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## The floral vascular supply in *Epilobium* and related genera

By

C. E. B. BONNER

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### INTRODUCTION

This subject was taken up in the hope of finding certain anatomical differences which would help in the distinguishing of the different species of *Epilobium*. The flowers of the commoner species of the genus are, however, very similar in structure; there are only very minor differences and these are principally of proportion.

Nevertheless the floral structure has some interesting points. For the purpose of comparison the flowers of *Oenothera* and *Fuchsia* and those of the irregular *Circaea lutetiana* were studied. For the same reason, *Lythrum salicaria* was also included.

The flowers of the *Epilobia* are all regular except those of *E. angustifolium* which are zygomorphic. They are built on a tetramerous principle and conform to the conventional formula

$$K.4 C.4 An.4 + 4 Gn. (\bar{4})$$

The inferior ovary is very long and is capped by a perianth tube from which arise the other portions of the flower.

The calyx and the corolla are spreading.

The petals are obcordate, about twice the length of the lanceolate sepals. The stamens are of two lengths: the outer whorl (antesepalous) being longer than the antepetalous whorl. The anthers are introrse. The ovary is quadrilocular and loculicidal. The ovules are numerous and anatropous. The style is usually exsert, the stigma globular, four-lobed or four-armed. The fruit is dehiscent, splitting into four longitudinal strips. The seeds are obovoid or fusiform topped with a tuft of pappus.

There are no distinct pollination mechanisms apart from that in *Epilobium angustifolium* where self-pollination is prevented by curvature of the style when the first stamens ripen. The stigma is thrust

out through one side of the perianth with its stigmatic lobes closed tightly together. The style becomes erect and the stigmatic lobes open out when the anthers have dehisced. The flower is thus protandrous.

Some species, such as *E. hirsutum*, *E. parviflorum* and *E. montanum* are nearly homogamous and are often self-pollinated by the bending back of the lobes of the stigma.

*The Perianth.* — Except in the group *Chamaenerion* and many *Fuchsias*, the bilobed nature of the petals is pronounced. They may be white, pink, purple, violet or lilac in colour; in *Fuchsia* red or purplish; yellow in *Oenothera* and white or pink in *Circaea*.

In *Fuchsia* the sepals also are petaloid. This character is also met with in the *Chamaenerion* group, where the colour may extend to the ovary and to the top of the pedicel. As already stated, the sepals and petals are four each, in number, *Circaea* being an exception in having only half the number of each.

*Lythrum* (not belonging to the family Onagraceae but of the closely related Lythraceae) has a variable number of members; 4, 5 or 6 oblong purple petals alternating with an equal number of sepals. (An epicalyx is also frequently present.)

In every case the perianth members are inserted along the edge of a tube, the perianth tube<sup>1</sup> surmounting the ovary. (Here also *Lythrum* is an exception, the ovary being superior, the perianth tube surrounds it and is connected to its base only.) This tube is long and well developed in *Oenothera*, of medium length and development in *Fuchsia*, relatively short in *Epilobium*, short and filiform in *Circaea*.

*The Androecium.* — The stamens vary chiefly in size. In the group *Chamaenerion* of the genus *Epilobium* the two stamen whorls are practically equal: the outer whorl has an insertion slightly below that of the inner. The group *Lysimachion*, however, display a considerable difference in length in the two stamen whorls: the outer being about  $1\frac{1}{3}$  times longer than the inner.

The anthers are short, about a quarter of the length of the filament. *Fuchsia* has a similar arrangement of its 8 stamens. In *Oenothera* the stamens are all equal having filiform filaments and linear anthers. In *Circaea* there is a reduction to 2 stamens. In *Lythrum* there are as many or twice as many stamens as petals, inserted below them on the perianth tube.

<sup>1</sup> *Perianth tube*: The region of the flower of an *Onagraceae* between the top of the ovary and the base of the perianth members. The terms *receptacle*, or *hypanthium* used by other authors might cause confusion, as their definitions imply a morphological conception other than that entertained by the present writer in connection with the flowers of the *Onagraceae*.

*The Gynaecium.* — In *Epilobium*, the styles and stigmas are varied. The cylindrical style is as long or longer than the stamens. In some species it is surmounted by a four-cleft or four-branched stigma, whilst in others it is club-shaped with a depression at the top. The ovary is long and slender with shallow rounded ribs, quadrilocular, with axile placentation. The ovules are numerous, papillaceous and bear a tuft of long unicellular hairs (an aril) at maturity. The fruit is a loculicidal capsule.

In *Oenothera*, the style is generally long and slender with a four-branched stigma. The ovary is rather shorter than in *Epilobium*, club-shaped in outline, frequently flanged or winged. They are quadrilocular with axile placentation. The ovules are numerous but without arils. The fruit is a loculicidal capsule.

In *Fuchsia*, the style is long, exserted, bearing an entire, or sometimes four-lobed stigma. The ovary is shorter than in the preceding genera, being globose or cylindrical, quadrilocular, placentation axile. The ovules are as in *Oenothera* but in some species are only few in number. The fruit is a berry.

In the genus *Circaea*, the style is long surmounted by a club-shaped stigma. The ovary is globular, uni- or bilocular containing only one ovule per loculus. The fruit is indehiscent, nut-like, and covered with recurved bristles.

In *Lythrum*, the style length is variable (the flowers are trimorphic). The stigma is capitate. The ovary is bilocular, having an axile placentation. There are numerous ovules. The fruit is a capsule.

## I. THE VASCULAR SUPPLY

### *Abbreviations used in figures and text.*

- $l^s$  — lateral strands in the sepals.
- $l^p$  — lateral strands in the petals.
- $a$  — vascular ring (annulus) in the perianth tube.
- $L$  — vascular cord running in the groove of the ovary wall (Apparent lateral strand of carpel).
- $p^L$  — Branch of  $L$ . to the petals.
- $f^L$  — Branch of  $L$ . to the stamens (filaments).
- $st^L$  — Branch of  $L$ . to the style and stigma.
- $gl^L$  — Branch of  $L$ . to the glandular region of the perianth tube.
- $D$  — outer vascular cord in the apparent midrib of the carpel leaf (dorsal).
- $l^D$  — branches of  $D$  in the ovary wall and the perianth tube.
- $s^D$  — branches of  $D$  in the sepals.
- $d$  — inner vascular cord in the apparent carpel midrib.



- $o^d$  — branches of  $d$  to the placentae (ovarium).  
 $c^o$  — branches of  $o^d$  to ovules (chalaza).  
 $gl^d$  — branches of  $d$  to the glandular region of the perianth tube.  
 $f^d$  — branches of  $d$  to the stamens (filaments).

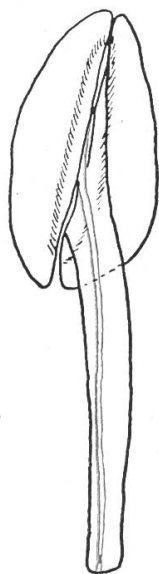


FIG. 10.  
*Epilobium angustifolium*.  
Stamen.

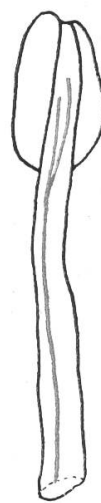


FIG. 11.  
*Epilobium montanum*.  
Stamen.

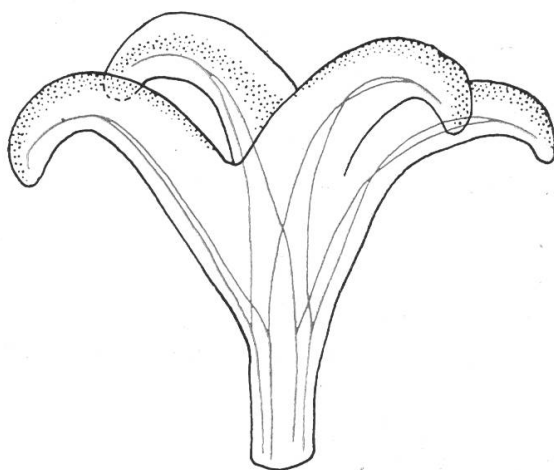


FIG. 12.  
*Epilobium angustifolium*.  
Stigma.

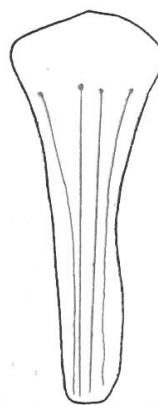


FIG. 13.  
*Epilobium roseum*.  
Style and stigma.

*The vascular supply in Epilobium.* — The venation of both the petals and sepals varies but little in the different species of *Epilobium* and their plans closely resemble those of *Fuchsia*, *Oenothera* and

*Circaea*. The vascular supply to each stamen consists of a single strand <sup>1</sup>, a hollow cylinder in the filament, but tapering to a point with a small branch curving into the connective. (Figs. 10 and 11)

The style has four vascular strands. In *E. angustifolium* and the other species of the *Chamaenerion* group, each strand divides into two and each stigmatic lobe receives a branch from each of the two nearest strands. (Fig. 12) *E. hirsutum* has this plan also. Those specimens of *E. roseum* and *E. alpinum* which were examined had strands remaining entire. (Fig. 13) In this way these latter species show a greater resemblance to *Oenothera*, *Fuchsia* and *Circaea*.

The ovary of *Epilobium* is, as already stated, quadrilocular. The placentation is axile, that is, there are four groups of two placentae built around a central axis. (Figs. 14, 15) The ovary is four-lobed. Four septa radiate from the axis to the median part of each lobe. (Fig. 15) There are eight vascular cords in the ovary. (Fig. 16) One large one in each lobe, and a much smaller one in each groove.

