STUDIES IN FLORAL ANATOMY

Part I. Gynæceum Constitution in the Cruciferæ[1]

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Received May 5, 1941

(Communicated by Dr. P. Maheshwari)

Introduction

The nature of the Crucifer gynæceum was a subject of much discussion in the past and some bitter controversies have been aroused once again during recent years over the number of carpels of which it is composed. A complete review of all the views and hypotheses proposed from time to time on the question seems to be unnecessary since this ground has already been covered by other authors (see particularly Eames and Wilson, 1928 and Bancroft, 1935). It should suffice to say that till recently the bi-carpellary theory was accepted by most botanists in spite of certain obvious difficulties in explaining the nature of the septum which bisects the ovary and the abnormal position of the stigmas which are situated not on the mid-ribs of the two carpels but on the commissures.

Attracted by the appearance of some abnormal ovaries of *Matthiola incana*, Miss Saunders (1923) made a fresh and detailed study of many crucifers and adduced evidence to show that the crucifer ovary consists of four members—two sterile "valve" carpels and two fertile "solid" carpels—, and that the septum, dividing the ovary chamber into two loculi, is true carpellary tissue, formed by the inward extension and subsequent fusion of the two fertile carpels.

Eames and Wilson (1928, 1930) have brought forward much anatomical evidence in support of this view. They hold that the carpel is fundamentally a three-trace organ and that the vascular supply of the two solid carpels is of the same nature as that of the valve carpels which are here sterile. The septum is believed to have been formed by an expansion of the ventral margins of the folded solid carpels. The ovules are extra-carpellary and are supposed to have been extruded out in phylogeny through the walls of the carpels.

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[1] Part of the thesis submitted in partial fulfilment of the requirements for a D.Sc. Degree of the Agra University.

On the other hand, Mrs. Arber (1931 *a*, *b*), from her work on the Cruciferæ, concludes that "the anatomical basis on which the quadri-carpellary theory rests, does not stand examination, and moreover this theory introduces unnecessary complexities from which the bi-carpellary theory is free".

Miss Spratt (1932) also supports the bi-carpellary view, but she delimits the carpels differently and is of the opinion that the ovules are borne on their mid-ribs and not on the margins. In a few cases she fails to find any vascular tissue in the two valve positions in young gynæcia of certain crucifers. In her opinion the mid-rib bundles are too important to be missing. Consequently the replum bundles, which according to the quadri-carpellary theory represent the mid-rib bundles of the solid carpels, are here regarded as the dorsal bundles of the two carpels and the ovules as being borne on them.

Eggers (1935) also disagrees with both Saunders and Eames and Wilson and writes: "Jedenfalls haben wir keinen Grund, aus dem Verhalten des Leitgewebes in der Schote auf deren Vierfruchtblättrigkeit zu schliessen".

On the other hand, Dickson (1934), who has made a thorough study of the Papaveraceæ, is in general agreement with the quadri-carpellary theory as conceived by Eames and Wilson.

It was this bewildering divergence in views and interpretations and at times even in the matter of observations that prompted me to study the question afresh. As also pointed out by Arber (1931 *a*), it was experienced that free-hand sections are of little real value in such studies. The material was, therefore, embedded in paraffin and cut on the microtome. The sections were stained with crystal violet and erythrosin since this combination brings out even the smallest bundles with considerable clearness.

The plants studied here fall into five different tribes of the family (Schulz, 1936). They will now be described in regular sequence and such observations as throw light on the morphology of the gynæceum will be discussed at some length.

Investigation

Brassiceæ

(i) *Brassica campestris* L. var. *sarson* Prain.—Fig. 1, A, shows a section of a flower bud at the point where traces for the four median stamens (St.) are passing out (those for the other two having departed earlier) and the whole vascular ring has broken up into two median segments, the replum

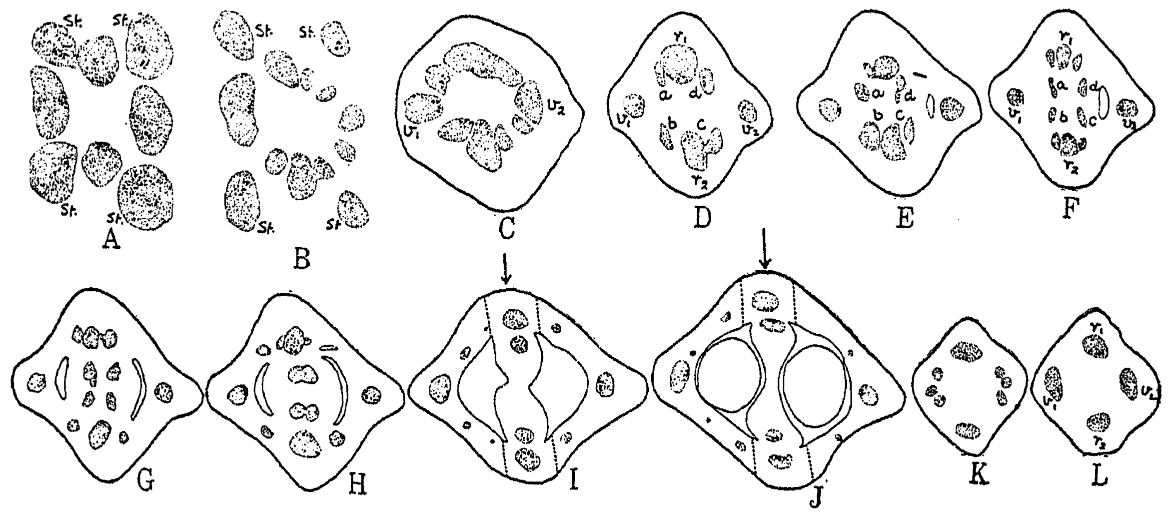

FIG. 1, A–L

T.s. of ovary of *Brassica campestris* (× 20). For explanation see text.

N.B.—Dotted lines in this as well as in the subsequent figures mark the limits of the carpels according to the tetracarpellary theory supported here whereas the arrows when produced towards the centre would delimit the two carpels on one side according to the bi-carpellary view.

strands, and two lateral segments, the valve strands.[2] A little higher up these four divide to form a more or less complete ring of vascular tissue (Fig. 1, B). From the positions of the valve strands one trace now passes out on each side as the median bundle of the valve (Fig. 1, C, bundles v_1, v_2). Out of the six bundles now left in the stele *a* and *d* proceed inward to approach the corresponding bundles *b* and *c* coming from the opposite side (Fig. 1, D–F). Without meeting in the centre they swing in and fuse in pairs to form the inversely oriented placental bundles on the inner side of the replum bundles (Fig. 1, G–I).

Just when *a*, *d* and *b*, *c* are passing in, one small bundle is cut off on each side of each replum strand. This passes out into the corresponding arm of the valve. The remainders of the replum strands constitute the replum bundles just referred to (Fig. 1, I).

Higher up in the style the two lateral bundles in each valve approach the median bundle and finally fuse with it (Fig. 1, K, L). These two bundles thus formed together with r_1 and r_2 (Fig. 1, L) continue right up to the base of the papillose stigma.

