

branching is primitive and the monopodial type has been derived from this through a stage like unequal dichotomy. The present observations, however, lead to the conclusion that in the Ophioglossaceae the dichotomous branching of the roots has been derived from the monopodial type. It is not a primitive condition but the result of reduction.

Both these conclusions concerning the root morphology of the Ophioglossaceae, the origin of monarch from polyarch structure and of dichotomous from monopodial branching, agree with the now generally accepted view of Bower, based primarily on the morphology of the stem, leaf, and spike, that 'within the family Botrychium and Helminthostachys appear to be relatively primitive genera and Ophioglossum more highly specialized'.

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THE CONSERVATE CHARACTER OF THE VASCULAR SYSTEM: COMPARATIVE ANATOMY OF NORMAL AND PENTAPHYLLOUS BICARPELLARY FLOWERS OF GAGEA FASCICULARIS.—It is generally believed by morphologists that the vascular system of an organ is more conservative than the external form. As Bower ('The Filicales', vol. i, Cambridge, 1923) says, 'Anatomical characters are apt tardily to follow evolutionary progress and thereafter to persist as vestigia.' Arber ('New Phytologist', xxxii, 1933), however, takes exception to this point of view and rejects the principle of conservatism of vascular bundles. To the question, 'Are we to consider it proven that the vascular bundles are more conservative than the external form, so that vestigial organs may be represented by their bundles, when all external trace of these organs has disappeared?', her answer is that 'we have no alternative but to discard the doctrine of the conservatism of the vascular bundles'. She cites a number of examples from her extensive work on floral morphology to show the existence of organs whose vascular supply has disappeared prior to the loss of the organs themselves and says, 'there seems to be no escape from the conclusion that there is a complete absence of positive evidence for the vestigial survival of vascular tissue after the organ which it supplied has ceased to exist'. Saunders ('New Phytologist', xxxiii, 1934), on the other hand, has criticized Arber's work and upheld the general view. In a recent review, Wilson ('Bot. Rev.', v, 1939) admits that in some cases what appear to be rudimentary organs have persisted with no corresponding vascular supply; still he says, 'it may be stated with confidence that, on the whole, vascular bundles are more conservative than external forms; that in general the vascular supply to an organ persists while the structure is in the process of disappearing'. In reply to a short criticism by the writer (Joshi, 'Nature', cxxxii, 1933), Arber pointed out the need for further investigation of the subject.

During a visit to Kashmir in 1937, the writer collected some floral material of *Gagea fascicularis* Salisb. (*G. lutea* Ker-Gawl.) from Khilanmarg. Most of the flowers in this material were found to have a normal liliaceous structure. They possessed a perianth of two trimerous whorls, two trimerous whorls of stamens, and a tricarpellary syncarpous gynaecium consisting of a trilocular superior ovary, one style and stigma. Among these normal flowers, however, one flower was found with only five quincuncial perianth leaves, five stamens, and a bicarpellary gynaecium. The variation was obviously the result of loss of one perianth leaf,

one stamen, and one carpel. It appeared possible that the study of the effect of such a loss on the vascular construction of the flower may throw some light on the doctrine of the conservatism of vascular bundles, particularly with regard to its application to floral morphology. For this reason the present investigation dealing with the comparative anatomy of the normal and variant flowers was undertaken.

Anatomy of the normal flowers.