The "midrib" cords (I will name the former as such, for they appear to be this at first sight) are composite; in transverse section a large crescent-shaped portion (*D*), and a smaller inner portion (*d*) (See Fig. 17).

The inner cord (*d*) gives rise to frequent branches *o<sup>d</sup>* which cross to the placentae through the septa dividing the loculi. (Fig. 16) *D*, on the other hand, merely gives off a number of very small laterals which remain near the periphery *l<sup>D</sup>*. On reaching the perianth tube *d* separates from *D* and supplies the antesealous stamens *f<sup>d</sup>*. Here *D* gives off a branch simultaneously to the left and right (*a*). (Figs. 18-19) What is left continues and becomes the midrib of a sepal *s<sup>D</sup>*.

Let us leave this cord for a moment and turn our attention to the smaller ones in the "grooves" (*L*). Whilst forming part of the ovary wall these give rise to no branches, but on reaching the perianth tube they split off a first branch internally *st<sup>L</sup>*; this with the three others corresponding to it form the vascular supply to the style and stigma. A second internal branch goes to the antepetalous stamens *f<sup>L</sup>*. What is left splits simultaneously to form an *a*-branch meeting that of each adjacent *D*-cord. In this way an apparent vascular ring is formed just beneath the point of origin of the petals and sepals. Part of *L* continues to form the petal-midrib *p<sup>L</sup>*, another small portion forms marginals to the two adjacent sepals *s<sup>L</sup>*. At intervals along the *a* branches are given off forming small laterals to both petals and sepals. The cords *d* and *L* are thus both composite. *D* is purely calyx. *d*

<sup>1</sup> *Vascular cord*: A composite bundle made up of strands of different morphological sources, as distinct from a *vascular strand*, which is a morphologically homogeneous bundle, and a *trace* a small bundle of minor significance in the leaf or the perianth members.

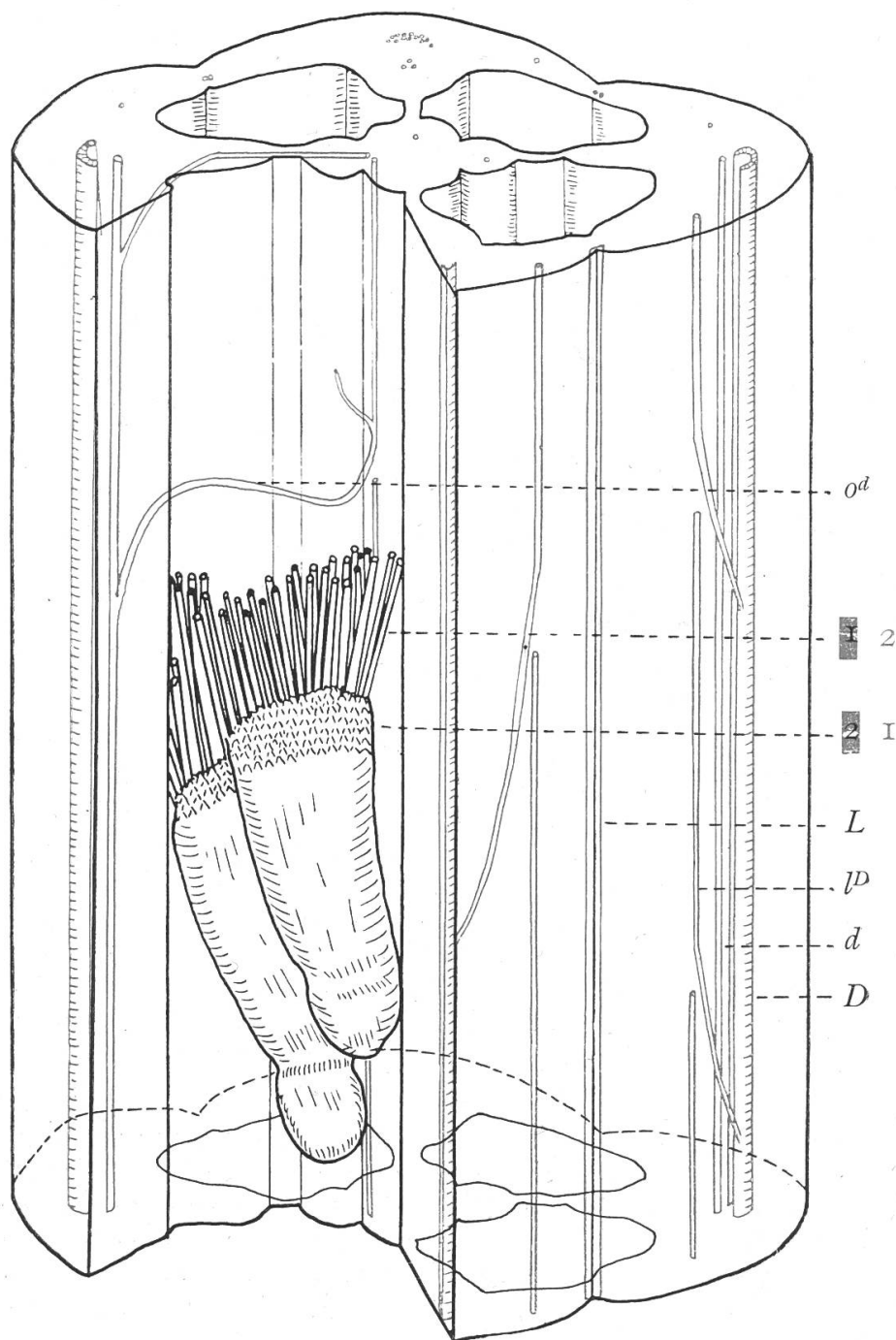


FIG. 14. — Reconstruction of a section of an *Epilobium* ovary showing distribution of the main vascular strands. (1) Papillae on surface of seed. These cover the whole surface of the seed although a few only have been shown to simplify the drawing; (2) Pappus, cut to about a quarter of their total length to permit visibility of internal structure.

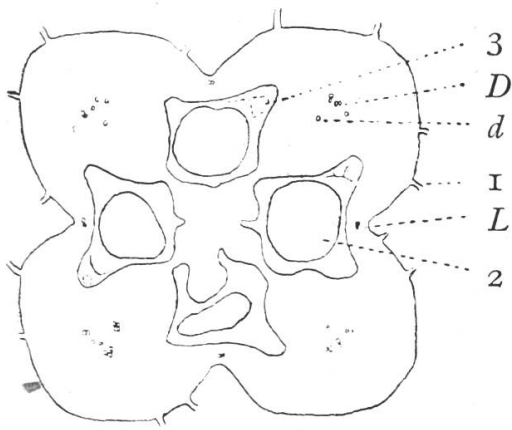


FIG. 15.  
*Epilobium palustre*. T.S. ovary  
( $\times 54$ ). (1) base of an epidermal  
hair; (2) ovule; (3) Loose tissue  
of future pappus.

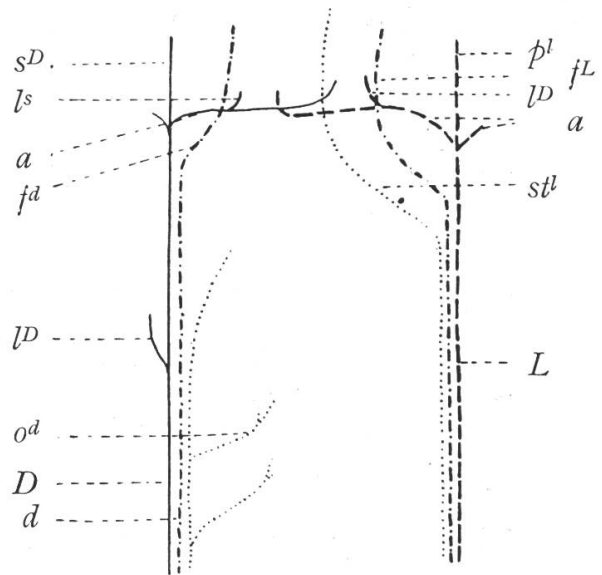


FIG. 16.  
*Epilobium*. Diagram of the general  
plan of the vascular supply to the  
flower. (Only one of the four pairs  
of cords in the *Epilobium* ovary are  
represented above. The diagram  
thus represents the system <sup>1</sup> though  
not the complete supply.)

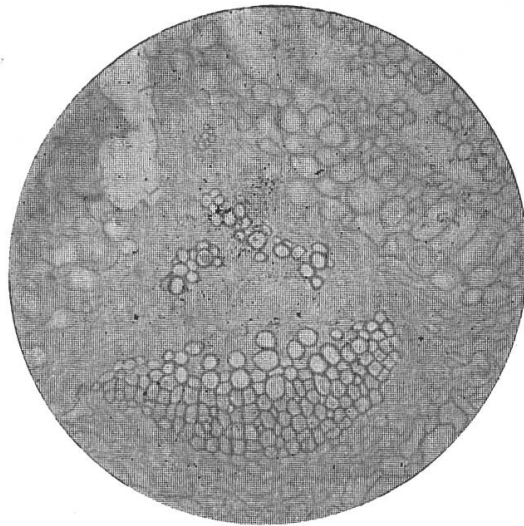


FIG. 17. — *Epilobium hirsutum*.  
Old ovary, D- and d-cords.

<sup>1</sup> Vascular system: A representative unit of the total floral vascular supply. Thus in *Epilobium*, the floral vascular system is in quadruplicate, it is composed of four identical units.

has the components for one whorl of stamens and the upper half of the gynaecium.

In the region of the *L*-strands there is a minute furrow in the young ovary which appears to be caused by a break in an outer epidermis, consisting at this point of very narrow cells. These cells in developing increase the depth and magnitude of the furrow. The cells separating the *L*-strand from the double inner epidermis form two lignified groups separated by a few cells which disintegrate in the final stages. Dehiscence takes place eventually in these thin zones, splitting the *L*-strand into two (Fig. 14). The central column and the radial septa are composed of loose parenchyma.