(ii) *Brassica oleracea* L. var. *gongylodes* L.—The vascular anatomy of the gynæceum of this species presents some significant variations with regard to the origin of the lateral bundles of the valves. Here, some of the bundles flanking the gaps caused by the passing out of the median bundles

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[2] The expressions "replum strands" and "valve strands" are used here in a purely topographical sense and without any previous commitment to any of the two existing theories.

of the valves cut off one bundle each for the corresponding arm of the valve before passing in. In Fig. 2, C–E the bundles *a*, *b* and *d*, for instance, have

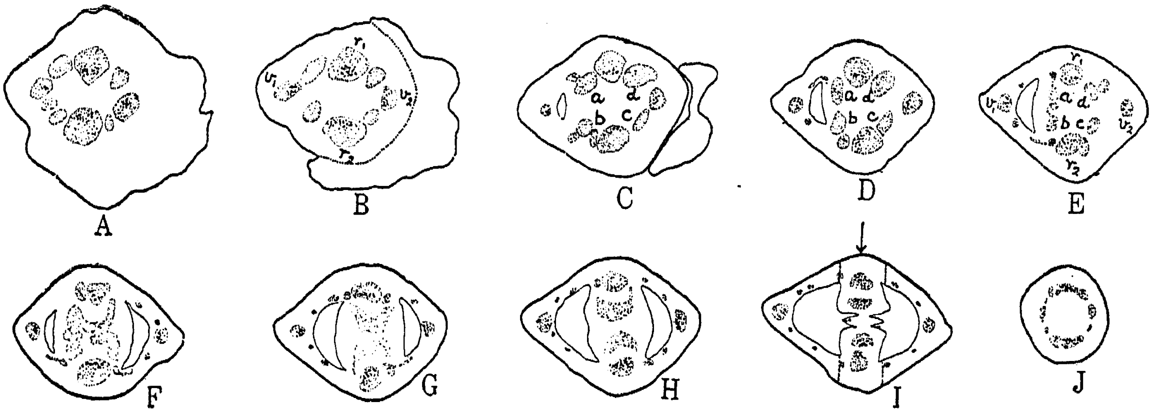

Fig. 2, A–J

T.s. of ovary of *Brassica oleraceæ* (× 20). For explanation see text.

cut off small portions for the margins of the valves but the bundle *c* passes in without doing so and consequently on this *c* side the first lateral bundle for the valve is cut off from the replum strand in the same manner as in the last species.

The remnants of *a*, *b* and *d* and the bundle *c* now proceed toward the centre and fuse there to form an X-shaped plexus of vascular tissue in which the component bundles cannot be distinguished (Fig. 2, F–G). Two groups of vascular tissue emerge out of this plexus in the antero-posterior plane (Fig. 2, H). They have their xylem elements facing those of the replum bundles on their outer side. They give out the ovular traces and are, therefore, the placental bundles. Though their components are not distinguishable there can be no doubt about their having been formed in the usual manner by the fusion of the marginal bundles. Many cases can be cited where due to an *early* fusion of the marginal bundles the placental strands appear as single bundles even at the point of their origin (see among others Eames, 1931; Dawson, 1936; Puri, 1939).

Fig. 2, J shows the vascular ring in the upper part of the style. Higher up only two bundles are left in the positions of the replums and they supply the stigma.

(iii) *Brassica rugosa* Prain.—In this species a ring of procambial tissue with only four xylem groups enters the base of the ovary (Fig. 3, A). The two lateral groups of xylem elements separate off as definite vascular bundles v_1 and v_2, which pass out as median bundles of the valves (Fig. 3, B). The remaining two arcs of vascular tissue, *i.e.*, the replum strands, occurring in the antero-posterior plane, contract a little, as it were, and become more concave on the inner side (Fig. 3, C) and cut off small bundles at either end

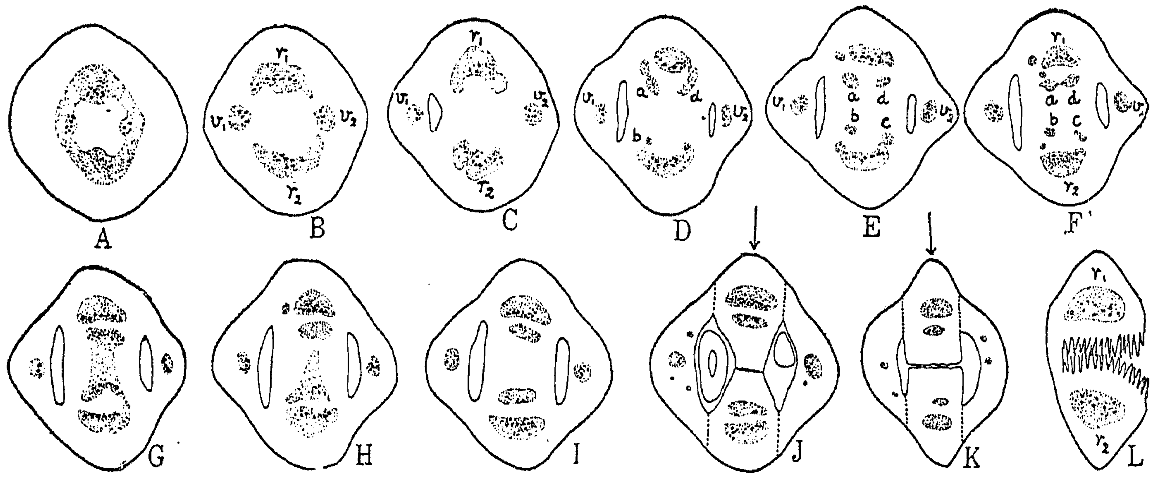

FIG. 3, A–L

T.s. of ovary of *B. rugosa* (× 20). For explanation see text.

(Fig. 3, D–E). While passing in the bundles *a* and *b* (Fig. 3, D) have left small portions on the periphery. In Fig. 3, F the bundles *a* and *d* have come to lie very close together on the inner side of r_1. Similarly the bundles *b*, *c*, occupy positions on the inner side of r_2. Immediately all the four bundles, *a*, *b*, *c* and *d*, are connected by a very light expanse of vascular tissue running across the centre (Fig. 3, G). This central expanse is, however, much fainter than the tissue at its two ends where the separate bundles have lost their individuality to produce the placental bundle seen in Fig. 3, H–I. In Fig. 3, H the central plexus has broken off from one of the placental bundles while in the next the whole of it has disappeared completely.

In some cases it has been observed that no central plexus is formed but the bundles cut off from the replum strands *directly* form the placental bundles.

It should be noted that in this species the valves do not receive any lateral bundles. In some cases very small traces are cut off but they disappear very early.

(iv) *Eruca sativa* Gars.—The passing out of the traces for the median stamens (St.) leaves only four stelar bundles in the receptacle (Fig. 4, A). A little higher up the latter divide to form a more or less complete ring of vascular tissue (Fig. 4, B). From the positions of the valve strands one trace now passes out on each side as the median bundle of the valve (Fig. 4, C, bundles v_1, v_2). The bundles *a*, *b* and *c*, *d* lying on either side of the gaps thus formed approach one another and the vascular ring is completed once again, but this time it is somewhat laterally compressed (Fig. 4, D–E). Fresh gaps are soon formed at the four corners of this ring due to the passing out of the lateral traces into each arm of either of the valves (Fig. 4, E–F).