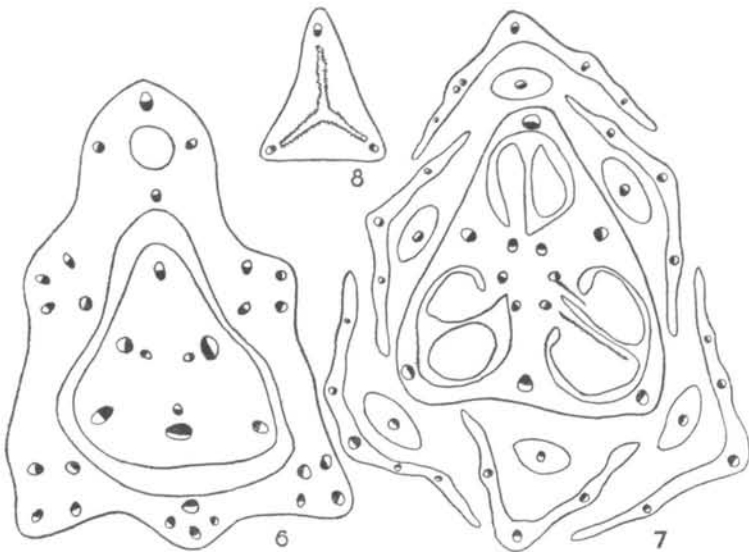
The anatomy of the normal flowers is illustrated in Figs. 1-8, which represent a series of transverse sections through a normal flower from the pedicel upwards.



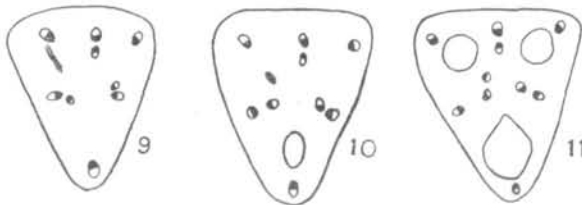
FIGS. 1-5. ($\times 30$.)

The pedicel has a triangular outline in cross section and shows typically six vascular bundles (Fig. 1). Three of these are small and are situated opposite to the angles, while the three bundles alternating with these are of a comparatively much larger size. As we approach the thalamus, the stele broadens out and the smaller bundles begin to pass outwards. They are further joined by two traces from the sides of the larger bundles (Figs. 2 and 3). These composite bundles form the vascular supply of the outer whorl of perianth leaves and stamens. At the level the small bundles and the lateral traces from the larger bundles begin to unite, three traces are given out from the middle of the larger bundles (Figs. 3 and 4). These form the vascular supply of the inner whorl of perianth leaves and stamens. Higher up each of these six perianth-stamen traces breaks up into four bundles (Figs. 4 and 5). Three of these are situated towards the outside and supply a perianth leaf, one forming the midrib bundle and two forming the lateral veins. The fourth one is situated towards the inside of the midrib bundle of the perianth leaf and supplies a stamen. The stamens are fused for some distance with the perianth leaves to form a short tube surrounding the base of the ovary (Fig. 6).

After the perianth and staminal vascular supply has been given off, the vascular tissue remaining in the centre of the thalamus again organizes into six bundles (Fig. 5). Three of these bundles which are on the same radii as the midrib bundles of the outer whorl of perianth leaves are smaller in size. Alternating with them



FIGS. 6-8. ($\times 30$.)

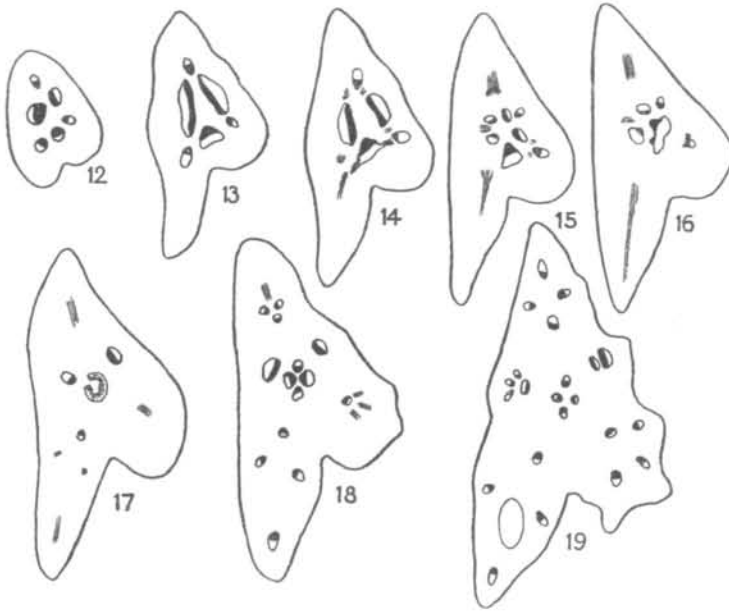


FIGS. 9-11. ($\times 30$.)