*The vascular supply in Oenothera.* — The general lay-out of the ovary is the same as in *Epilobium*. (An axile placentation composed of four groups of two placentae built around a central axis; a four-lobed ovary in which four septa radiate from the axis to the median

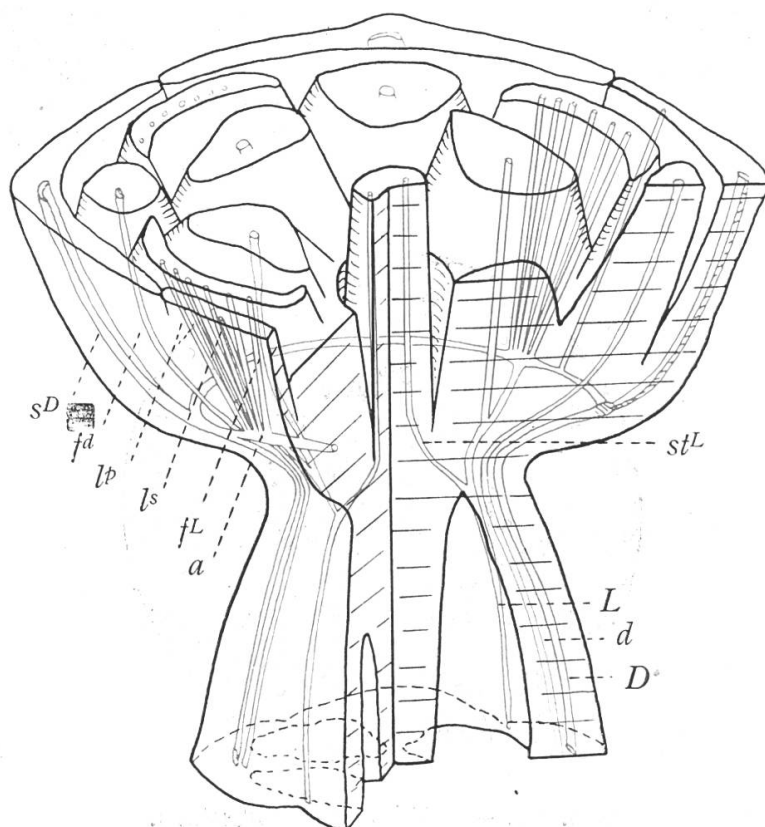


FIG. 18.

Reconstruction of a flower of *Epilobium*, group *Chamaenerion* from the top of the ovary to the base of the perianth.

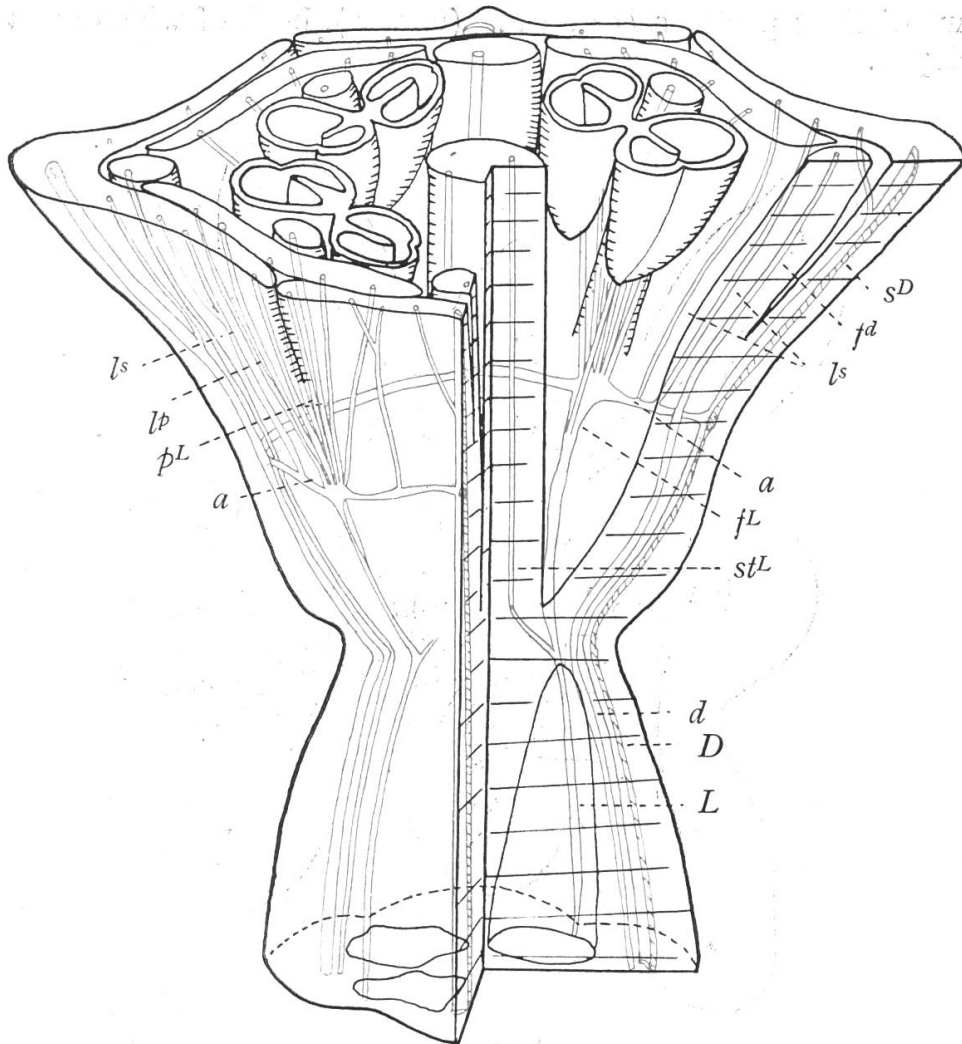


FIG. 19.

Reconstruction of a flower of the group *Eu-Epilobium*  
from the top of the ovary to the base  
of the perianth.

part of each lobe.) There are eight vascular cords in positions equivalent to those in the ovaries of the genus *Epilobium*. They will therefore be referred to by means of the same set of abbreviations.

The "midrib" cords are composed, as in the previous genus, of two distinct portions *D* and *d*. (Fig. 20), both of which are well developed.

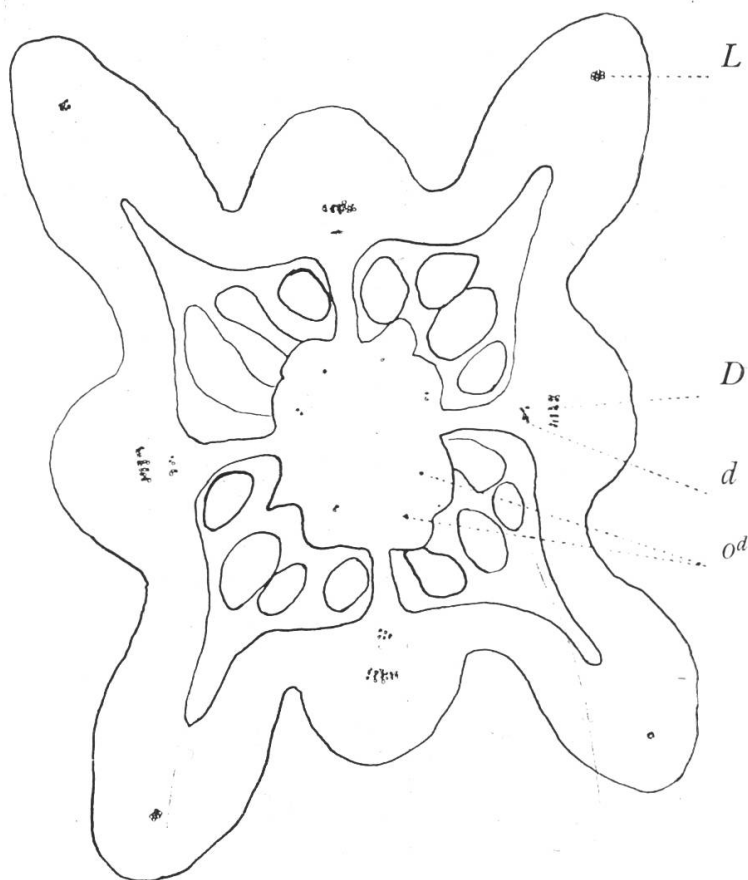


FIG. 20.

*Oenothera* sp., T.S. through an ovary ( $\times 40$ ).

The *D*-cord gives off small branches  $l^D$  within the ovary wall (Wrongly attributed to *d* by VAN TIEGHEM (1871: 236 Pl. VII, Fig. 223), and others, which are more highly developed, in the walls of the perianth tube (Figs. 21 and 22) These latter branches continue up to the vascular ring (*a*), an arrangement not found in *Epilobium* owing to the relatively poor development of its perianth tube. Near the top of the tube two branches leave the main-cord horizontally to form part of *a*. The remainder of the cord becomes a sepal midrib,  $s^D$ .

The  $d$ -cord gives off branches in the ovary wall  $o^d$ , which cross to the central axis via the septa, where they divide to form the funicular traces  $c^o$ . In the basal region of the perianth tube a further small trace branches off towards the inner face of the tube,  $gl^d$ , in an area composed of glandular tissue (Fig. 21). No further branches separate and the remaining strand  $f^d$  passes into the filament of an antesepalous stamen (Fig. 22).

