

STUDIES IN THE CAPPARIDACEÆ

VI. Floral Structure in *Crataeva religiosa* Forst., with special reference to the Morphology of the Carpel

BY PROF. T. S. RAGHAVAN, M.A., PH.D. (LOND.), F.L.S.

AND

K. R. VENKATASUBBAN, M.Sc.

(From the Department of Botany, Annamalai University)

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I. Introduction

IN a previous paper (Raghavan, 1939), attention was drawn to some important general structural features of the Capparidaceous flower mainly from the point of view of floral anatomy. In this communication, *Crataeva religiosa*, a genus not dealt with in the previous paper, has been investigated in some detail from an ontogenetic as well as anatomical point of view with the object of throwing some light upon the morphology of the carpel especially. The morphological interpretation of the gynæceum of the Capparidaceæ has been a matter of discussion along with that of the more widely discussed Crucifereæ. In the hope of elucidating further evidence on the subject, this detailed study was undertaken. Though the gynæceum has naturally claimed

the bulk of the paper, the anatomy and developmental history of organs like the gynophore, the septum, etc., have also been described in detail not only because no details of these are available in the literature (so far as we know), but also because it was found that their structure supported the view that has been adopted in this paper, of the nature of the carpel.

The terminology employed in the description and figures is based upon the classical concept of the carpel, that is that carpels form a whorl of only one kind of members, implying a monomorphic as opposed to the polymorphic hypothesis. The placenta is the joint outgrowth from the united carpellary margins. The term commissure is intended to include the region external to the placenta, just at the place of fusion of the carpel margins. In other words, the placenta may be considered as the joint outgrowth from the commissural region.

II. Ontogenetical

The organs of the flower arise in acropetal succession. The origin of the sepal is indicated by a fold in the outer layer. By periclinal divisions of the cells below the fold, the sepals are formed. The petal initials are likewise formed in the second layer of the apex beneath a slight fold in the outermost layer (Pl. VI, Fig. 1). In fact this formation of a slight undulation in the apex always precedes the activity of the cells of the layer below, which results in the formation of the respective organs. It was also observed that the sepals do not originate either from the same level of the axis or simultaneously. Their ontogeny reveals a spirality. The median posterior petal is the first to be formed. After the cells of the petals have been initiated and have grown to some extent by repeated divisions, the apex which was almost conical (Pl. VI, Fig. 2) assumes gradually a broadened form (Pl. VI, Fig. 3). This broadening takes place in such a manner that there is a central rounded protuberance. Histologically this broadening is accomplished by repeated periclinal divisions in the second layer of the apex except at the central dome. In the formation of the stamen primordia the usual folds are formed in the "shoulder" (Newman, 1936) and by cell divisions in the layer beneath the folds, the stamens arise. After all the stamen primordia have been initiated, the central dome shows a fold in the outer layer of cells on one side (Pl. VI, Fig. 4) and the cells below the fold form the carpel primordium by division. It is important to remember two facts, firstly that the two carpels of which the gynæceum of *Crataeva* is composed, do not arise simultaneously, nor in the same level on the dome. They exhibit a spiral sequence even as the other floral members. Secondly, the initials of the carpels are towards the two sides of the domed apex and never in the centre of the dome. The two carpels arise as infolded structures from the margin of the dome and as

they grow towards one another around the dome the carpellary margins fuse leaving the extreme apex of the dome unused. The full interpretation of this is discussed at the end of the paper. Pl. VI, Fig. 5 shows the two carpel primordia in longitudinal section having grown some length and the swelling represents the unused apex of the dome and the difference in level of the origin of the carpels is also clearly seen. The fusion of the two carpels along the margins is clearly seen in a transverse section at about this stage, and as this has already been demonstrated for Gynandropsis in Pl. XII, Fig. 1 of the previous paper (Raghavan, 1939), that stage is not reproduced here again. Pl. VI, Fig. 6 is a longitudinal section of gynæceum of about the same age.

Some interesting observations were made in connection with the origin of the floral whorls and the members thereof. In the differentiation of the calyx the median posterior sepal is the earliest (Text-fig. 1). This is made out not only by its first separation but also by the vascular strands of the central stele leaving for this organ earliest. Following the ontogeny of the sepals as could be inferred from the differentiation of the members of the calyx whorl, one finds that it follows a clockwise direction in the matter of their release (Text-figs. 1-4). Next to the posterior sepal the right-handed lateral, then the anterior and lastly the left-handed lateral. This implies unmistakably two important things, firstly that the organs do not arise simultaneously and secondly they do not originate from the same level of the floral axis. In other words, the sepals exhibit a clear spiral sequence in their origin. The same is the case with the petals. The members of the corolla are distinctly spiral in their differentiation. The earliest petal is the one between the posterior sepal and the right-handed lateral. And the interesting point is that in their differentiation an anti-clockwise direction is observed. In the matter of the andrœcium the differentiation of the staminal whorls in a spiral manner though quite evident as a whole, their large number made it difficult to follow the differentiation of individual members of the different whorls. It can however be made out that the 28-29 stamens which usually compose the andrœcium, are in three whorls of eight, four and sixteen and in the differentiation of these, one finds that while the first whorl exhibits an anti-clockwise direction its immediate next shows a clockwise direction. This disposition in whorls can, however, be made out by close observation of very young flower buds, especially the release of the vascular supply for the developing stamens. In a slightly older stage all these whorls are jumbled together giving no indication of their arrangement in such definite cycles.