are three larger bundles. The latter give off towards their inside another branch (Fig. 6), which is inversely orientated. The ovary at its base thus shows nine bundles arranged in two rings. The outer ring has six normally orientated bundles. The smaller ones of these form the dorsal traces of the carpels and the alternating larger bundles are the median laterals. The inner ring has three inversely orientated bundles. These are the fused ventrals of adjacent carpels and by their division higher up form the ventral traces of the carpels (Fig. 7), which supply the ovules. At the top of the ovary, the ventral and the median lateral traces of the carpels come to an end. The style has triangular outline in transverse section and shows three bundles (continuations of the dorsal bundles of the carpels) in the three angles (Fig. 8). The stylar canal is tri-radiate, of the hollow type, and lined by the glandular transmitting tissue.

Figs. 9-11 represent a series of three sections through the base of the gynaecium

of another flower with normal parts. It shows the origin of the ventral traces on two sides (the upper and the right in the figure) in the normal manner. They arise simply as branches from the median laterals, become inversely orientated by turning round as they move inwards and divide to form the ventrals of the adjacent



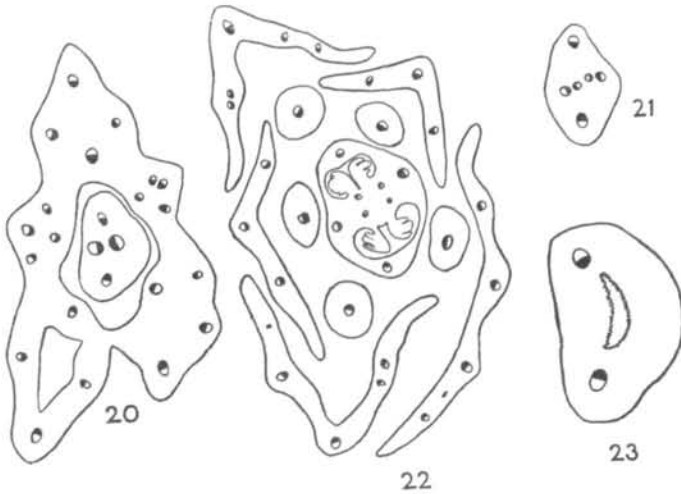
FIGS. 12-19. ($\times 30$.)

carpels. On the left-hand side, however, one of the ventrals is seen to arise from the median lateral bundle of that side, while the second one is given off from the dorsal bundle of the carpel. This origin of a ventral trace from the dorsal trace and not from the neighbouring median lateral is very significant and shows the plasticity of the vascular tissue.

Anatomy of the abnormal flower.

The anatomy of the flower with five perianth-leaves, five stamens, and bicarpellary gynaecium is illustrated by Figs. 12-19 and 20-23. Figs. 12 and 13 show the structure of the pedicel. It differs from that of normal flowers in the development of a conspicuous groove on one side. The groove starts from the very base of the pedicel and continues right up to the separation of the perianth leaves. This can be easily seen by following the series Figs. 12-20. The development of the groove is obviously the result of loss of one of the perianth leaves and stamens from this side of the flower. The vascular structure of the pedicel, however, is quite similar to that of normal flowers, and traces for the outer whorl of perianth leaves and stamens are also given off in the same manner (Figs. 14-19). After the departure of these, three large bundles are left in the centre. One of these is just to the inside of the groove on the pedicel. From the middle of the other two bundles traces come out for the two inner perianth leaves and stamens in the same manner

as in normal flowers (Fig. 15), but there is absolutely no sign of any vascular trace from the groove-opposed bundle which would have supplied the missing perianth leaf and stamen. The vascular bundles of the thalamus after the departure of the perianth and stamen traces come close together and unite to form roughly a



FIGS. 20-23. (Figs. 20-22 $\times 30$; Fig. 23 $\times 90$.)

