. Lining of glandular cells around the stylar canal from a transverse section of style.

(d., dorsal bundle; v.s., ventral strand.)
The vascular supply of the pistillate flowers is similar to that of the gynoecium of a perfect flower. However, the basal pistillate flowers derive their vascular supply directly from the rhizome.

**DISCUSSION AND CONCLUSIONS**

The presence of two pistillate flowers at the base of the inflorescence axis, the morphological nature of the flower, the presence of three dorsal bundles in the so-called monocarpellary gynoecium are some of the points which deserve attention. They will be discussed at some length.

Campbell (1898) stated that, “The homologies of the two pistillate flowers which usually occur near the base of the shaft of the inflorescence are not entirely clear, but they probably represent shoots of the same nature as the innovations which occur in the axils of the leaves”. Thus according to Campbell (1898) these flowers are equivalent to axillary shoots. Since these flowers like the inflorescence axis, derive their vascular supply independently from the rhizome, Campbell’s statement appears to be correct.

The perfect flower of *Lilaea* has been in some controversy. While it has been considered as a normal hermaphrodite flower by the majority of authors, some have interpreted it as a secondary inflorescence consisting of a staminate and a pistillate flower. It was Campbell (1898) who suggested, probably for the first time, that the so-called perfect (hermaphrodite) flower is a secondary inflorescence made up of a staminate and a pistillate flower, the former subtended by a bract. He further stated that when single flower is present in the axil of the bract it is formed by direct transformation of a primordium of young shoot into the carpel or stamen but when a carpel and a stamen are present together the primordium divides dichotomously into two equal parts, one giving rise to a stamen and the other to a carpel. Uhl (1947) also expressed a similar view when she interpreted the so-called flowers of *Lilaea* as representing reduced lateral branches of an inflorescence bearing unisexual flowers. She pointed out that the condition in *Lilaea* has been derived from that in other members of the family like *Triglochin* and *Scheuchzeria* by shortening and telescoping of the lateral branches. The resultant short branches are adnate to the main axis and bring the bract, the staminate flower and the pistillate flower so close to each other that they appear like a perfect flower.

The perfect flowers are present in a concavity in the inflorescence axis and each derives a single trace from the vascular bundles of the inflorescence axis. This trace extends horizontally before entering into the flower. This should not have been the case if the flowers were borne on lateral branches.
which are adnate to the main axis. The perianth, stamen and carpel (which form a perfect flower) receive a single trace which indicate that these structures form a single unit, not the two independent flowers. Thus it appears that the perfect flower of Lilaea is a normal bisexual flower.

The perianth segment subtending a male flower has been interpreted differently. Campbell (1898) described it as a bract equivalent to a leaf at the base of the main shoot. Jepson (1925, quoted from Hutchinson, 1959), Uhl (1947), Lawrence (1951), etc., also considered it to be a bract. However, Hutchinson (1959) interpreted it to be a single perianth segment equivalent to that in some species of Aponogeton. The present observations also indicate that this bract-like structure is a perianth segment since its structure and vascular supply is similar to that of the perianth segment of Potamogeton which subtends the stamen (see Singh, 1965 a). In Lilaea the perianth segment is adnate to the base of the stamen and the single bundle which supplies the staminate flower splits into two, one of which supplies the perianth and the other the stamen.

The ovary of Lilaea is unilocular and the solitary ovule has been described as basal. The vascular supply consists of four bundles, one of these forms the ovular supply and is, thus, the ventral strand of the carpel. The other three bundles are restricted to the three angles of the ovary wall and continue into the style and, therefore, they are the dorsal bundles. Out of the three dorsals, two separate at a slightly lower level while the third remains fused with the ventral strand for some distance.