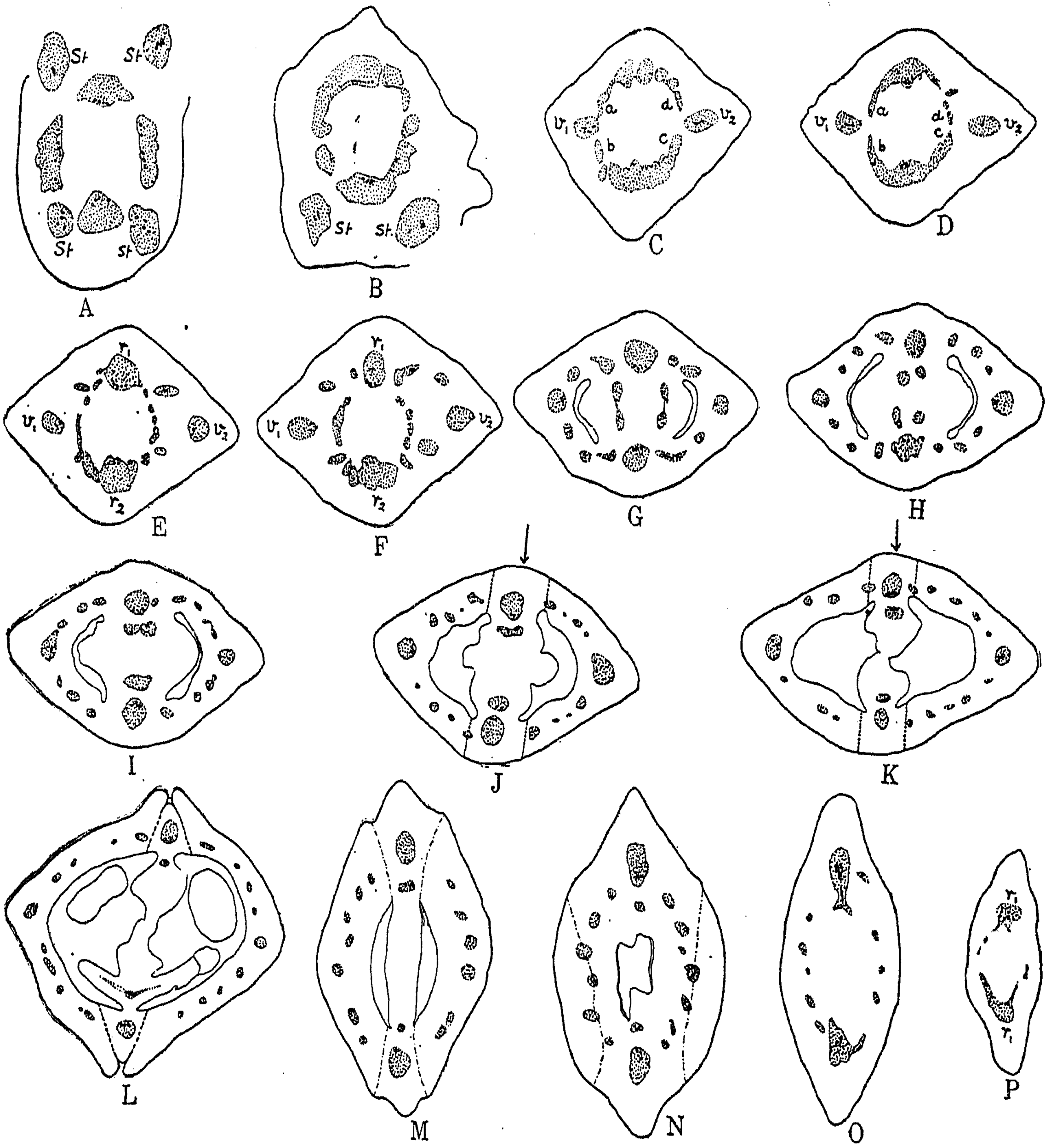

FIG. 4, A–P

T.s. of ovary of *Eruca sativa* (× 26). For explanation see text.

Due to the disappearance of some of the vascular tissue, the lateral bridges, which connect the two replum strands r_1 and r_2, gradually fade away and finally four bundles emerge out of them (Fig. 4, G). These swing inward in opposite directions in such a way that they come to lie in pairs just on the inner side of the replum bundles (Fig. 4, H). Here they fuse to form the placental bundles with inverse orientation (Fig. 4, I).

In Fig. 4, J, small protuberances of tissue are seen marked off, one on each side in the middle of the septum. A little higher up both of them become detached and gradually disappear. It is quite likely that these are the degenerating glands of the type very often seen in the axils of, or alternating with, the stamens (see Arber, 1931 *a* and Norris, 1941). The residual septum then becomes deeply constricted in the middle (Fig. 4, K). Fig. 4, L shows the condition as seen in the middle of the ovary where the valves have over-grown, as it were, to cover the replum. The ovular traces arise from the placental bundles.

Higher up towards the style, the valves decrease in size and the replums show a corresponding increase (Fig. 4, M–N). The style and stigma are thus composed only of the replum tissue (Fig. 4, O). The stigma receives only the two replum bundles (Fig. 4, P).

(v) *Raphanus sativus* L.—This species has already been studied by several authors and the observations made here tally with those of Arber (1931 *a*). However, there is some difference in the interpretation, and hence I consider it worth-while to summarise the results very briefly.

Fig. 5, A–B, represent the condition during and after the departure of the stamenal traces (St.). Soon after the passing out of the median bundles of the valves the smaller bundles *a*, *b* and *c*, *d* flanking the gaps, begin to approach one another towards the centre (Fig. 5, C–D). They branch and anastomose and with the help of some other very small bundles, cut off from the replum strands, almost close the gaps caused by the median bundles of the valves (Fig. 5, E–F). Just when this ring is being completed new gaps are formed by the passing out of lateral traces for each arm of the valves. Then the median strands constitute the replum bundles and four main bundles emerge out of the remaining tissue of the stele (Fig. 5, G). These four bundles swing in to their positions on the inner side of the replum bundles and finally fuse together to form the inversely oriented placental bundles (Fig. 5, H).

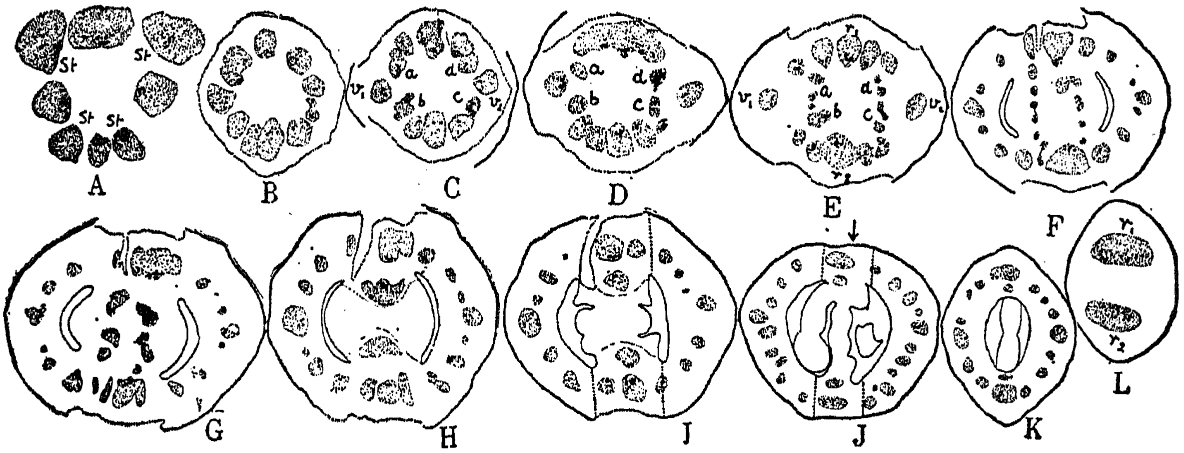

Fig. 5, A–L

T.s. of ovary of *Rephanus sativus* (× 26). For explanation see text.

The septum presents the same appearance as in the last species (Fig. 5, I). The stigma receives only the two replum bundles (Fig. 5, L).

It is interesting to note that as we approach the stigma the size of the vasuclar bundles slightly increases. This is a feature common to many of the species studied by me. Arber (1931 *a*), who also observed it, thinks that this may be "connected with the hindrance to the further flow of the sap, when the distal region of the organ is approached". As pointed out by Hunt (1937), it is also likely that they may refer to the massive stigmas once possessed by these species or their ancestral forms, now lost during evolution.