As regards the carpels, we find that the observation made on longitudinal sections was corroborated by transverse sections of very young

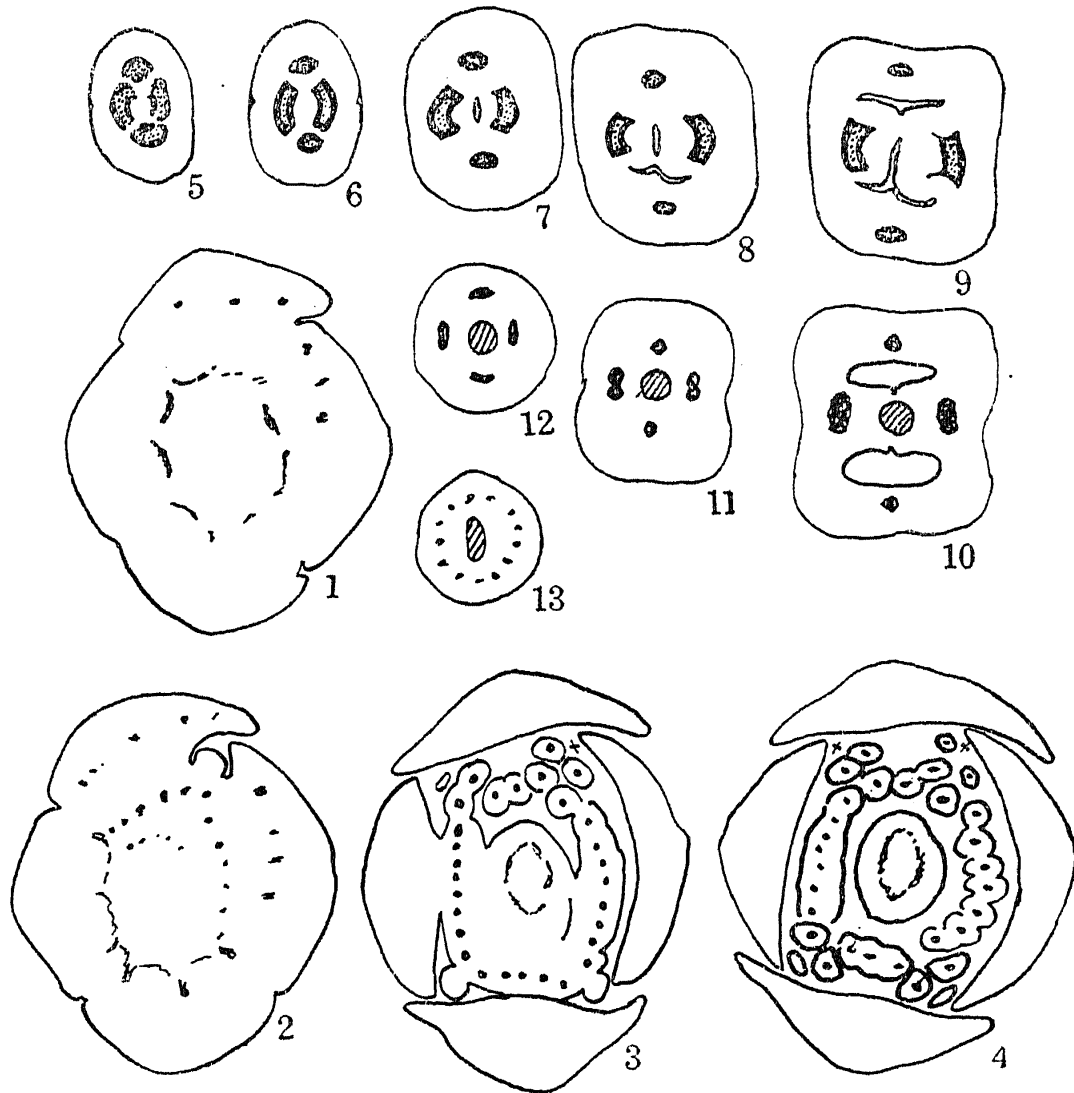
gynæcia. The loculi do not appear simultaneously indicating that the two inrolled carpels by whose marginal fusion the loculi are formed, arise neither from the same level nor simultaneously. Thus the spiral occurrence of the innermost floral whorl, *i.e.*, the carpellary leaves, is also unmistakably evident. The same sequence is observed in the disappearance of these members. The earliest petal to differentiate is the first to disappear; so also with the stamens and the carpels. This also implies that these organs do not arise from the same level of the axis.

III. Anatomical

At the base of the flower bud, there is a ring of vascular bundles. From this the strands for the posterior median sepal are the first to separate (Text-fig. 1). Next the lateral sepal strands are given out (Text-fig. 2). The median sepals are the outer and overlap the lateral (Text-fig. 3). After the petal strands are differentiated the bundles of the stamens separate in a spiral sequence. Most commonly there are twenty-eight stamens for which there are as many bundle supplies. As already stated, in the differentiation of the stamens and their vascular supplies a spirality can be unmistakably traced in respect of each whorl. By tracing the exit of these stamen strands the disposition of the staminal whorls can be inferred. There are eight outermost stamens two on either side of and internal to each petal. Alternating with these pairs are four stamens forming the next inner whorl. Internal to this is a whorl of sixteen.