The  $L$ -cord which ran in the groove of the ovary in *Epilobium* is found near the apex of the flange in the mature ovary of *Oenothera*

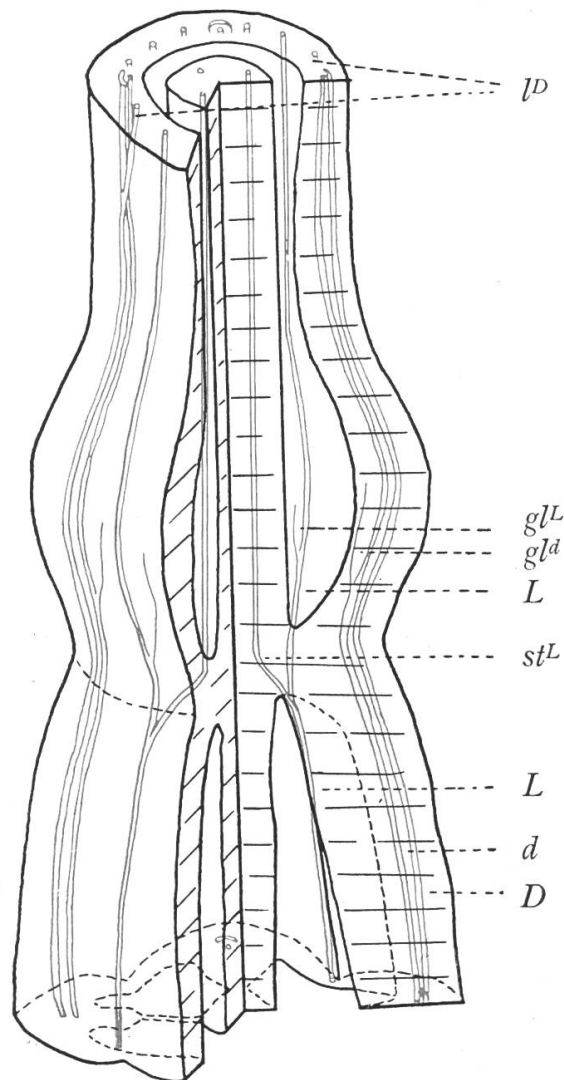


FIG. 21.

Reconstruction of a flower of *Oenothera* from the top of the ovary to the lower half of the perianth tube.



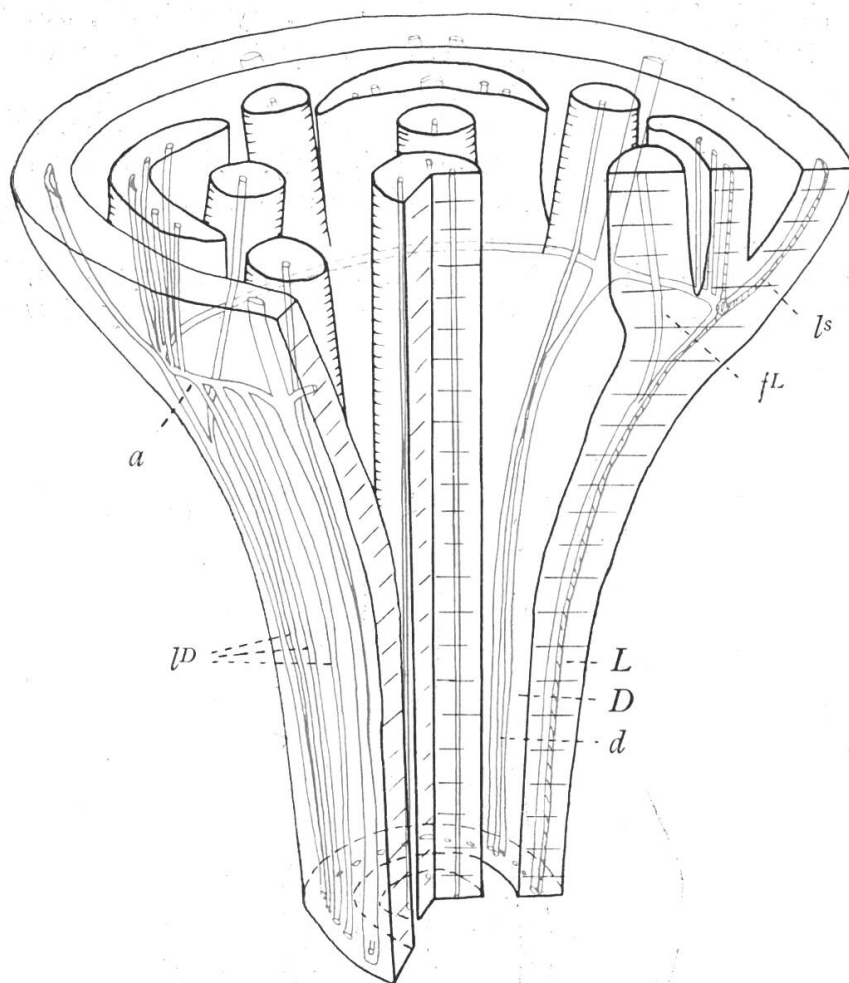


FIG. 22.

Reconstruction of a flower of *Oenothera* ;  
upper half of the perianth tube.

(Fig. 20). It curves inwards abruptly at the top of the ovary giving off a strand  $st^L$  which runs up the style. The remainder of the cord then ascends in the wall of the perianth tube without branching except for a small trace  $gl^L$  in the glandular area. At the top of the tube a strand curves inwards up the filament of an antepetalous stamen  $f^L$ , whilst shortly afterwards the cord gives off two lateral  $a$ -branches which meet and mingle with the  $a$ -branches from the neighbouring  $D$ -strands, and at the same time it divides to form a petal midrib  $p^L$  and sepal laterals  $l^s$ .

The  $a$ -ring is thus complete and well developed. In addition to the branches from the  $L$ - and  $D$ -cords which compose it, the  $l^D$  strands join it also. Both petal and sepal laterals originate from the ring.

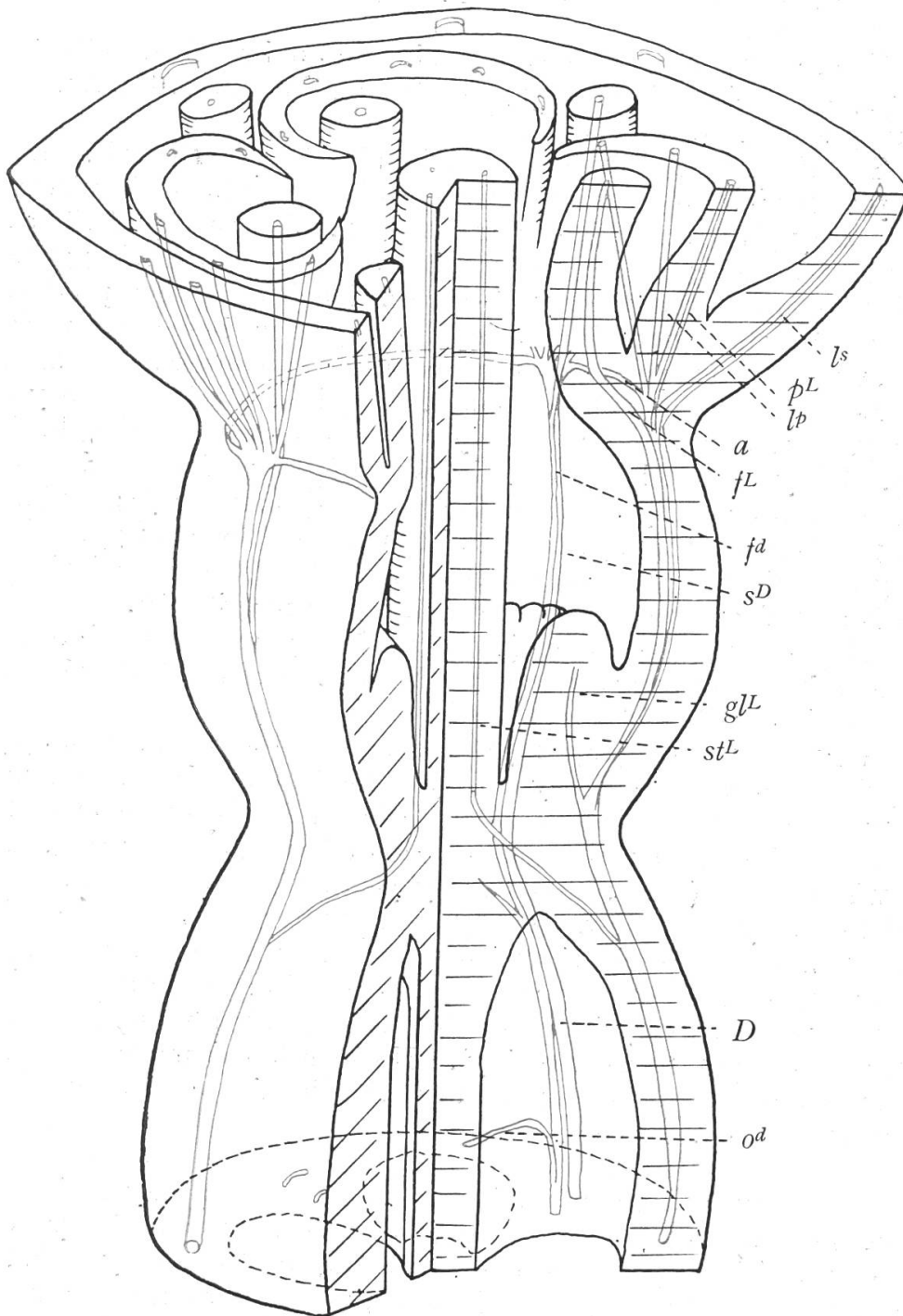


FIG. 23.  
Reconstruction of a flower of *Fuchsia*.

*The vascular supply in Fuchsia.* — The lay-out is as in the previous genera: a quadrilocular ovary in which there are eight vascular cords.