Lepidieæ

(i) *Iberis odorata* L.—In this species the origin of the placental bundles could not be made out in young gynæcia (Fig. 6, A–G). In older ones, however, an inversely oriented placental bundle is visible on the inner side of each replum bundle (Fig. 6, H). It may be on account of great reduction that the placental bundles do not get distinctly separated from those of the replums. But it seems pretty certain that their mode of formation is, in all essential respects, similar to that found in above-described species.

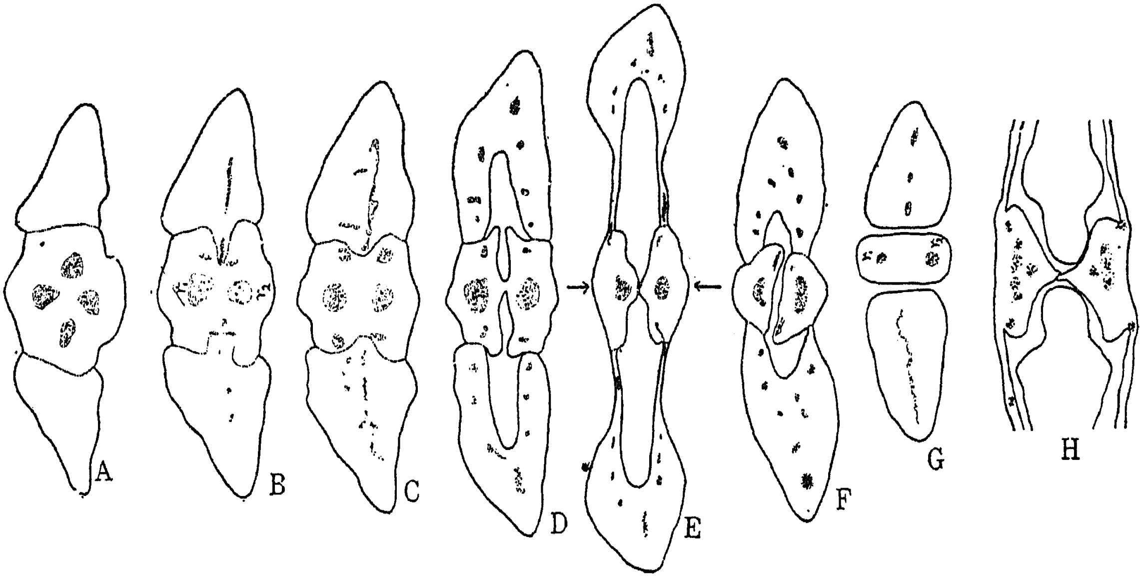

FIG. 6, A–H

T.s. of ovaries of *Iberis contracta* (× 20). A–G, young ovary; H, older ovary. For explanation see text.

(ii) *Capsella bursa-pastoris* (L.) Medikus.—As usual there are four bundles entering the base of the ovary. A little higher up the replum strands cut off one bundle on either side. Out of the total of eight bundles thus formed v_1 and v_2 now pass out to become the median bundles of the valves (Fig. 7, A). The bundles *a*, *d* and *b*, *c* then proceed toward the centre and fuse there into an X-shaped plexus (Fig. 7, B–C). Later on the plexus breaks up into two parts each of which lies on the inner side of the replum

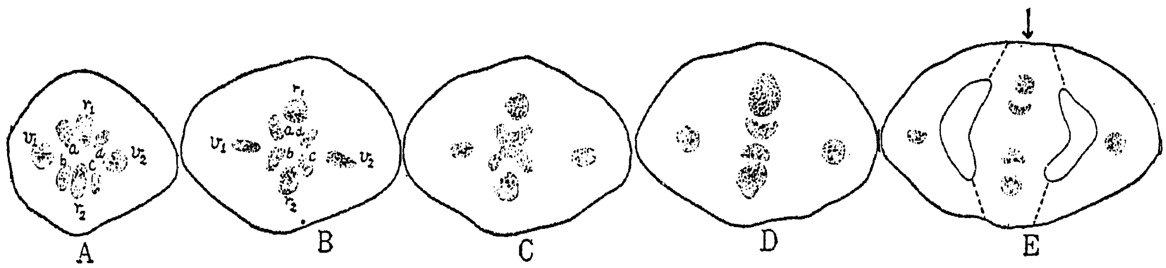

FIG. 7, A–E

T.s. of ovary of *Capsella bursa pastoris* (×40). For explanation see text.

bundle. This is the placental bundle with the usual inverse orientation (Fig. 7, D–E).

Arabideæ

(i) *Cardamine hirsuta* L.—This species represents a comparatively simpler condition. The passing out of the median bundles of the valves, v_1, v_2, leaves only six bundles in the stele (Fig. 8, A). Of these the median

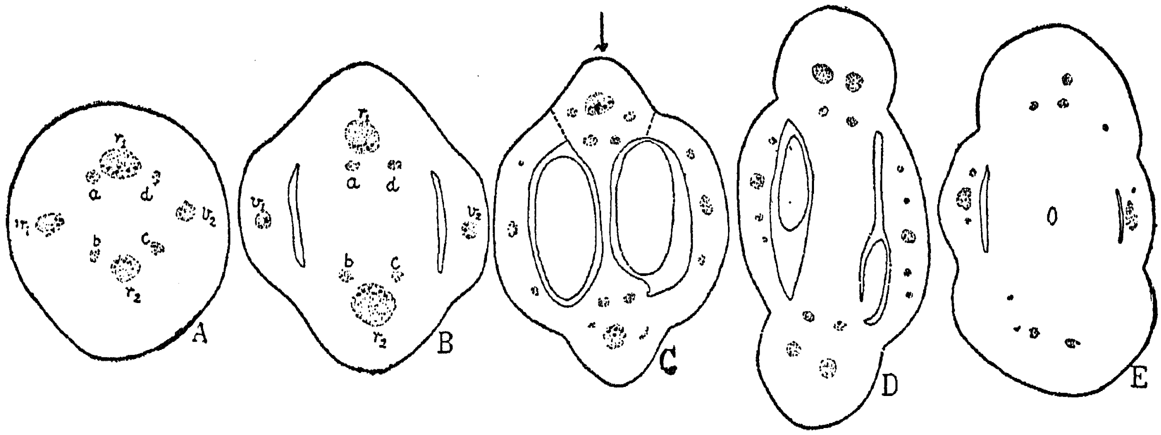

FIG. 8, A–E

T.s. of ovary of *Cardamine hirsuta* (× 40). For explanation see text.

ones, r_1, r_2, form the replum bundles while those lying on the sides swing slightly inward and take up positions on the inner side of the replum bundles (Fig. 8, B). They remain distinct throughout and supply ovular traces separately (Fig. 8, C).

Higher up each of the replum bundles divides into two (Fig. 8, D). Towards the apex the bundles of the valves and the replums decrease in size (Fig. 8, E) and finally disappear almost simultaneously.

Matthioleæ

(i) *Matthioloa annua* (L.) S W.—Fig. 9, A, shows the four bundles entering the base of the ovary. They branch and soon form more or less a complete ring (Fig. 9 B–C). After the passing out of v_1 and v_2 the smaller bundles *a* and *d* approach *b* and *c* coming from the other side (Fig. 9, D–E).