After the supplies for the stamens have left, there remains the receptacular stele from which the vasculature of the gynæceum originates (Text-fig. 3). Theoretically this residual stele represents the termination of the axis. Arising laterally from this axis are the two carpels which by the fusion of their inrolled margins forms initially a unilocular gynæceum. At the base of the ovary, there is a ring of four prominent vascular strands, two median and two lateral. The loculi make their appearance one by one in a median plane. That is, the carpels are disposed in the antero-posterior plane, a condition which was also recorded for *Euadenia eminens* (Raghavan, 1939). It may be added that generally in this family the carpels are lateral as seen from the drawings of Payer (1857) and Eichler (1875). The lateral bundles are more prominent and bigger than the median. Connecting these are very small minor strands. When the top of the gynæceum is reached we find the lateral bundles showing distinct duality and this is correlated to the spitting of the placental region which delimits the two individual carpels. It is obvious that these two bundles are the marginal strands of the adjacent carpels, which in the lower level of the ovary are in a united condition. The two median bundles represent the midrib bundles of the two carpels. At very

young stages of the ovary when the ovule primordia have not yet been initiated these marginals alone constitute the only bundles at the commissural region. Later on when ovules are being formed one finds a few changes. Firstly, the united marginals assume a concentric configuration



with the phloem almost surrounding the xylem. Secondly, strands passing to ovules make their appearance (Pl. VI, Fig. 7). These may be designated the placental strands. The duality of the marginal strands is a clear indication of the formation of that region by the fusion of the adjacent carpellary margins. One of the reasons of Saunders (1923) for calling this region the 'solid' fertile carpel is that near the top of the receptacle there remain, after the stamen traces have departed, four bundles. These she considered as the four carpel traces. But as we have shown, these are not carpel traces, but represent the receptacular stele which consists of four bundles. The flower is a highly metamorphosed shoot and has a stele made up of discrete bundles which are still further divided by the gaps of the traces proceeding to the floral organs. So the bundles remaining after the departure of the

uppermost stamen traces are not true carpel traces but represent the stele of the receptacle. From these, strands are given off for the innermost floral whorl, the carpels.

IV. *Ontogeny of the Gynæceum*

By studying the gynæceum at different stages of its development, some interesting observations were made. At a very early stage one is able to identify the duality of the carpellary margins at the placental region and this is very much clearer near the top of the ovary than lower down. It may be added that care was taken not to confuse structural changes occurring in space with those occurring in time. The adjacent margins soon fuse and a clear space in the form of a narrow strip is visible separating the two commissures (Pl. VI, Fig. 8). At this stage of development, the gynæceum is unilocular with two parietal placentas. A little later, the middle portion of each placenta slightly protrudes into a gentle convexity in such a manner that they both fuse in the centre, converting a unilocular into a bilocular ovary (Pl. VI, Fig. 9). A critical examination of this fused portion reveals that there are one or two layers of cambial cells dividing tangentially. The cells have very prominent nuclei with no vacuoles. As the ovary advances in age, a clear partition wall is formed connecting the two placentas (Pl. VI, Fig. 10), obviously due to the activity of the cambial cells referred to above. Thus the ovary is distinctly two-celled till about the stage of fertilization. The ovules are anatropous till after fertilization and the campylotropous curvature is initiated only thereafter. The ovules increase in size greatly and so does the ovary as a whole. This results in the rupture of the septum (Pl. VI, Fig. 7). To our mind this rupture is brought about primarily by a spatial necessity. Near the torn ends of the septum can be seen very distinctly ordinary vacuolated parenchyma cells arranged one above the other in such a manner as to recall to one's mind the secondary cortical cells developed during periderm formation. Obviously these rectangular cells superimposed in a serial fashion are the products of the activity of the cambial strip mentioned above. And it is also safe to infer that rupture has taken place at the cambial region. From now onwards the ovary (or rather the young fruit) is unilocular right up to the mature stage. In tracing therefore the ontogeny of the ovary, one finds that it is unilocular at a very early stage, bilocular till after fertilization and again attains the unilocular condition during the post-fertilization changes.

V. *The Gynophore*

(a) *Ontogeny*.—The gynophore is an organ of frequent occurrence in the Capparidaceæ. In genera like *Gyanandropsis* and *Cadaba*, there is present

an androgynophore by which not only the gynæceum but also the androecium, is raised far above the level of the flower. In *Cratæva religiosa*, there occurs a very long gynophore bearing an almost spherical ovary at its tip. Although an organ of such frequent occurrence little is known of its anatomy or of its developmental history relative to that of the ovary it carries. In an ontogenetic study of the floral organs, it would be of interest to find out how and at what stage of the formation of the carpels, the gynophore comes to be formed.

In the earlier stages, it was shown that the carpels arose as inrolled organs from the sides of the floral axis, leaving the extreme apex unused. The carpellary margins fuse forming a unilocular ovary with two parietal placentas. The primordia of the ovules arise from the placental regions and till this stage there is no sign of the gynophore (Pl. VI, Figs. 5 and 6). The subsequent formation of the gynophore is due to the activity of a few meristematic layers at the base of the gynæceum. These cells are arranged in linear rows indicating their having been cut off by repeated tangential divisions of the cells of the meristematic layer. It is by such repeated divisions and subsequent enlargement of these cells that the gynophore attains its length.