ring of vascular tissue (Figs. 16 and 17). This breaks higher up into four bundles (Figs. 18-20), two large alternating with two small ones, which organize into the dorsal, median lateral, and ventral bundles of the two carpels in the same manner as in normal flowers (Figs. 21 and 22). The smaller bundles continue as the dorsal bundles. The larger ones give off ventrals towards the inside and then form the median laterals. The only notable point is that the dorsal bundles of the two carpels are not situated exactly opposite to each other as they should be in a normal bicarpellary syncarpous gynaecium. One side of the ovary thus appears to be slightly better developed than the other (Fig. 22). In the style as in the normal flowers the ventral and the median lateral traces fade away, and only the dorsal bundles continue, but their arrangement is very lop-sided. Ordinarily in a bicarpellary syncarpous gynaecium with a single style, the style appears in transverse section either circular or elliptical and shows two bundles facing each other in a perfectly symmetrical fashion. In the present case the style appears in transverse section nearly triangular (Fig. 23) and approaches the style of normal flowers of *Gagea fascicularis*. Further the two vascular bundles occupy two angles of the triangle, so that one side is far more developed than the other.

Discussion.

In recent years there has been a great revival of interest in floral anatomy, particularly due to the work of Saunders and Arber in England, Eames in America, and Troll in Germany. This work has often led to much controversy with regard to the morphology of the various floral parts, especially the gynaecium. As a good deal of such controversy ultimately depends on how much importance one

attaches to the vascular system in the solution of morphological problems, a proper evaluation of the doctrine of conservatism of vascular bundles should be of great service to future investigations in this line. An attempt, therefore, will be made in the present and subsequent investigations to study the effect of the loss or increase in the number of parts of the flower on its vascular system.

Comparison of Figs. 2 and 3 clearly shows that the abnormal flower of *Gagea fascicularis* with 5 perianth leaves, 5 stamens, and 2 carpels has been derived from the normal flowers by the loss of one of the inner perianth leaves, one stamen and one carpel. The study of the vascular system of this flower, although it is not separated even by one generation from the normal flowers, shows the total absence of any rudimentary vascular traces of the lost parts. It is, therefore, clear that in this case no bundles persist after the organ which they supplied has ceased to exist.

The vascular plan of the flower as a whole, however, does not change so rapidly, and a great deal of resemblance is found between the vascular plans of the abnormal and normal flowers. Thus although the perianth leaves in the abnormal flower are arranged in a quincuncial manner and are nearly equally spaced around the periphery of the thalamus, their vascular traces arise in the same manner as in normal flowers, i.e. in two whorls. The two inner alternate with the outer; the only difference is the absence of one of the inner perianth-stamen traces. In the ovary it is found that the dorsal bundles of the two carpels are not exactly opposite one another and lack the symmetry seen in a normal bicarpellary gynaecium. This is particularly marked in the style. Here the two bundles, which are continuations of the dorsal bundles of the carpels, are so situated as to occupy the angles of a triangle. They have the same position as in a normal tricarpellary gynaecium—only one of the angles of the triangle is not occupied by any bundle—, and indicate by their asymmetric disposition the loss of one of the carpels.

Externally the loss of one of the perianth leaves and stamens is shown by the development of a groove along the whole length of the pedicel, even though its vascular system is quite similar to that of the normal flowers. Such a groove is not seen in normal pentaphyllous flowers of other plants. Its presence, therefore, indicates recent loss of some parts. Incidentally, this fact lends support to the 'leaf-skin Theory' of Saunders (1922), according to which the outer cortical portion of the stem is formed by downward prolongation of the leaf-bases.

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A PRELIMINARY ACCOUNT OF THE LIFE-HISTORY OF PORPHYRA UMBILICALIS (L.) AG.—During an investigation into the phases of colonization of newly constructed concrete surfaces in the littoral zone at Mumbles Head, Swansea, it was found that *Porphyra umbilicalis* was a dominant constituent of the algal flora during both pioneer and subsequent phases. Advantage was taken of the opportunity thus provided to study its development and life-history. As soon as the ecological work is completed a full account of these observations will be published; the following is a brief summary of the life-history of this alga as it is found at Mumbles Head.