Agarwal (1952) while working out the embryology of Lilaea made a casual mention of the vascular supply of the flower. He described that the single bundle of the pistillate flower branches at the base of the ovary, one of the branches forms the dorsal bundle, while the other divides once again to form two ventral bundles. One of these bundles gives off an ovular trace. Thus, according to him the vascular supply of the ovary consists of only three bundles—two ventrals and one dorsal. It appears that what he considered the ovular trace is actually the ventral bundle of the carpel which remains fused with one of the dorsal bundles for some distance and is completely used up in supplying the ovule. While the two bundles, which he calls as ventrals, are in reality the dorsal bundles.

It is interesting of Lilaea that there are present three dorsal bundles in the ovary, indicating tricarpellary nature, a point also emphasized by Uhl (1947). In other members of the family Scheuchzeriaceae like some species of Triglochin there are six carpels. Reduction in carpel number from six to three is common in other species of Triglochin. In Scheuchzeria
the usual number of carpels is three. In both the genera the carpels are fused along their inner margins for some distance. Thus, it appears that the condition in *Lilaea* has been brought about by an intimate fusion of three carpels of which two have become suppressed and one remained fertile. The dorsals of the three carpels persist while the ventral supply is reduced to a single strand.

There are two possibilities as regards the nature of the ventral strand. Either it is a fusion product of the ventrals of all the three carpels or of only the surviving fertile carpel. The second possibility appears to be more logical. Since the two carpels have suppressed, their ventrals might have also disappeared. Only the ventrals of the fertile carpel, which remain fused with its dorsal for some distance, persist to supply the ovule. The so-called monocarpellary condition in *Lilaea* has been brought about by the suppression of two of the three carpels, therefore, the apparently basal position of the ovule also appears to be a derived one (cf. *Najas*, Singh, 1965 b).

There is some difference of opinion regarding the systematic position of *Lilaea*. It has been retained by most authors in the family Scheuchzeriaceae (*see* Hooker, 1894; Engler and Prantl, 1889; and others), but Hieronymus (1892) and Schumann (1892; quoted from Campbell, 1898) suggested its segregation to a separate family. Small (1909; quoted from Lawrence, 1951) first time treated it in a unigeneric family Lilaeaceae. Recently this view has been concurred by Lawrence (1951), Hutchinson (1959), etc.

Markgraf (1936) considers that *Triglochin* and *Lilaea* are more closely related to each other. However, *Scheuchzeria* forms a sort of connecting link between the Helobiae and *Liliales* and might be placed in a separate family. Agarwal (1952) who has studied the embryology of *Lilaea* concludes that *Lilaea* is more closely related to *Triglochin* than to *Scheuchzeria*. He states that on embryological grounds when *Triglochin* and *Scheuchzeria* can be placed in the same family there is no justification for removing *Lilaea* to a separate family.

The floral structures of *Lilaea* show many dissimilarities to that of *Triglochin*, *Scheuchzeria*, etc. Besides the number of perianth segments and stamens, the gynoecium of *Lilaea* also differs from that of other members in the vascular supply and number of ovules though the basic number of carpels is three in all the genera. Therefore, the statement of Uhl (1947) appears to be convincing that the genus *Lilaea* probably was derived from *Triglochin* like ancestral types and is now sufficiently far removed from the present-day *Triglochin* to justify its recognition as a family.
V. Singh

Summary

The vascular anatomy of the flower of *Lilaea scilloides* has been described in this paper. The flowers are polygamous. Each perfect flower consists of a perianth segment, a sessile stamen and a closely appressed carpel. The perfect flower of *Lilaea*, that has been considered by some authors as a secondary inflorescence consisting of one staminate and one pistillate flower, is regarded here as a normal bisexual flower.

The presence of three dorsal bundles in the gynoecium of *Lilaea* suggests its tricarpellary nature and the so-called monocarpellary condition appears to have been brought about by suppression of two of the three carpels. It appears logical that the ventral strand, which supplies the solitary ovule, is the fusion product of the ventral bundles of the only surviving carpel.

The present investigation also gives some support for segregating *Lilaea* to a separate family.

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References


* not seen in original.