(b) *Anatomy*.—At the base of the young gynophore is an ellipse of vascular bundles (Text-fig. 5) in conformity with the general configuration of the gynophore at that region. A slight depression is also seen in the middle of each long side of the ellipse. Though the vascular strands are placed so close together as to obscure to some extent their discreteness, it can be made out that four bundles constitute the ellipse. Of these, two lie in the median plane and two along the lateral plane. The terms median and lateral are used relative to that of the floral axis. That is in the same sense in which the outer pair of sepals are the median pair and the other at right angles to the former, the lateral pair. The lateral pair are situated along the long sides of the ellipse and are much longer than the median pair which are disposed along the short sides. These four strands are sheathed on the outside by a sclerenchyma band; so is the case with the inner margin, so that a hollow region of parenchyma is left as a central ring. As one proceeds higher up, the ellipse gradually becomes circular and correlated to this is the fact of the outer sclerenchyma sheath curving inwards at the boundary of each vascular strand in such a manner that soon each bundle comes to be surrounded by the sclerenchyma sheath (Text-fig. 6). The four strands, while closely appressed at a lower level, become separated higher up and at the base of the ovary, the gynophore shows four widely separated

strands, each pair at right angles to one another (Text-fig. 7). The lateral pair still continues to be the bigger. The ovarian cavities make their appearance one after another and from now upwards the unilocular ovary becomes prominent (Text-figs. 8 and 9). It can now be seen that the lateral bundles which were quite prominent right from the beginning of the gynophore, are the fused marginals of the adjacent carpels (Figs. 10 and 11). Further up, at the top of the ovary, a splitting is seen in the placenta demarcating the individual carpels and correlated to this is the division of each united marginal into two, one going to each half placenta on either side. In other words, one strand comes to lie in each margin of the carpel. The transmitting tissue appears still further up (Text-fig. 10), and the duality of the marginal bundles is maintained throughout (Text-figs. 11 and 12) except at the extreme top of the stigma where all the strands lose their identity due to splitting and form together a diffuse vascular cylinder of a number of minor strands (Text-fig. 13).

The close aggregation of the four bundles in a tubular fashion at the base of the gynophore is undoubtedly a result of the mechanical need of the organ which has to withstand a bending strain. And hence it is that one finds that the ring of vascular bundles reinforced both inside and outside by a sheath of sclerenchyma. As the top of the gynophore is reached, the individuality of the bundles becomes gradually clear and no sooner is the top of the ovary reached than the duality of the marginal bundles becomes evident.

It is needless to say that it is these marginals, that when traced downwards to the gynophore appeared as the elongated lateral strands and these by a close approximation with the median which in their turn are the downward continuation of the midrib bundles, formed a compact ring. Ontogenetically it was shown that the gynophore was brought into existence by the meristematic activity of the base of the gynæceum. It is now found that anatomically it conforms in all details to the vasculature of the base of the ovary.

It was said that the carpels originated as two inrolled structures from the margins of the domed apex leaving the extreme tip unused. And in tracing the vasculature of the gynæceum it was found that the base or the lower portion of it exhibited four strands of which the median were the midrib bundles and the lateral represented the united marginals. Their duality became distinct as the top of the ovary was reached. If we imagine the basal portion of the ovary to undergo elongation, however great, naturally the strands originally present at the basal portion of the ovary

also elongate proportionately and hence it is that we find that the vasculature of the gynophore is essentially that of the ovary. But due to mechanical requirements of the organ, the strands have become closely aggregated and reinforced by the occurrence of sclerenchyma sheaths around them. Being a long organ and having to bear a weight at the top in the shape of a heavy ovary, the organ is subjected to the strains of bending to which a normal aerial stem is exposed. And, hence we find the bundles in the form of a compact ring sheathed by sclerenchyma. The important thing to remember in connection with the gynophore is that it comes to be formed only after the carpels have been fully formed, more or less in a secondary manner by the meristematic activity of the gynæcial base and as such it possesses the vasculature of the latter though in a slightly modified manner in keeping with the mechanical requirements.

VI. Discussion

(a) *The Floral Whorls*.—The nature of the floral organs occurring in *Cratæva religiosa* and the indications they show for the interpretation of the floral parts in general and the carpel in particular will be briefly discussed.

That the flower is a 'determinate branch' (Eames and Wilson, 1930) is to our mind demonstrated amply by the ontogeny of the floral whorls. Not only do the forms of the various members imply this concept, but the fact that the members of each whorl arise in a spiral, also supports this. One may find something incongruous in using the term spiral, in describing a whorl. Capparadaceæ belongs to the cyclic series of the dicotyledons and as such exception may be taken to the use of the word spiral in the description of the floral members. Though there are various floral whorls, the members of each whorl arise in a spiral sequence. If the ontogeny of the sepals is followed, one finds that seldom do they originate simultaneously; so the petals and the stamens. Even in the matter of the gynæceum it has been shown that the carpels are initiated in a spiral manner. In Pl. VI, Fig. 4 only one of the two carpel primordia is in evidence while the other arises later on and in a slightly different level. This is also indicated by the appearance and disappearance of the loculi in a spiral sequence. Coulter and Chamberlain (1903) doubted whether the members of a whorl ever arose simultaneously. Newman (1928) came to a similar conclusion in respect of the members of each floral whorl in *Doryanthes excelsa*, though according to Engler, the Amaryllidaceæ belong to the cyclic series of monocotyledons. This spiral origin could however be traced only by a critical examination of the ontogeny of the various floral whorls.