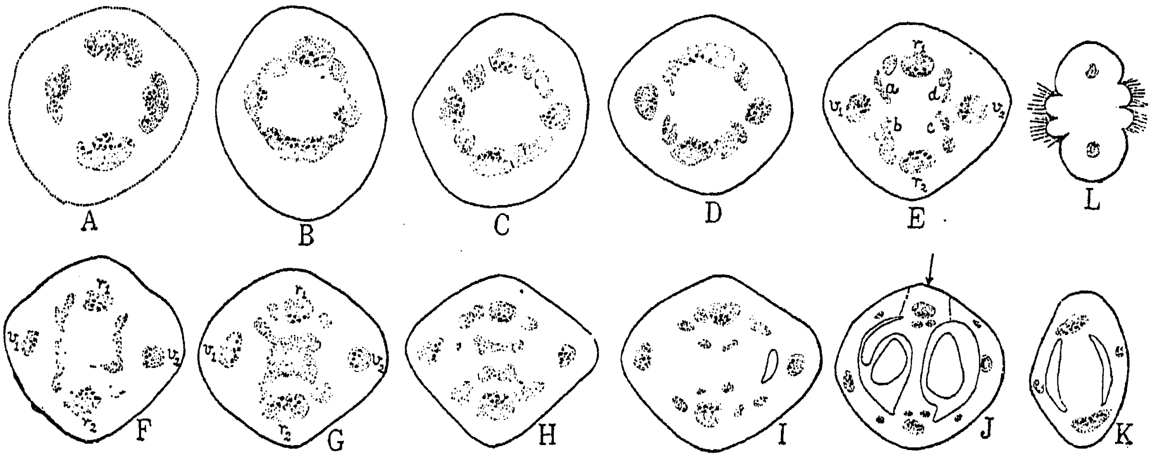

FIG. 9, A–L

T.s. of ovary of *Matthiola annua* (× 26). For explanation see text.

They fuse in the centre to form an X-shaped plexus (Fig. 9, F–G). In Fig. 9, H, the plexus has lost some of its central tissue and has split up into two parts, each of which again loses its central portion and results in two bundles lying right and left inside the replum bundles (Fig. 9, I). They remain quite distinct throughout their course and give out ovular traces.

In this species the lateral bundles of the valves, if present, are cut off from the replum strands after those which form the central plexus (Fig. 9, I–J).

The style receives only four bundles out of which the replum bundles are more prominent than the median bundles of the valves (Fig. 9, K). Fig. 9, L represents the six-lobed stigma which receives the two replum bundles only. The lateral lobes of the stigma are, however, very small and are upward continuations of the valves.

Hesperideæ

(i) *Cheiranthus cheiri* L.—The course of events in this species is illustrated in Fig. 10, A–K. The behaviour of the bundles *a*, *d* and *b*, *c* is more

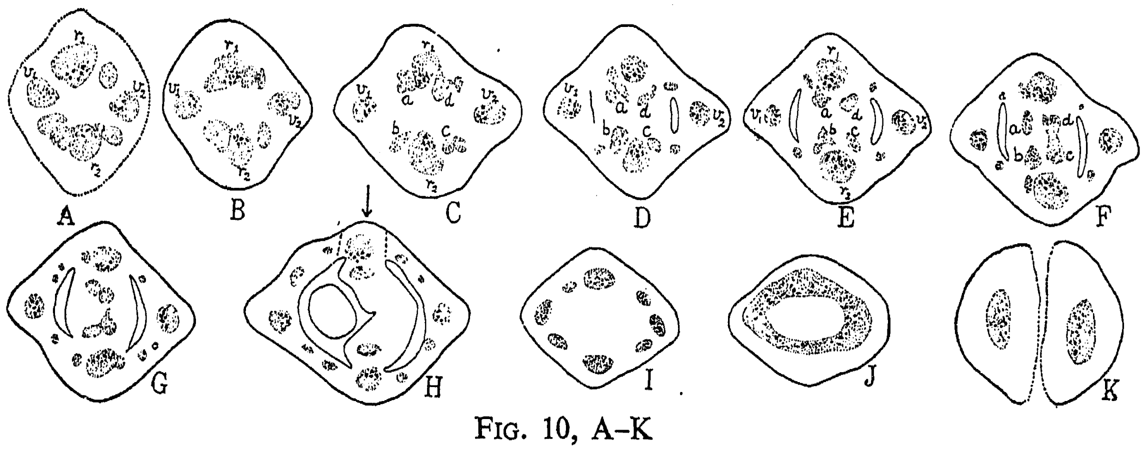

FIG. 10, A–K

T.s. of ovary of *Cheiranthus cheiri* (× 26). For explanation see text.

or less similar to that in *Brassica rugosa*. In Fig. 10, F the bundles *d* and *c* are seen connected together by a short expanse of vascular tissue. In the next figure this 'bridge' has disappeared and there are left two bundles on the inner side of each replum bundle (Fig. 10, G). A little later they fuse into placental bundles (Fig. 10, H).

Fig. 10, I shows eight bundles passing into the basal region of the style. Higher up all the bundles anastomose to form a complete ring of vascular tissue (Fig. 10, J). As the stigma is reached the latter breaks up into two arcs which finally resolve into two bundles occurring in the positions of the replum bundles (Fig. 10, K).

In addition to these *Cherianthus allionii*, *Nasturtium officinalis*, *Senebiera pinnatifida*, *Lepidium officinalis* are some of the other species examined but they all show the same ground-plan as described above and hence it is no necessary to deal with them separately.

Discussion

(i) *Ground-plan of the Vascular Supply of the Gynæceum*

In all the plants studied here four bundles usually enter the base of the ovary. A little higher up they give out small branches on either side and tend to form a ring of vascular tissue. From this there arise four distinct systems of vascular bundles, two median and two lateral. Each of these typically comprises three bundles—one mid-rib and two laterals. In the median system the lateral bundles often swing inward and fuse to produce inversely oriented placental bundles.

These four systems are, however, to be clearly distinguished from the replum and valve strands with which they may not necessarily correspond.

(ii) *Nature and Number of the Carpels*

(*a*) *The Bi-carpellary Theory.*—According to this view the Crucifer gynæceum is composed of two carpels with a valve-like contour. The two smaller areas with their inward prolongations represent the carpellary margins which are believed to have become hypertrophied due to their ovule-bearing function.

The chief objection to this interpretation has always been that in most genera the stigmas are situated over the commissures and not over the mid-ribs of the carpels the normal position for the stigmas.

The method of dehiscence, apparently neither loculicidal nor septicidal, is also difficult to explain on this interpretation.

Further, the nature and behaviour of many of the bundles entering the base of the ovary cannot be satisfactorily explained on the basis of this interpretation.

The exponents of this theory regard the median bundles of the lateral systems the mid-rib bundles of the carpels and the three bundles of the median system (two after fusion) to be branches of the same placental bundle. There is however, no justification for such a presumption since it has been shown that in most of the species described above the marginal bundles of the median systems have no direct connection, whatsoever, with its median bundle.

Then, in what manner the inverse orientation of the bundle supplying ovular traces is brought about has also failed to receive a satisfactory explanation.[3] Merely suggesting that the inversion is a physiological necessity (Eggers, 1935) does not, in any way, carry us nearer the solution of the problem.

As pointed out before, Spratt (1932) has suggested different limits for the two carpels and holds that the ovules are borne on the mid-ribs of the carples and that the placental bundles are simply branches cut off from the mid-rib bundles for supplying ovular traces. It may be pointed out in this connection that ovules are so far known to be borne only on the margins of the carpellary " leaves " and there appaers to be no special reason why the Crucifers should be treated as exceptional by assigning their ovules to the mid-rib. Moreover, some of the other objections mentioned above also apply to this interpretation.

(*b*) *The Tetra-carpellary Theory.*—According to this view there are four carpels in the Crucifer gynæceum, occurring in the same whorl or in two different whorls of two each. The so-called valves of the ovary make up the sterile carpels while the segments between the valves constitute the fertile and solid carpels. During recent years Saunders (1923, 1937) on one hand and Eames and Wilson (1928, 1930), on the other, have been great exponents of this view. They, however, differ considerably in detail and it is, therefore, desirable to deal with their conceptions separately.