The *D*-cords are well developed but run unbranched to the top of the perianth tube, where they give off lateral *a*-traces, the remainder forming sepal midribs (Fig. 23).

The *d*-cords are almost equal in size to the *D*-cords. In the ovary wall *o<sup>d</sup>*-strands branch off through the septa to the placentae, where they give rise to funicular traces *c<sup>o</sup>*. At the top of the ovary a final *o<sup>d</sup>*-strand leaves each cord, but ends without having gone far or having given rise to any *c<sup>o</sup>*-traces. Each cord then produces a strand *gl<sup>d</sup>* in the region of the glandular ring at the base of the perianth tube, while the rest passes into the filament of an antesealous stamen.

*L*-cords are also well developed. At the top of the ovary they each give off a strand *st<sup>L</sup>* to the style and then a trace to the glandular ring. They do not branch in the wall of the perianth tube except at the top where they divide as follows:— 1) a strand *f<sup>L</sup>* goes into an antepetalous stamen; 2) Lateral *a*-branches are formed; 3) strands *l<sup>s</sup>* are given off which become the marginal laterals of the neighbouring sepals and 4) the remainders form the petal midribs *p<sup>L</sup>*.

The *a*-ring is continuous (as in *Oenothera*) through the interlacing of the *a*-branches from the *D*- and *L*-cords. From this ring branches run into both petals *l<sup>p</sup>* and sepals *l<sup>s</sup>*.

VAN TIEGHEM'S (1871: 72) account of the vascular supply in *F. fulgens* corresponds fairly closely to that given above. He makes no mention, however, of the *a*-ring formed at the upper end of the perianth tube, or of the vascularisation of the glandular ring. HENSLOW'S account (1890: 181) twenty years later is far less accurate, and not easy to follow. The present writer does not agree with HENSLOW'S description of the origin of the placental strands. Nor does he agree with the formation of a central mass of lignified tissues at the top of the ovary (from which must arise the strands to the style, stamens and petals, presumably). No mention is made here either, of a vascular ring at the top of the perianth tube or of a vascularised glandular region.

*The vascular supply in Circaea.* — The general layout is on the same plan as for the preceding genera, although the ovary is only bilocular. There are four cords running in the ovary wall; two "midrib" cords at the ends of the septa and two *L*-cords midway between them (Fig. 24). The *D* and *d* components of the midrib cords are hardly distinguishable from each other, so closely are they merged (Fig. 25).

The *D*- and *d*-cords. A single branch *o<sup>d</sup>* crosses each septum to the centre of the ovary where it becomes the funicular trace to the

single ovule in each loculus. (Fig. 25). Laterals are also given off in the ovary wall  $l^D$ , where they may branch again to form a leaf-like network. The perianth tube region is not hollow. The central tissues end as a glandular cushion around the base of the style. Into this cushion the  $D$ - and  $d$ -cords send  $gl^d$ -strands which divide repeatedly to form numerous short traces (Fig. 26).

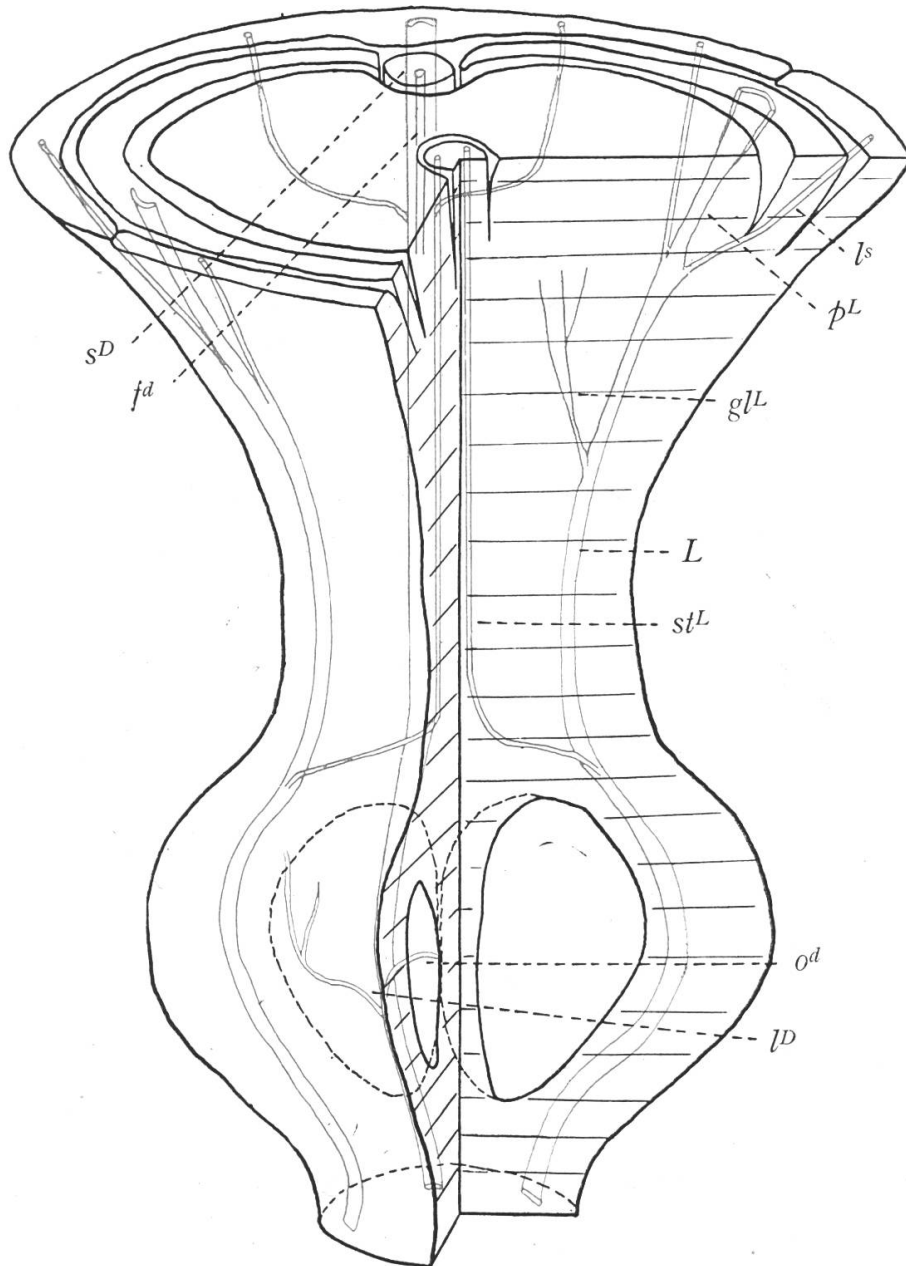


FIG. 24. — Reconstruction of a flower of *Circaea lutetiana* up to the base of the perianth.

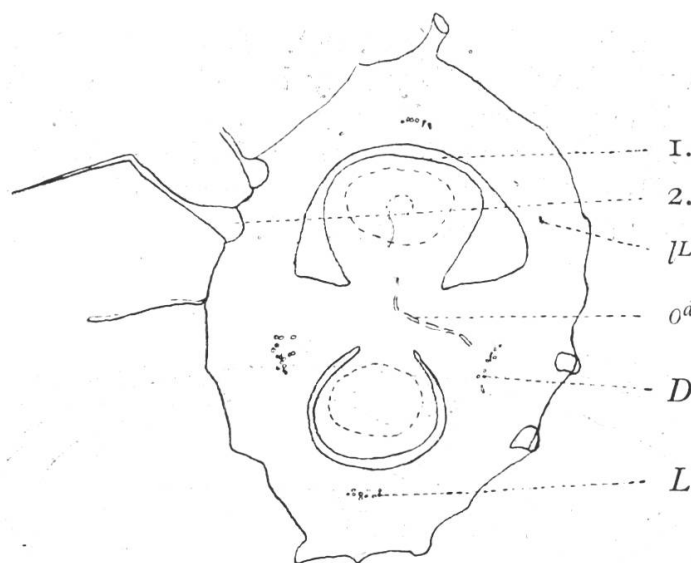


FIG. 25. — *Circaea lutetiana*, T.S. ovary. (1) ovule ; (2) epidermal hair characteristic of the ovary region.

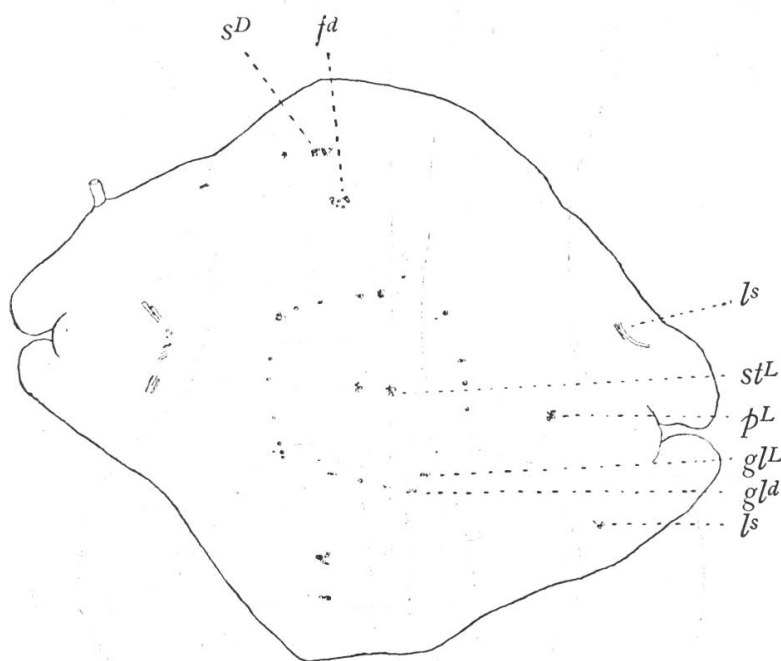


FIG. 26. — *Circaea lutetiana*., T.S. flower bud, perianth tube ( $\times 70$ ). Separation of the strands feeding the glandular disc.