The vasculature of the members of the floral whorls fully bears out their foliar nature. Each whorl consists of members arranged in close spirals and to each member pass out as traces the stelar bundles of the condensed floral axis. The vasculature of the latter is that of an ordinary branch or vegetative axis composed of discrete bundles. And just as stelar bundles of the axis leave as traces for the vascular supply of the leaves, so also are gaps formed by traces to the floral organs. These gaps are of course soon bridged and some of these again pass out as traces to the next upper whorl and so on.

(b) *The Carpel*.—The carpel needs some special mention, for while the foliar nature of the other floral whorls is more or less generally accepted, the morphology of the carpel has been the subject of wide controversy. McLean Thompson (1929, 1934) for instance, abolishes the carpel altogether. His views on the angiospermic flower and its parts may be summarised as follows: the flower is a sporogenous axis the basal portion of which is sterile while the superficial portion is potentially sporogenous. Bracts, sepals, etc., are products of the sterile base. Microsporangium is an emergence from the lower portion of the sporogenous tissue. Toral growth is commonly dominant over apical growth from an early stage. It may extend beneath the bracteoles and sepals and consequently the maturing axis is cup-shaped when toral growth prevails. An inferior ovary is thus initiated. The emergences which are diverted from spore production mature as stigmatic organs each of which may be a component of a future style. Thus stigmatism is merely a state of tissue. The superior ovary results by the erection of prominent emergences (carpels) from the megasporangium consequent upon the maintenance of apical growth in the axis. On this theory the ovule bearing organ of the Leguminosæ is a flattened phylloclade. According to him so far as the gynæceum is concerned, the erection of emergences by toral growth known as carpels implies nothing of transmission by descent. All that is obligate by descent is a sporogenous axis which may be moulded according to the nature of its growth. The whole problem to him is one of physiology of the growth of the sporogenous axis.

Barring this a carpellary theory, the other chief views on the morphology of gynæceum grant the existence of such a thing as the carpels and its foliar concept. The classical view of the carpel implies a monomorphic concept. First propounded by Goethe (1790) and regarded by Brown (1840) as generally accepted, the classical theory of the monocarpellary gynæceum is that of a modified leaf (megasporophyll) with the margins fused to form the placenta, the apex of the folded carpellary leaf forming the stigma. This

has been restated and elaborated by Goebel (1905) in his classical organography. The polymorphic concept of the carpel (Saunders, 1923, 1925, 1929) and its fancifulness was discussed in some detail in a previous communication (Raghavan, 1939). So far as it affects the Capparidaceæ, it may be stated that it is said to be composed of carpels of two types, the solid fertile and the sterile valve carpels. Thus it implies that the usual three main functions of the gynæceum are divided between the two types of carpels. The solid fertile concerned with reproduction and reception (being ovule bearing and stigmatic) while the sterile valve has only to form the protective covering of the ovary.

Having these in our minds let us consider what the observations regarding the Capparidaceous gynæceum herein recorded would lead us to conclude. For this we have on hand some amount of anatomical and ontogenetic data. Tracing the developmental history of the gynæceum right from the earlier stage, one finds, that as with the other floral members (sepals, petals and stamens) the carpels also arise in a spiral sequence, never simultaneously, nor from the same level of the axis. Pl. VI, Fig. 4 shows a very early stage of the initiation of the carpels primordia. Only one of the two carpels has been initiated. The other arises later and at a slightly higher level. Similarly at a slightly later stage when the loculi are just being formed by the fusion of the adjacent carpellary leaves, one finds that the cavities appear in a spiral order and not simultaneously; the same sequence is followed in the disappearance of the two loculi. These facts necessarily imply that the carpel must be in the nature of a leaf or a leaf-like organ. If it is morphologically a leaf, though very greatly metamorphosed beyond all recognition, then its origin from the axis must throw some light also. Leaves, whether ordinary or metamorphosed, are always lateral in origin. Never do they terminate the growing apex. In a normal flower, however, one finds the innermost floral whorl, namely the gynæceum, right in the centre in such a position that if one examines the flower even at a very early stage of development, one would unhesitatingly conclude that it has terminated the apex of the floral axis. In other words, in the formation of the carpels, the whole of the apical region including the terminus, has been involved. This can be disproved however by a critical study of the manner of initiation of the carpel primordia from the domed apex. It was stated that after the initiation of each floral whorl—and it must be remembered that the members of each whorl arise in spiral succession—say, petals, the periclinal divisions of the cells extend from the petals to about a third of the distance on the convex upper surface of the axis and this results in the formation of a smooth slope or shoulder from which the central dome stands out prominent. And on this shoulder are initiated the stamen primordia. It is from this what may be