The Conception of Saunders.—According to her the four carpels occur in the same whorl and every one of them is individually represented by one of the four bundles entering the base of the ovary. The lateral carpels, which are of the " valve " type, are always sterile while the median ones are

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[3] Arber (1938) has attempted to explain it on " mechanical grounds ' in some of the Papaveraceæ but that interpretation cannot be applied to the Cruciferæ.

of the "consolidated" type and are always fertile. The latter show the following features: (1) They bear a row of ovules on either side of the mid-rib. (2) They possess a pair of well-developed bundles close to the mid-line, which furnish traces to the ovules. (3) They bear the stigmas which need not be considered now as commissural.

The "consolidated" type of carpel is believed to appear in two forms which, however, intergrade with one another. When contracted to a column or radial sheet of tissue, as is the case in ovaries developing into siliqua fruits, it is conveniently distinguished as a "solid" carpel; in its most reduced form it is believed to be composed merely of a fibro-vascular cord. When expanded, so that in outward shape it resembles the valve type, it is said to be "semi-solid", as is the case in ovaries forming the silicula type of fruit.

Such an enunciation of the tetra-carpellary theory has been subjected to much adverse criticism by Arber (1931 *a*, 1931 *b*), Eames (1931) and Eames and Wilson (1928, 1930). Without going into details I will simply refer to some of the more important objections raised by these authors.

By tracing the course of the vascular bundles in serial sections Arber (1931 *b*) has shown beyond doubt that the bundles seen in the base of the ovary do not always correspond to the four bundles seen higher up in it. She has also made it clear that the placental bundles are formed by a contribution from both the valve and replum strands and concludes (Arber, 1931 *b*, p. 178) that "this interdependence of the valve and replum bundles seems irreconcilable with E. R. Saunders' interpretation of them as belonging to different carpels".

Referring to the "semi-solid" carpels of Miss Saunders, she writes: "In a typical narrow siliqua, each valve which becomes detached on ripening is described as consisting of one sterile lateral carpel alone, whereas each valve which falls from the silicula of *Lunaria* is described as representing one much reduced sterile lateral carpel, together with one half of each of the two fertile semi-solid median carpels. But it will be recognised on comparing—a transverse section of a very young ovary of *Lunaria annua* L.—with a corresponding section of any typical Crucifer with narrow siliqua—that they are essentially identical; to explain the nature of the valve on different lines is wholly arbitrary and unconvincing" (Arber, 1931 *a*, p. 38).

The Conception of Eames and Wilson.—Though Eames and Wilson also uphold the tetra-carpellary theory, their method of approach to the subject is fundamentally different from that of Saunders. According to them the four carpels are arranged in two whorls of two each. The outer whorl is made up of two valve-like open carpels bearing no ovules. The inner whorl consists of two solid or closed ovule-bearing carpels in which the loculus has disappeared by gradual reduction. They have based this interpretation mainly on anatomical grounds. The solid carpels have fundamentally the same vascular supply as the valve carpels with the only difference that the ventral bundles of the former often fuse together to form an inverted placental bundle which supplies traces to the ovules.

Such a view not only gives a convincing explanation of the peculiarities of the vascular supply of the gynæceum but also meets the various objections levelled against the bi-carpellary theory. Every one of the four systems seen in the base of the ovary (see p. 176) thus represents the vascular supply of a single carpel.

The present wirter, although sharing the views of Eames and Wilson on the nature of the carpels, finds some difficulty in agreeing with them in the details involving the origin and behaviour of the ventral bundles of both the valves and solid carpels. It is, therefore, proposed to discuss this point at some length; for it is not only important in determining the nature of the carpels but will also throw some light on the nature of the septum and the position of the ovules.

The Marginal Bundles of the Valve Carpels.—Generally the marginal bundles of the valve carpels arise from the sides of the replum bundles when

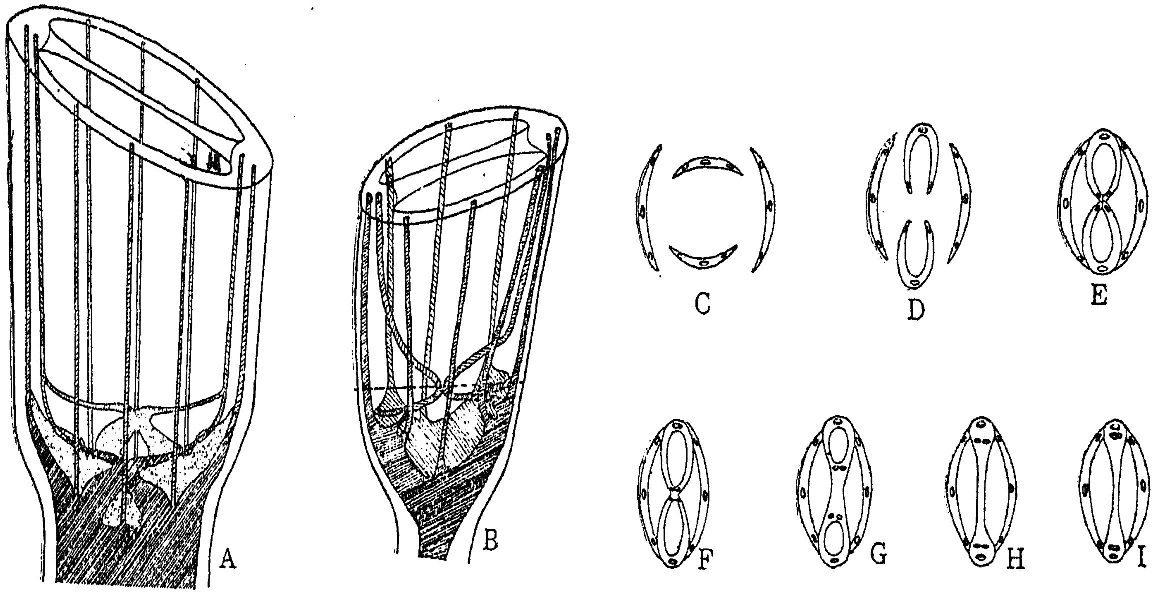

FIG. 11

A.—Theoretical diagram to illustrate the vascular ground-plan of the *Crucifer gynæceum.*

B.—After Eames and Wilson's (1928) Fig. 5 to show their conception of the *Crucifer gynæceum.* According to the interpretation suggested here the bundles passing in towards the centre have to be regarded as stelar bundles up to the level of the dotted line and not as ventral bundles of the solid carpels.

C–I.—Reproduction of Eames and Wilson's (1930) Fig. 5 to show the mode of solidification of the carpels.

the four smaller bundles, *a*, *b*, *c* and *d* (see Figs. of *Brassica campestris*, *Raphanus*, *Eruca*, etc.) have left for the centre. Arber (1931 *a*) has also reported a similar condition in *Brassica campestris* and some others. But Eames and Wilson do not draw any attention to this fact. On the other hand, they appear to suggest in a general way that the bundles lying on either side of the mid-rib bundles of the valve carpels pass out as their marginal bundles (see Eames and Wilson, 1928, Fig. 5, reproduced here as Fig. 11, B).

In some cases they may arise directly from the bundles *a*, *b*, *c* and *d* before the latter pass inward (see Figs. of *Brassica oleracea*, *Cheiranthus cheiri*, etc.). In still other cases the marginal bundles of the valve carpels may be entirely absent as in *Iberis* and *Capsella* or they may be visible at the base and disappear a little higher up as in *Matthiola* and *Brassica rugosa*.

The Marginal bundles of the Solid Carpels.—Since these are the last traces to arise and the receptacular stele does not usually continue beyond the level of their origin to an appreciable extent, it becomes very difficult to determine the exact place of origin of the marginal bundles of the solid carpels.