The strands of the two stamens (both being antesealous) spring from the *D*- and *d*-cords as *fd*-strands. These *fd*-strands therefore represent the remainders of the *d*-cords, and the other branches, which then give off two laterals each and then become sepal midribs *sD* must be equivalent to the *D*-cord remainders in other genera. The two

laterals do not form *a*-branches properly speaking, but after diverging widely from their parent cords, they pass into the sepals as laterals  $l^s$ .

The *L*-cords give off a strand each at the base of the perianth tube. These two strands  $st^L$  form the vascular supply to the style and stigma. Each *L*-cord emits a small strand  $gl^L$  which divides to form several small traces in the glandular cushion (Fig. 26). There are no  $f^L$ -strands or any branches which might be considered as their equivalents. Two lateral branches leave each *L*-cord to become the marginal laterals  $l^s$  of adjacent sepals, whilst the remaining portions become the midribs of the two petals  $p^L$ .

There is no continuous *a*-ring formed as the lateral branches from the *D*- and *L*-cords, that is, the  $l^s$ -branches do not overlap. It is interesting to note the absence of  $l^p$ -branches.

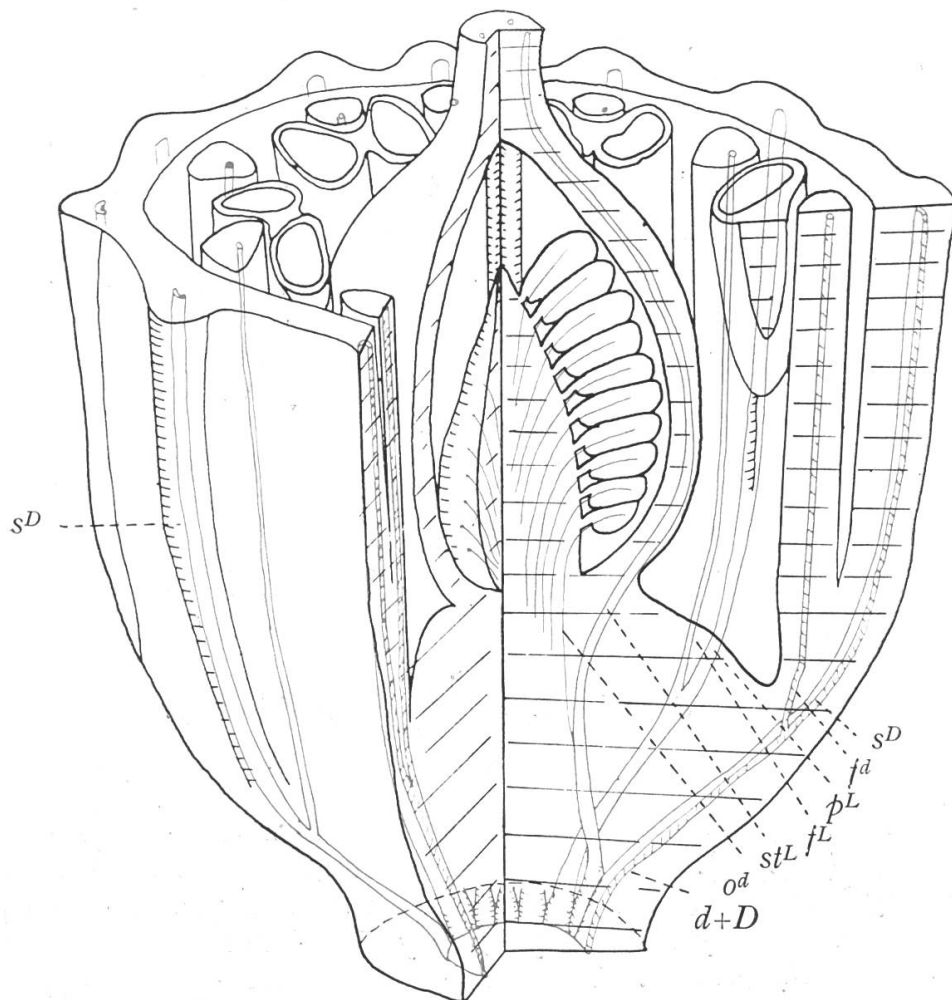


FIG. 27.

Reconstruction of a flower of *Lythrum Salicaria*.

*The vascular supply in Lythrum.* — The ovary in this genus being superior, there appears to be little resemblance, at first sight, between the plan of the vascular supply here and in *Epilobium*. Yet it is possible to recognise cords equivalent to *L*- and *D*-cords of the *Onagraceae*. These cords vary in number from eight to twelve and are

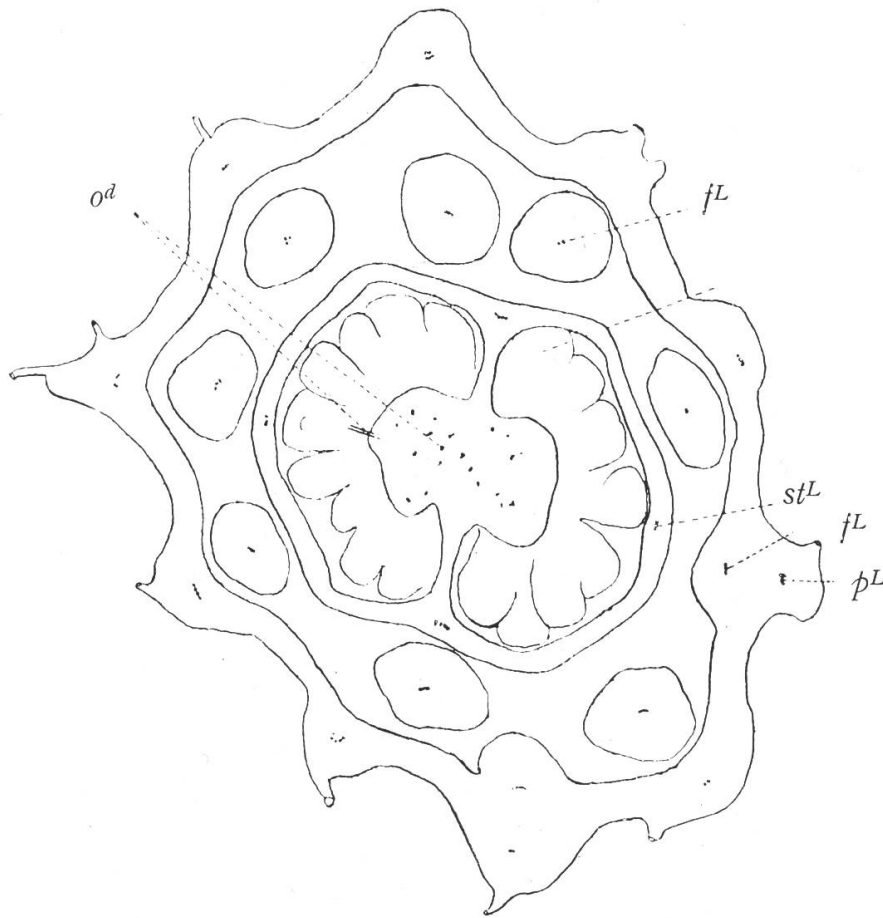


FIG. 28.

*Lythrum Salicaria*, T.S. flower bud, midovary.

arranged in a tight circle at the base of the flower, *L*- and *D*-cords alternating (Fig. 27). Four of the *L*-cords give off a strand each at the very base of the flower. These four strands pass up through the walls of the ovary to the style; they therefore represent the *stL* strands of the *Onagraceae*. The number of these *stL*-strands appears to remain constant at four, irrespective of the number of *L*-cords present. Shortly after, each *L*-cord gives rise to a strand *fL* which supplies an antepetalous stamen. No further branching occurs and

the  $L$ -cord passes into a petal, forming its midrib  $p^L$ , at the same time receiving two lateral branches from the neighbouring  $D$ -cords (Fig. 29).

The  $D$ - and  $d$ -cords branch in a fashion similar to the  $L$ -cords, at the base of the flower. These strands  $o^d$  collect towards the central

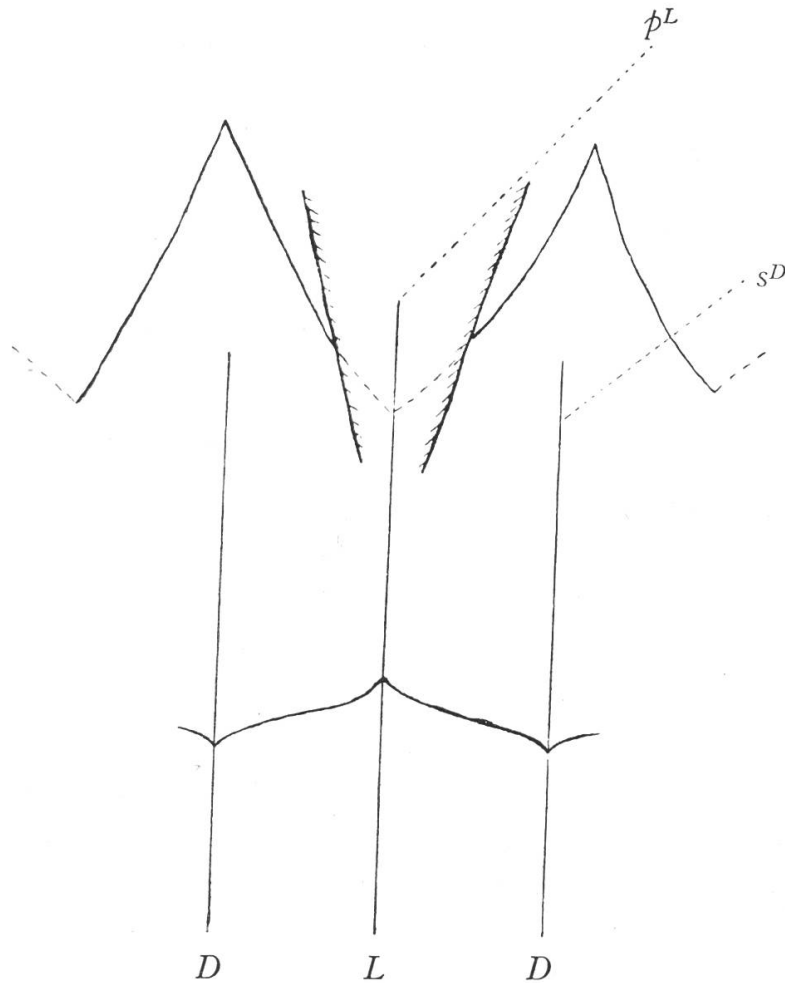


FIG. 29.