termed the residual axis that the carpels take their origin. It will be seen from an examination of the photographs that one of the two carpel primordia arises from one *side* of the apical dome, while a bit later and at a slightly different level the second carpel primordium originates from the opposite *side* of the domed apex. In a longitudinal section (Pl. VI, Fig. 5) these carpel primordia appear as finger-shaped protuberances. But actually these are in the nature of two incurved semicircular outgrowths from the two opposite margins of the domed axis. Naturally the extreme apex is left unused. And in a longitudinal section we see in the centre of the dome between the two carpel primordia a darkly stained tissue which obviously represents the unused apex of the dome. In a slightly older stage, when the two carpels have grown some distance, there is what may be termed a swelling at the base of one of the carpels. This indeed represents the residual unutilised apex and its position more towards one side rather than right in the middle of the two carpels, is due at once to the non-simultaneous origin of the two carpel primordia and their initiation at slightly different levels along the margin of the domed axis. Arber (1938) has described the four carpels of very young ovaries of *Papaver argemone* Linn. as surrounding a minute central area of tissue which she calls the vestigial apex of the floral axis. These observations prove beyond doubt that so far as it pertains to their origin the carpels are definitely lateral and not apical and much like that of any lateral member, a leaf.

The anatomical evidence on hand also supports the foliar conception of the carpel. The flower is a highly condensed shoot of limited growth. The vasculature of the floral axis is that of an ordinary vegetative axis, composed of discrete strands. The vasculature of the various floral members, as has been described already, closely conforms in all essentials to that of a normal leaf. The vasculature of the carpels is essentially that of a lateral appendage, leaf. Each carpel has a dorsal bundle representing the midrib and two ventral bundles representing the marginal strands taking their origin from the receptacular stele. The duality of these marginal bundles does not become clear till the top of the ovary is reached. At lower levels of the ovary, they are single being the united marginals of the adjacent carpels. Higher up, slits between appressed placentas appear, separating the two individual carpels. In correlation to this splitting, the fused marginals divide, each passing to the carpel to which it belongs. One of the arguments for considering the fused carpel margins with their placental outgrowths as the contracted carpels (Dixon, 1935) is that the vascular bundles of the contracted carpel remain unchanged throughout their course. In the present investigation it has been amply shown that the fused marginal bundles do

not remain unchanged throughout their course but each invariably separates into two halves near the top of the ovary, one half passing into the carpellary margin on either side.

The placental strands on whose inverted nature (relative to that of the marginal) Eames and Wilson (1928, 1930) based their interpretation of the Cruciferous and Capparidaceous gynæceum, make their appearance only at a comparatively late stage when the ovules have been formed (Pl. VI, Fig. 7).

It was shown that at such a stage the united marginals assume a concentric configuration. When a portion of such a concentric strand is detached on the side towards the placenta, it naturally has its xylem turned towards the parent bundle. Thus the inversion of the placental strands can be explained. The reason why the united marginals assume a concentric structure is explained by Arber (1938) on quite simple mechanical grounds. Each placenta is internal to these fused marginals. A collateral bundle cannot supply a vascular system for a structure internal to itself on the same radius. It is a special case of the general problem of how a collateral bundle can give off a branch on its xylem side. In *Cratava* this problem is solved by the bundle becoming concentric. Therefore much importance cannot be placed upon these inverted placental strands. Thus from the evidence on hand there is no reason to call the commissural region as anything other than the fused carpellary margins. There is no evidence at least so far as the gynæceum of *Cratava* is concerned to endow this commissural region with the individuality of a distinct type of carpel, the solid.

Since this paper was prepared for the press, we have seen a paper by Kausik (*New Phytologist*, Vol. 37, p. 396) on the morphology of abnormal flowers in some Angiosperms. Some of his observations seem to corroborate the view herein recorded of the morphology of the carpel. In *Allamanda grandiflora* in some abnormal ovaries he has recorded a single terminal vegetative bud between the two carpels (*cf.* his Fig. 3 *e*). This, to our mind, is a clear case of an exaggeration of the growing point which normally is left unused during the formation of the carpels. In another case he has noted two leaf-like carpels. The author himself says (p. 406) that the carpels are the nearest placed to the growing point of the floral shoot and the latest formed *lateral* organ—an observation which has been proved in this paper by detailed ontogenetic and anatomic studies. The author regards these recorded cases of virescence and phyllody as reversions in which there is a reappearance of ancestral characters. In the same breath he says however that “it is not even remotely suggested that the floral parts are in any sense metamorphosed foliar appendages”. What else are these cases of reversions to, it is hard to

understand, unless it be that these are considered as organs *sui generis*, of which there is however no mention.

There are also some interesting observations in respect of what is called "gynophore" which occurred as an abnormality in *Allamanda*. Its anatomy according to the author would appear to conform to the vasculature of the floral axis, composed of a ring of vascular bundles. In that case these would be true stelar bundles from which the carpellary strands must be given out. Theoretically these stelar bundles would end somewhere, denoting the termination of the axis. Thus according to the author the gynophore originates as an elongation of the floral axis. This is only an inference that we are led to, as there is no detailed account of the ontogeny of the gynophore-like organ. We would only point out that in the case of *Cratava* where the gynophore is an organ of normal occurrence, it is formed by the elongation of the basal portion of the ovary; its vasculature is essentially that of the gynæceum and not of the axis. How far the structure of a normal gynophore and that of one that comes to be present only as an abnormality, differ from one another in this important detail, can be confirmed and generalised only after further critical comparative examination of gynophores in other genera of the Capparidaceæ and those occurring in a state of atavism.