Eames and Wilson (1928, pp. 254–55) have described a wide range of behaviour for these bundles:

(1) In many species they are said to arise from the sides of the mid-rib bundles of the solid carpels and then turn in and fuse with each other. The bundle so formed approaches the corresponding of the opposite carpel and meets it in the centre of the ovary. Then the two swing outward and take their positions just inside of the dorsal bundles (see Fig. 5 of Eames and Wilson, reproduced here as Fig. 11, B).

(2) In some cases " they may not fuse but approach the centre of the ovary and then retreat to the position just inside of the dorsals, meanwhile remaining distinct ".

(3) " Again, all four such traces may meet in the centre and form a somewhat confused mass of vascular tissue in which the component parts are distinguishable with difficulty."

(4) " In other cases the ventrals of each carpel fuse without passing far toward the centre of the ovary, and then swing slightly backward and follow up inside the dorsals."

(5) " In a few species the ventrals, after fusing near the centre of the ovary split apart again and swing back, taking position to the right and left

I am unable to confirm the first-named behaviour although this is reported to be the commonest. The nearest approach to it, that I could find, was in *Brassica rugosa* where the fusion products of *a*, *d* and *b*, *c* respectively are connected by a small bridge of vascular tissue. But in order to fit this example in the case in question we have to regard the bundles *a*, *b*, *c* and *d* as the marginal bundles of the solid carpels which is not correct.

In the third-named behaviour the four marginal bundles are said to fuse together in the centre to form a confused mass of vascular tissue. If this be so it would mean that the whole of the receptacular tissue has disappeared even at such low a level as the origin of the marginal traces. As long as we believe that carpels are appendicular organs (Prof. Eames himself is a strong exponent of this view) we must presume that the tissue of the receptacle and in many cases even the vascular supply of the same, must continue for some distance (say a few microns) above the origin of the carpellary traces if not above the carpels themselves.[4] The contention that the ventral bundles of the opposite carpels fuse together in the centre so near the level of their origin, is a complete negation of this apparently logical and reasonable presumption. Besides, in cases like *Coringia orientalis*, *Cheiranthus allionii*,[5] etc., (Eames and Wilson, 1930, p. 651) even the vascular tissue of the receptacle continues for some distance after the origin of the ventral traces of the solid carpels, to say nothing of the ordinary receptacular tissue which must necessarily end at a still higher level than the last traces of its stele.

The fifth type of behaviour also does not appear to be quite convincing. In determining the nature of the carpels, Eames and Wilson have depended entirely on the behaviour of the marginal bundles and have always regarded them as representing the course and behaviour of the margins of the carpels. If the case under reference is interpreted in this light it should mean that the carpels first became closed since the ventrals had fused and then opened again allowing the ventrals to split apart! This, however, is highly improbable.

These are the difficulties which one encounters if the views of Eames and Wilson are to be accepted *in toto*. All of them are evidently due to their mistaking the stelar bundles *a*, *b*, *c* and *d* for the marginal bundles of the solid carpels. In a later communication (Eames, 1931) Eames has devoted

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[4] Arber (1937) has brought together interesting evidence about the prolongation of the receptacular tissue beyond the origin of the carpels.

[5] With the herbarium material of this species, which alone was available to me, I could not confirm this point.

considerable attention to the question, "When is a trace not a trace but a receptacular bundle?", and there he has clearly shown that in *Illicium anisatum* the two bundles left after the passing out of the mid-rib bundles of the carpels cannot technically be regarded as marginal bundles although for all intents and purposes they *are* marginal bundles. He seems to have overlooked the fact that a similar condition exists in the Cruciferæ.

I shall now pass on to explain the view to which I have been led as a result of my study of the Crucifer gynæceum. I maintain that the bundles *a*, *b*, *c* and *d* in the species described above are true stelar bundles and that it is from these that the marginal traces of the solid carpels are derived. If they are themselves regarded as marginal bundles then the later origin of the marginals of the valve carpels from between them and the replum bundles (the mid-rib bundles of the solid carpels) cannot be justified. I have recognised five types of behaviour of these bundles before they give rise to *true* marginal traces. These can, however, be regarded only as convenient classes which are not separated from one another by any hard and fast rules, but which, nevertheless, cover all the possible variations in the behaviour of the bundles in question.

(1) In *Eruca sativa*, when the dorsal traces for the valve carpels have made their exit, the bundles *a*, *b* and *c*, *d* approach one another. During their inward course they branch, anastomose and with the help of some other bundles cut off from the sides of the replum strands complete the vascular ring again. From the sides of this ring marginal traces for the valve carpels are given out and the replum bundles become the dorsal traces of the solid carpels. Out of the remaining tissue then there emerge out four bundles which swing in pairs in opposite directions as the marginal bundles of the solid carpels and ultimately fuse in pairs as the inverted placental bundles.

In *Raphanus sativus* also the bundles *a*, *b*, *c* and *d* exhibit a similar behaviour.

(2) In *Brassica campestris* the bundles *a*, *b*, *c* and *d* proceed toward the centre and without undergoing any fusion they (or remains thereof, for some of the tissue must have disappeared in their upward course) swing backward and inward as marginal bundles of the solid carpels and fuse in pairs just on the inner side of the mid-rib [*cf.* case (2) of Eames and Wilson].

(3) In *Capsella* also the bundles *a*, *b*, *c* and *d* proceed inward but here they fuse to form an X-shaped plexus of vascular tissue which for reasons already discussed can only be regarded as stelar in nature. Very soon the plexus breaks up into two groups, each constituting an inverted placental

bundle on the inner side of the mid-rib bundles of the solid carpels. *Brassica oleracea*, *B. rugosa* and *Cheiranthus cheiri* all show slight variations of the same type [*cf.* case (3) of Eames and Wilson].

(4) In *Matthiola* also the bundles *a*, *b*, *c* and *d* fuse into an X-shaped plexus of vascular tissue, which breaks up into two parts by losing its central portion. The marginal bundles, though differentiated, are still connected together for some distance by very small portions of the receptacular tissue which soon disappears leaving two distinct bundles, one on either side of each of the mid-rib bundles belonging to the solid carpels [*cf.* case (5) of Eames and Wilson].

(5) *Cardamine* appears to represent an extreme case where the bundles *a*, *b*, *c* and *d* do not *apparently* carry any stelar tissue with them. They swing slightly inward and take up their positions as the marginals of the solid carpels.

Thus in all cases the bundles *a*, *b*, *c* and *d* are true stelar bundles. It is only after their stelar part of tissue has disappeared that they can be regarded as true marginals. (See foot note 6.)

(iii) *Solidification of the Carpels and Position of the Ovules*

The inverted state of the placental bundles—a condition met with only in the multicarpellary gynæceum with axile placentation—indicates very clearly that the carpels, although without loculi, are of the closed type, in which the margins have turned in and fused opposite to the mid-rib bundles. Hence it is concluded that the median carpels in the Cruciferæ are solid.

Eames and Wilson (1930) have given a series of diagrams to show the way in which this solidification of the carpels might have occurred (see their Fig. 5, reproduced here as Fig. 11, C–I). There is, however, some difficulty in accepting their suggestion *in toto*. The figures referred to above may be interpreted to mean that the carpels have suffered only lateral contraction; for while the margins of the solid carpels remain joined together in their original position and maintain the same distance from the mid-rib, the placental bundles are made to shift outward. This moving out of the placental bundles has been regarded by them as a strong evidence for a contraction of the carpels. It is, however, difficult to understand a contraction which can shift the marginal bundles from the centre to the periphery without affecting the margins themselves.