*Lythrum Salicaria*, the vascular strands at the top of the perianth tube.

axis and at the same time divide to form a large number of funicular traces  $c^o$  (Fig. 28). The  $f^d$ -strands separate at about the same level as their neighbouring  $f^L$ -strands. At the top of the perianth tube, two  $a$ -branches are given off which join, as stated above, the  $L$ -cords on either side to form the petal midrib  $p^L$ . The  $D$ -cord then becomes a sepal midrib  $s^D$ .

The  $a$ -ring is thus present in this genus also but in a very simplified form.



*Circaea*, *Oenothera* and *Fuchsia* have a glandular region to which go a number of small traces. ( $gl^d$  and  $gl^L$ .) In *Circaea* this region is in the form of a disc at the base of the style. (Figs. 24 and 26). In *Oenothera* it is situated at the base of the long perianth tube; (Fig. 21) the secretion appears to be mucilagenous. In *Fuchsia* it is a ring protruding out of the wall at the base of the perianth tube (Fig. 23). In *Epilobium* the region just below the stamens functions as a nectary (Figs. 18 and 19).

These glandular regions are of a certain interest in that the genera *Fuchsia*, *Oenothera* and *Epilobium* display a graded sequence from a definite vascularised glandular organ to a non vascular but merely glandular area. It was not possible in this study to assess the morphological significance of this organ as the number of genera investigated were too limited. It might be suggested, however, that they may represent the vestiges of additional whorls of stamens such as are found to be present in certain *Lythraceae*.

## II. THE INTERPRETATION OF THE GYNAECIUM

During the past few years there has been much controversy as to the general interpretation of the gynaecium. As the ovary of *Epilobium* is inferior, it will, in its structure afford an excellent test. One theory maintained that the inferior ovary was sunk within the inflorescence axis. This latter completely encloses it and the outer whorls of the flower are born on its rim. The other theory as advocated by E. R. SAUNDERS (1937) states that the inferior ovary is not enclosed within the floral axis, but that the outer floral parts originating below the ovary are extended along its walls and fused to them, only separating at the top. EAMES and MACDANIELS (1925) come to the same conclusion for some plants in their *Introduction to Plant Anatomy*. A further hypothesis put forward by SAUNDERS claims the existence of a whorl of sterile carpels in the gynaecium of some plants. These carpels may be so reduced as to be present only as a vascular cord. This, of course, quite revolutionises the old conception of the ovary being made up of a number of leaf-like carpels fused edge to edge to produce a parietal placentation, or with their edges meeting at a common centre to produce an ovary with exile placentation; or a free central placentation where the carpels (admitted sterile), enclose the ovules which are born on a prolongation of the inflorescence axis into the centre of the ovary.

It is interesting to apply these two conceptions in turn to the *Epilobium* ovary, or to that of *Oenothera* or *Fuchsia*; for all three are built on the same plan.

Firstly let us consider the gynaecium itself. There are eight cords which all have some relation to the ovary.

The ovary is quadrilocular and could be interpreted as being composed of four carpels, each carpellary leaf being folded into an "O" shape with fusion of the margins of each carpel. The transverse septa are formed through the fusion of the carpels.

In order that this plan should conform to the vascular supply just described, the large cord *L* should contain the carpel mid-rib, whereas *d* should contain two fused lateral strands from adjacent carpels. This is apparently frequently the case. (EAMES and MACDANIELS, 1925 : 282.)

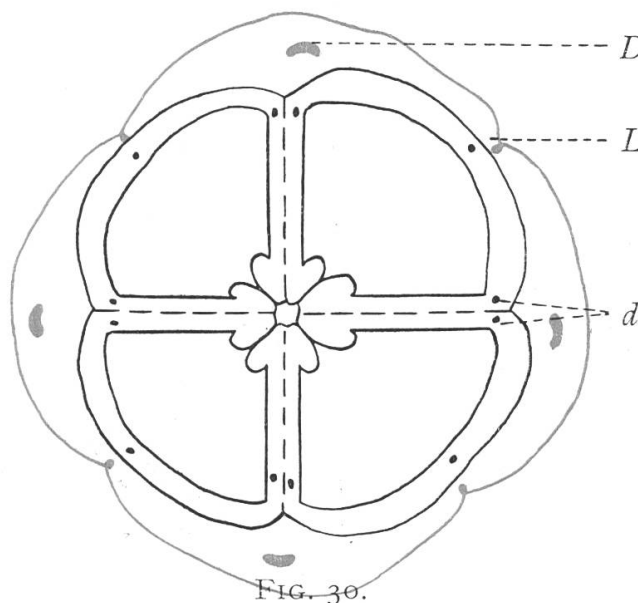


FIG. 30.  
*Epilobium*. Suggested arrangement of the carpels.  
(Bundles in red belong to perianth and andrecium.)

This conception thus produces a type of carpel leaf, which has a mid-rib running direct to the stigma, the carpel leaf-tip giving off no secondary branches, whilst two lateral strands branch frequently towards the margin, but send no branches towards the centre. One visualises a leaf with a structure similar to Fig. 30. If one adopts the conception put forward by E. SAUNDERS, eight carpels can be assumed. An outer whorl of four semi-solid fertile carpels (Type F of Fig. I in *Floral Morphology*, by E. R. SAUNDERS, Vol. I, p. 11), and an inner whorl of sterile valve carpels (Fig. 31) (Type B of Fig. 1 in *Floral Morphology*).

These two types of carpel as found in *Epilobium*, fit very well the description of similar types found in other plants.

So far Miss SAUNDERS' conception fits the case of *Epilobium* better than the former ; for it does away with an awkward carpel leaf venation which has no similarity to that of the foliage leaves.

Next comes the problem of the nature of the ovary wall. If the ovary is inferior in the old sense, then the carpels are enclosed and fused to the prolongation of the floral axis, the other floral whorls originating above.

In the other conception the ovary is only apparently inferior as it is fused with basal portions of the much elongated outer floral whorls.

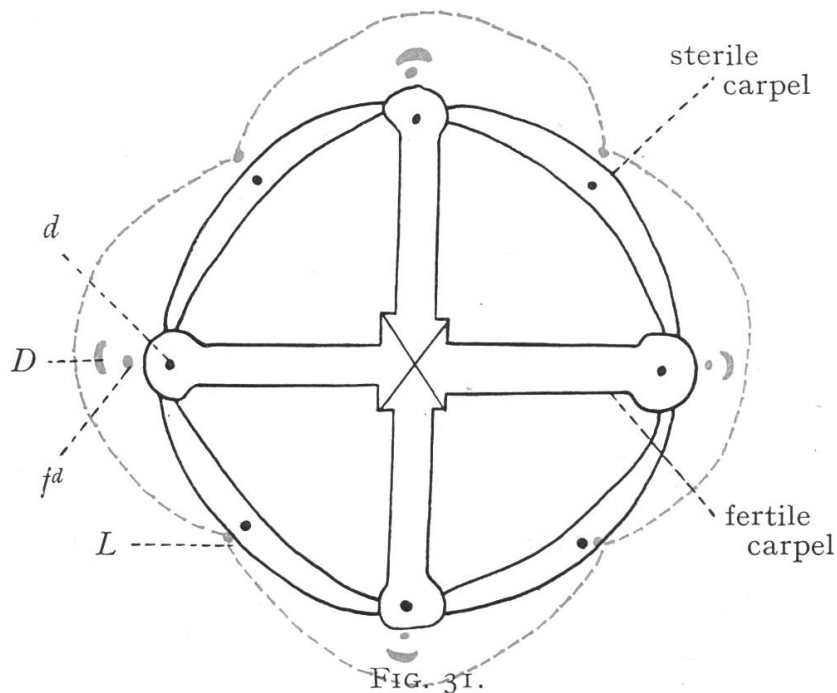


FIG. 31.  
*Epilobium*. Arrangement of the carpels according to the theory of carpel polymorphism.

As the vascular cylinder is already subdivided into bundles it is difficult to recognise signs of the floral axis in the ovary wall. On the other hand it is easier to distinguish signs of floral leaf structure.

The following are signs which may indicate a floral leaf structure :

- (1) The mid-rib cord is obviously composite in nature. (See Figs. 15 and 17).
- (2) The portion *D* throws out small lateral branches as does the mid-rib of a dicotyledon leaf.
- (3) The "grooves" in the ovary correspond in position to the continuation of the sepal edges.