(c) *The Septum*.—A word may now be said of the septum that is a feature of constant occurrence in the ovary till after fertilization. It consists of a partition stretched between the commissures. At low levels of the ovary the septum is thicker than at a higher level. Ontogenetically at a very young stage the two commissures are just free so that the ovary is unilocular. Later the central portion of the commissures touch one another, a narrow strip of meristem is formed by whose repeated tangential divisions the septum is brought into existence. Rupture takes place presumably at the cambial region and the bilocular ovary becomes uni-locular once again after fertilization. The occurrence of what is termed a spurious septum is sometimes described in connection with the Capparadaceæ. No detailed account of the method of its origin or its duration in the different genera of the family is available. It was therefore considered desirable to trace its origin and fate. The septum lasts till after the fertilization of the ovules. In the related genus *Cadaba indica* the septum is a permanent feature. It is present for a brief space of time in genera like *Cleome* and *Gynandropsis*. It is therefore inferred that the septum formation in this family may throw light upon the formation and the nature of the septum in the Cruciferæ, where it is a feature of constant occurrence and which has been the subject of discussion at the hands of morphologists. The morphology of the Cruciferous

septum to which terms like dissepiment, false partition, replum, etc., are variously applied, has been differently interpreted.

de Candollé (1821) believed that the two carpels were fused together as in a normal syncarpous ovary with axile placentation; the septum then would be made up of the ventrals or the margins of the two carpels. Chodat and Lendner believe the septum to be the receptacle prolonged and flattened. Payer (1857) and others have held that the septum is a placental outgrowth. Eames and Wilson (1928) hold that the septum is carpellary in nature. It must be remembered that according to them the commissure of the classical concept of the gynæceum represents the solid carpel, in which the locus has wholly disappeared and the usual dorsal and ventral strands are present in close apposition. On this basis, the part lying inward of the inverted ventral bundles must represent the narrow strip of tissue on the ventral margin of the folded carpel. This strip in this case is said to be much extended and forms a broad wing on the reduced carpel. The wings of the two carpels meet in the centre and the septum is formed.

Applying these views to the Capparidaceous septum, which to our mind is very similar to the Cruciferous septum, we find that on the evidence of ontogeny, the septum is unmistakably the product of activity of the cambial strip which is formed at the place of the union of the two commissural margins at a very early developmental stage of the gynæceum. Definitely it is a lateral (relative to the floral axis) placental outgrowth of a secondary nature. A critical examination reveals that not the entire fused margin of the placenta forms the meristematic strip. It is formed in the middle. Each carpel is an inrolled leaf so that the tips are free to bear the ovules. True it is that it is the fused product of the adjacent carpellary margins that constitutes the placenta. But in this case the central portion of the placenta takes part in what may be termed the secondary origin of the septum while the ends representing the tips of the inrolled carpels are free to bear the ovules. This can best be seen in Pl. VI, Fig. 7, where the carpellary tips bearing the ovules are seen quite distinct from the central portion in which alone are seen the remnants of the septum.

de Candollé's (1821) interpretation of the septum would involve an axile placentation for the cruciferous and Capparidaceous gynæceum. That this is not so is made clear by a study of the ontogeny of the gynæceum, whose placentation is unmistakably parietal at least in the initial stages. Chodat and Lendner's axillary concept of the septum, would mean that all the axis is prolonged to the top of the ovary. For this, there is neither ontogenetic nor anatomical evidence. There is no stele nor any evidence of a vascular

tissue even of a vestigial nature in the septum and this should be present if it were axial in nature. Eames and Wilson's (1928) interpretation of the septum as being carpellary, is based on the assumption that the placentas represent the contracted solid carpels. There is no evidence, however, at least so far as Capparidaceæ is concerned to look upon the placenta as anything other than the fused margins of the adjacent carpels. According to them the presence in the septum of the inverted bundles is sufficient proof that the septum is not a mere placental outgrowth, in which there is usually no fundamental vascular system.

In *Cratæva*, no bundles, inverted or otherwise were found either in the septum or even in the placental region. Another argument of theirs in favour of the carpellary nature, is that the outer cell layers of the septum are epidermis like and in some cases provided with stomata. So far as *Cratæva* is concerned, stomata were found only in the abaxial side of the carpellary leaf. None were found either in the adaxial surface or in the funiculus or the septum. Nothing in this paper is said of the origin of the ovule, whether from the abaxial surface of the carpellary margin or from the adaxial. It is therefore with hesitation that we venture to offer an explanation for the presence of stomata in the partition. Stomata are of frequent occurrence on the abaxial surface of the carpel. Rarely they occur also on the adaxial (the side lining the ovarian cavities). If in the species of Eames and Wilson stomata occurred only on the abaxial surface, could it not be that the septum represents an outgrowth of the abaxial margin? This would imply that the ovules arise from the abaxial margin of the carpellary leaf. For such an origin of the ovules there is evidence. Newman (1928) has proved the abaxial origin for the ovules of *Doryanthes excelsa* and also *Acacia Baileyana* (1933). Goebel (1905) also states that the occurrence of ovules on the undersurface of the carpels is not rare. On the other hand there is the possibility of stomata occurring on both the surfaces of the carpel. Orr (1921) for instance has noted the occurrence of stomata in the inner ovariaian wall of *Cleome spinosa* and *Isomeris arborea*. If that is so, this assumption of the abaxial outgrowth is not necessary, for the septum may then be regarded as an outgrowth of the abaxial margin of the carpellary leaves.