Such an interpretation is, of course, unavoidable if we accept that the septum is carpellary in nature (Eames and Wilson, 1928). But it must be pointed out that this introduces a serious inconsistency in the tetra-carpellary theory, for when it comes to explaining the nature of the median carpels the course and position of the ventrals are regarded as absolute guides to the course and position of the carpellary margins (Eames and Wilson, 1928, p. 264), but here the two structures are described to have no apparent relation with each other.

With regard to the ovules these authors had to suggest, although "reluctantly", that they have extruded out by penetrating through the wall of the carpels. This is the only possibility if the marginal bundles and consequently the margins of the solid carpels are supposed to fuse in the centre. Spratt (1932) appears to have discarded the tetracarpellary theory of the Crucifer gynæceum merely on this account. She does not think it likely that such tender structures as ovules could ever have made their way out of the carpellary walls.

The mode of solidification of the carpels suggested here in Fig. 12, A–L. The writer believes that the extrusion of the ovules took place before the margins of the carpels fuse together to close the loculus and that the ovules were pushed out of the loculus—probably due to lack of space—through the open margins into the cavities enclosed by the valve carpels. It was only after extrusion of the ovules that the margins of the fertile carpels fused

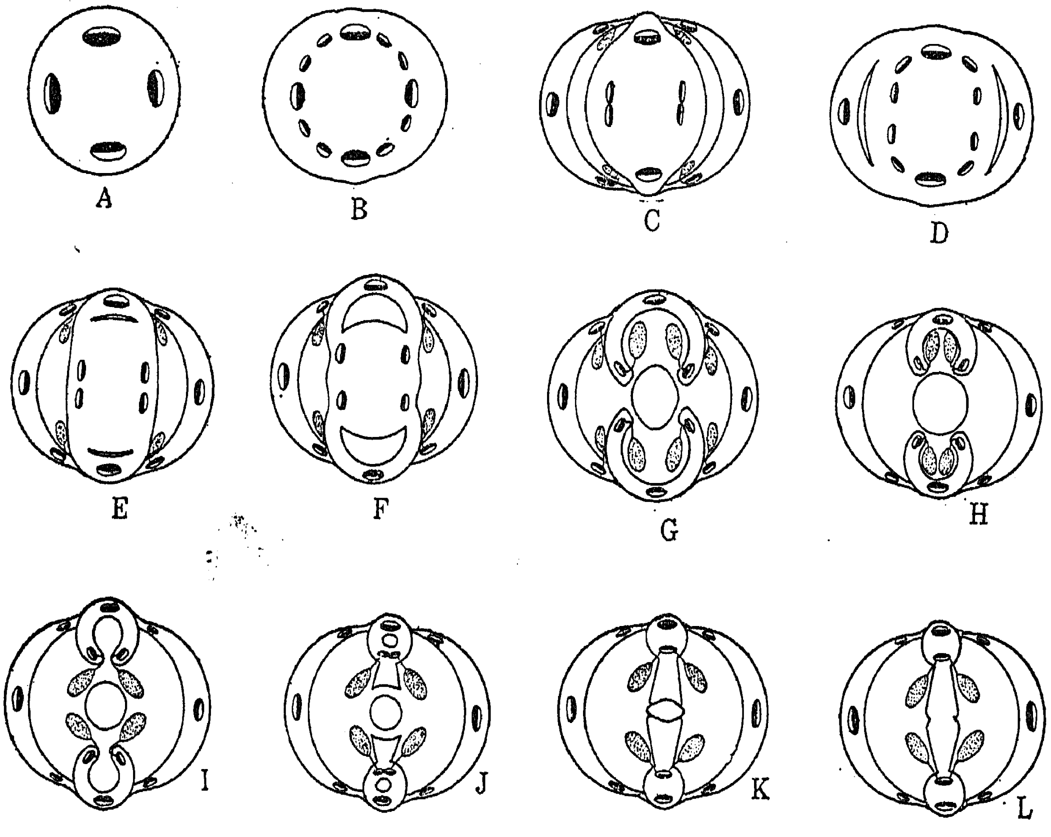

FIG. 12, A–L

Theoretical diagrams to show the author's conceptions of the mode of extrusion of the ovules, solidification of the carpels and formation of the septum.

together (Fig. 12, I–J). Further consolidation resulted in complete elimination of their loculi and the carpels became solid (Fig. 12, K).[6]

(iv) *Nature of the Septum*

According to Eames and Wilson the septum is carpellary in nature' *i.e.*, it is formed by the fusion of the margins of the two solid carpels. The main evidence, and probably the only one, on which this view is based is the supposed meeting of the ventrals of the solid carpels in the centre.

In the first place it has already been shown that the marginal bundles do not meet in the centre and what are believed to be ventrals are really stelar bundles (see foot note 6 below) so that the tissue in which they run cannot be regarded as other than receptacular.

Secondly, even if it is accepted that the bundles in question are really the ventral bundles of the solid carpels, their outward movement towards the mid-rib bundles must lead to the conclusion that the margins of the solid carpels have also receded (for the behaviour of the ventrals cannot but be regarded as representing the behaviour of the carpellary margins themselves). The septum could then arise only by out-growths from the margins of the solid carpels.

The orthodox view that the septum is false still seems to be most satisfactory. In the basal region it is mainly receptacular but as we go upward the axile portion goes on decreasing and the placental in-growths go on increasing until they fuse together in the centre. However, these in-growths arise from the margins of solid and not from the fused margins of the valve carpels as the orthodox view demands.

Eames and Wilson's main objection against the false nature of the septum is best put in their own words (Eames and Wilson, 1928, pp. 251–52):

> " If the dissepiment is false, that is of placental origin and not morphologically formed from the carpel walls then the placentæ are normal parietal placentæ and the ovules are borne in a loculus falsely divided into two chambers. Anatomical evidence, already used by earlier students, and again brought forward by the writers, shows that the ovules are not attached to the placentæ in the manner in which ovules are normally borne on parietal placentæ. The placentæ are clearly not parietal and the above interpretations are not correct."

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[6] In a personal letter Professor Eames has expressed himself as in agreement with my interpretation of the nature of the bundles *a*, *b*, *c* and *d* as also with the mode of extrusion of ovules suggested here.

It is quite apparent that the above objection applies to the false septum as it is conceived in the bicarpellary theory. It does not hold good for the present case where the septum is believed to have been formed by the placental out-growths of the solid carpels (Fig. 12, G–L).

The anatomical data obtained here are so uniform that it is not possible to draw any conclusions concerning relative degrees of evolutionary advancement among the genera whose representatives have been examined by me as also by Arber (1931 *a*, 1931 *b*). The only noteworthy feature is the behaviour of the last stelar bundles which give rise to the marginal traces of the solid carpels. But no importance can be attached to it since in the tribe Brassiceæ alone practically all the variations in the behaviour of these bundles can be noticed.

Summary

A detailed study has been made of the vascular supply of the ovary of about a dozen of species belonging to eight different genera.

The tetra-carpellary theory of the Crucifer gynæceum, as proposed by Eames and Wilson, has been supported and placed on firmer grounds.

A conception, different from the one given by Eames and Wilson, is suggested for the solidification of the carpels and the extrusion of the ovules. The fusion of the margins of the fertile carpels is believed to have taken place only after the ovules had been extruded from the loculus into the cavity enclosed by the sterile carpels.

The septum is believed to be mainly receptacular in the basal region and placental in the upper.

I am thankful to Dr. P. Maheshwari for the help he rendered in the preparation of this paper. I am also indebted to the Director, Royal Botanic Gardens, Kew, for kindly sparing some of his herbarium material for the sake of comparison. My sincere thanks are also due to Prof. A. J. Eames and Prof. R. R. Gates for some helpful criticism.

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