- (4) An additional indicator is present in *Epilobium angustifolium*, where the calyx is coloured as well as the petals. This colouring extends uniformly from the sepal-tips to the base of the ovary.
- (5) In *Oenothera*, where the receptacle is highly developed, the *D*-cords give rise to laterals above the ovary. These all join the *a* (Fig. 22).

The significance of the third point is based on the evidence put forward by E. SAUNDERS (1922: 135). Among the evidence was that of *Epilobium parviflorum* where the leaves show a continuation below their point of insertion on the stem. The author points out that the edges of the petiole are continued some way down the stem as small ridges. The same phenomenon is also visible in other species besides *E. parviflorum*: *E. hirsutum* and *E. angustifolium* for example. If such a feature is used as a proof of the continuation of a leaf beyond its apparent end it can surely have an equal significance in the case of the floral leaves.

The dehiscence of the fruit appears a more natural process if the lines of cleavage are looked upon as coinciding with the margins of a whorl of the floral leaf system, than it would appear if it were regarded as a bursting of the floral axis.

The ovary of the *Onagraceae* is thus, strictly speaking, not inferior, but superior, the apparently inferior position being due to the fusion of the basal portions of the outer whorls to the gynaecium.

*Lythrum salicaria* which is not in the family *Onagraceae*, but the closely related *Lythraceae*, has a flower whose structure affords a most interesting comparison (Figs. 27 and 28). *Lythrum* has a superior ovary which is surrounded by a "corolla tube" on the top of which are inserted the petals and sepals. Here the perianth and androecium have fused together to form a tube, a definite perianth tube. The great point of interest is, however, that the vascular cords of the tube behave in exactly the same way as do those of *Epilobium*: The sepal midrib gives off branches at its base which join the petal mid-rib (See Fig. 29). The flowers of *Lythrum* have thus a great structural resemblance to those of *Epilobium*. The latter might be regarded as of the *Lythrum* type wherein the ovary had become fused to the perianth tube.

The vascular ring in the receptacle is rather interesting. It has been referred to above as though it were composed of branches from the *D*-cords. Its exact composition is, however, rather obscure. In *Epilobium roseum* where this "ring" is but little developed, the branches forming the *a* do not reach the *L*-cords and these latter do not send out any lateral branches to meet the *a* (Fig. 32). A most striking point here is that the end of the *a* instead of becoming marginal

traces in the sepals, become laterals in the petals. This phenomenon could be explained in two ways : either, that the petals are composite structures made up of a central portion which could be regarded as a true petal and two lateral portions of sepal origin ; or, that the petal mid-ribs have given rise to the first pair of lateral traces below the ovary and these have become fused with the adjacent vascular cords along the length of the perianth tube.

If one assumes that the perianth "leaves" originate at the base of the ovary along with the other whorls, the second assumption fits it very nicely. In any case, the first assumption appears most unlikely.

In *Epilobium angustifolium* the *a*-ring is complete (Fig 33), laterals from the *L*-cords mingling with those from the *D*. The inser-

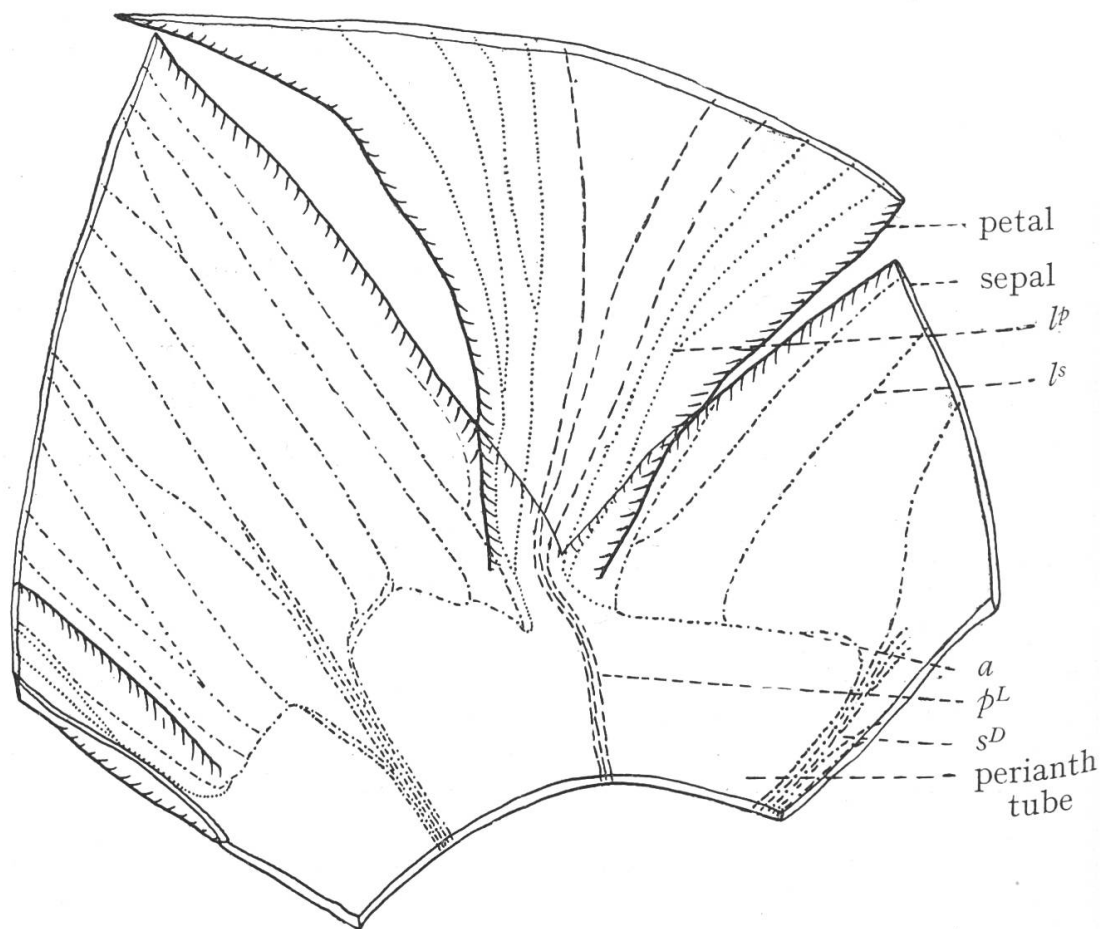


FIG. 32. — Drawing of dissected portion of a perianth tube and bases of the perianth members of *Epilobium roseum*. The preparation showed up clearly the non-continuous nature of the vascular ring in the perianth tube, and also the double origin of the lateral veins in the petals.

tion of the petals is also much broader. The composition of the *a* ring is most probably that of the diagram (Fig. 16). But as the *L*-branches and *D*-branches in the *a* are fused, it is not possible to say whether any of the laterals entering the petals come from strands by way of the *D*-cords. The other species studied exhibited intermediate degrees between *roseum* and *angustifolium*. As there is no reason for classing *E. roseum* as an exception it is reasonable to suppose that in all species the *D*-cords contain, fused to them the lateral traces of the adjacent petals.



FIG. 33. — *E. angustifolium*. T.S. base of perianth tube region of the flower ( $\times 30$ ). The section is slightly oblique. The top half cuts through a portion of the perianth tube. Small portions of lateral strands to the sepals are seen near the top edges. The migration of the stigma strands is only just beginning.

In *Circaea* the whorls are reduced by a half and the ovary is only two seeded, but the general plan of the vascular strands is the same as in *Epilobium*. The *a*-ring is complete, but in this case the *L*-cords furnish the laterals to the sepals in addition to the petal traces, whereas the petals receive no traces from the *D*-cords. In this genus therefore the *L*-cords contain fused to them the lowest laterals of the sepals (Fig. 25).

In *Oenothera*, as has already been stated, the *D*-cords produce laterals between the ovary and the *a*-ring, these all join the latter. The *a* becomes in this way an intricate network of elements. The petal and sepal lateral traces both arise from this ring. Both the *D* and *L*-cords produce *a*-branches, thus it may be that in *Oenothera* both the *L*- and *D*-cords may have fused to them the laterals of the adjacent "leaves".

It would thus appear that, assuming the ovary to be pseudo-inferior (apparently inferior because of the accretion to it of the basal portions of the outer floral whorls) it is equally feasible to assume that the ovary is constituted of four carpels only, as the venation of such a carpel leaf would correspond fairly closely to that of the laterals originating from the ovary base. Thus, in the case of the *Onagraceae* studied, it is not necessary to assume the presence of a second whorl of solid carpels of the type described by E. R. SAUNDERS.

### CONCLUSIONS

From the material discussed in this paper the following conclusions are permissible :—

- (1) The flowers of the European species in the genus *Epilobium* differ but very little in their anatomy.
- (2) The floral vascular supply in both sub-groups of the genus are but slight variations of the same plan.
- (3) The plan of the floral vascular supply in *Epilobium* is identical to that in *Oenothera* and *Fuchsia*.
- (4) The floral vascular supply in *Circaea* differs only through the reduced number of floral parts.
- (5) The arrangement of the floral vascular supply in *Epilobium* is such, that the ovary wall can be regarded as of composite nature. Namely, that the ovary may be a superior ovary to the walls of which the basal portions of the outer floral whorls have fused.
- (6) The fact that some of the petal laterals and the laterals of the neighbouring sepals originate from a common strand suggests the composite nature of the strand. This could be explained thus: The first pair of laterals for each of the perianth members arises at the base of the ovary and becomes fused to the midrib strands of the neighbouring member on each side.
- (7) A study of the floral vascular supply in *Lythrum Salicaria* reveals it to be on a plan very similar to that in the *Onagraceae*. This suggests that the *Lythraceae* may be a more primitive form similar to an ancestor of the *Onagraceae*. The accrescence of the outer whorls to the ovary and the reduction in the number of floral members being regarded as signs of specialisation.



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