Thus from the present investigation the septum is definitely a placental outgrowth of a secondary nature. There is no evidence to endow it with a distinct carpellary affinity. It is, however, carpellary to the extent that the placenta, of which this is an outgrowth, is undoubtedly an important portion of the carpels.

VII. Summary

Floral ontogeny and anatomy in *Crataeva religiosa* Forst., have been investigated in some detail and on the basis of the following observations, some conclusions drawn on the nature of the floral organs, especially the carpel.

The floral organs arise in acropetal succession and the members of each floral whorl exhibit a distinct spirality in their origin. The two carpels are lateral in origin and the terminus (residual apex) is always left unused. They do not arise either simultaneously or from the same level indicating a spirality in their origin.

The vasculature of the floral organs is found to be essentially that of a lateral appendage. The floral axis has a stele of discrete bundles which are further divided by the gaps of the traces proceeding to the floral organs. The bundles remaining after the departure of the uppermost stamen traces are, on this basis, interpreted as the residual stele of the receptacle (which theoretically represents the termination of the axis) and not as carpel traces direct.

The gynæceum is composed of two carpels disposed in the antero-posterior plane, with the parietal placentas made up of the fusion of the carpellary margins. The duality of the marginal strands is also recorded. At first unilocular, a septum is soon developed by cambial activity and this bilocular condition of the gynæceum persists till fertilization. The ultimate unilocular condition is reached by post-fertilization rupture of the septum.

The origin and development of the gynophore are described in detail. The formation of the gynophore is the result of the activity of a few meristematic layers at the base of the young gynæceum. The anatomy of the gynophore conforms to that of the gynæcial base. The median bundles are the downward continuation of the carpellary dorsal strands, while the laterals which are more prominent, are the fused ventral strands which at ovary region exhibit their duality clearly, especially towards the top. In the light of these observations, the foliar concept of the floral organs (including the carpels) is upheld, and there is no evidence at any rate in this genus to consider what has been found to be the commissures, as the solid carpels. The inverted placental strands which are used as a strong argument in favour of this concept, are found to appear comparatively late. Their inverted nature is merely a case of the general problem of how a collateral bundle can give off a branch on its xylem side. Here this is solved by the fused marginals assuming a concentric configuration and when a portion of it is

detached to supply the ovules, the separated placental strand has naturally its xylem turned towards the parent bundle.

The various views on the nature of the Cruciferous and Capparidacious septum are discussed in the light of the present findings and the conclusion is reached that it is a placental outgrowth of a secondary nature.

VIII. Acknowledgment

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EXPLANATION OF PLATE FIGURES

PLATE VI

All the figures are photomicrographs (ca × 75. Fig. 10 × ca 20).

- FIG. 1. L. S. of young flower bud. Note the median posterior sepal has arisen earliest; origin of petal primordium from the hypodermal cell in the 'fold'.
- FIG. 2. Slightly later. After the petal primordium has been initiated the apex is conical.
- FIG. 3. The conical apex has broadend; the stamen primordia are being initiated.
- FIG. 4. L. S. The initiation of one of the carpel primordia from the residual apex.
- FIG. 5. L. S. Later stage. Both the carpels have been initiated. Note the swelling towards base representing the vestiges of the residual apex.
- FIG. 6. L. S. still later stage. Only one of the two carpellary chambers has appeared.
- FIG. 7. The placental region of a mature ovary in T. S. The septum has ruptured the remains of which may be seen to be composed of serially arranged rows of cells. Note also the carpellary ends curved away and quite distinct from the central region.
- FIG. 8. T. S. of young ovary; unilocular condition.
- FIG. 9. T. S. of slightly older stage; beginning of the bilocular condition.
- FIG. 10. T. S. of mature ovary (central portion alone shown) showing the septum.

TEXT-FIGS. 1-4 (× ca 80)

Serial T. S. of young flower bud at sucessively higher levels.

- TEXT-FIG. 1. The separation of the posterior median sepal and next the right-handed lateral. Note the vascular supplies of these have already left the central stele.
- TEXT-FIG. 2. The origin of the first petal between the median posterior and the right-handed lateral. Note the separation of the staminal strands in a spiral manner.

TEXT-FIG. 3. The differentiation of the sepals in a clock-wise direction. The first petal to appear (*i.e.*, the lowest) has disappeared at this level, and the next towards the left has almost disappeared. Thus in the differentiation of the petals an anti-clock-wise spiral direction is followed.

TEXT-FIG. 4. T. S. of the base of the ovary. The posterior petals have disappeared. Note the arrangement of the stamens (the filaments) in whorls and each whorl being a spiral).

TEXT-FIGS. 5-13 (\times ca 80)

TEXT-FIGS. 5- 8. T. S. from gynophore to base of ovary taken at successively higher levels. Description in text.

TEXT-FIGS. 9-13. Serial T. S. from base of ovary to stigma at different levels. Note at the top of the ovary the transmitting tissue (cross-hatched). Still further up (Fig. 11) the duality of the marginal strands. At the stigma there is a diffuse ring of small strands surrounding the transmitting tissue.

