

THE CLASSICAL CONCEPT OF ANGIOSPERM CARPEL: A REASSESSMENT*

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THE so-called classical concept of the angiosperm carpel, like any other concept of plant morphology, has received much adverse criticism during the past 150 years or so it has been in existence. Some of this criticism is just and has enabled morphologists to modify the concept somewhat and to recognize its limitations and imperfections. If the concept has not been abandoned so far by many a morphologist it is not because it explains everything satisfactorily but because there is no other concept that can replace it for the entire group.

Some of the adverse criticism, however, is not warranted as it is based on findings that can still be explained, and perhaps better, in terms of the classical concept. Attention will be focused here on some recent assertions in this respect but before doing so it may be useful to state in a few words the essentials of the classical concept.

The so-called classical concept of the angiosperm carpel we owe to A. P. de Candolle who saw close *parallelism* or *equivalence* between a foliage leaf and a carpel. Subsequent authors elaborated it further so that in the current understanding, the carpel is envisaged as a leafy structure *involutely and adaxially folded on its midrib and bearing ovules on its margins*. This interpretation of the carpel morphology was based on studies of comparative morphology but subsequently it received substantial support also from anatomical studies (*see Eames, 1931*). It must, however, be pointed out that such an interpretation has no historical basis. It is just a way of resolving a carpel in terms of a foliage leaf; it should not be taken to mean that at any time in its evolution a carpel was necessarily an open leaf or it is derived from it.

Both the attributes of the carpellary leaf referred to above have been challenged during recent years on the basis of a detailed study of carpel structure in a number of primitive ranalian families; and

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it has been suggested that the primitive ranalian carpel is a *conduplicately folded leaf, bearing ovules on its adaxial surface* and not on the margins. For the sake of convenience of description this view may be designated as *conduplicate concept*. It must, however, be emphasized that the two inferences involved are not complementary to each other. For instance, it cannot be argued that since the placentation in a particular case is laminar the carpel is necessarily conduplicately folded, or *vice versa*. A carpel with superficial placentation, as in the Nymphaeaceae, Butomaceae, etc., may still have evolved through involution of its margins as is envisaged in the classical concept. It is, therefore, necessary that both of these inferences should be substantiated by facts separately—a point that has perhaps not been adequately appreciated so far.

Support for the conduplicate concept is derived from the following considerations:

- (1) The location of placentae on the supposed adaxial side of the megasporophyll, and not on its margin.
- (2) The vascularization of ovules from both the ventral and dorsal systems of carpellary bundles.
- (3) The *apparent* similarity of very young carpels, carpelodes and styles with a conduplicately folded foliage leaf.

More recently Periasamy and Swamy (1956) have offered some additional ontogenetic evidence in support of this concept. They assert that in the anonaceous *Cananga odorata* the marginal meristems of the carpellary primordium mature even earlier than the differentiation of placentae. This led them to suggest that in the carpel of this species "laminal differentiation attains normal completion before the inception of the placental ridges". Such a situation according to them "negates the possibility of an assumption of involute margins" as is assumed by the supporters of the classical concept.

Another point which Periasamy and Swamy have brought out is that "the ovules are vascularized by branches of the dorsal strand" and not by the ventral bundles even though the latter are much nearer to the placentae. This, according to them, is proof of laminar placentation and is believed to support the conduplicate concept.

A critical examination of all the arguments reveals that the data presented in support of the conduplicate concept admit of yet another interpretation which appears to be more in accord with the known facts and which is also in conformity with the so-called classical interpretation of the carpel (*cf.* Puri, 1955, 1959). It will, therefore, be desirable to discuss these points at some length here.

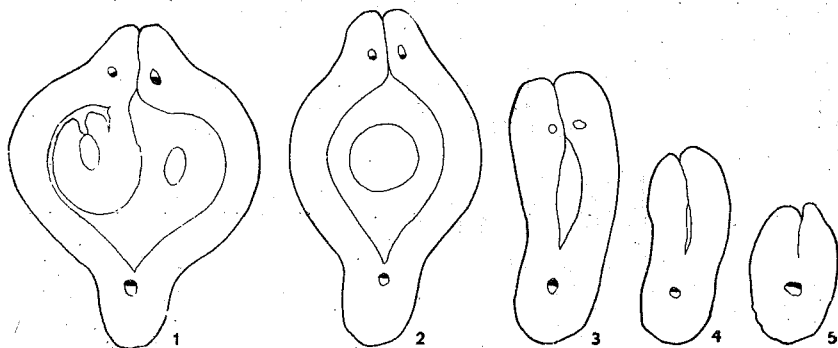
The location of the placentae.—The location of placentae, whether marginal or laminar, is an important point in any consideration of the nature of carpel. Bailey and Smith (1942) suggest that the margins of carpels in *Degeneria* are not infolded or coherent during ontogeny,

but tend to flare apart externally. They further assert that the placentation in this species is clearly laminar and that at anthesis, "broad areas (between margins and the placentae) of the adaxial surface of the megasporophyll are closely approximated", as they do in conduplicate leaves. No evidence seems to have been given for interpreting the surfaces, which stand face to face, as the ventral surface of the carpellary leaf.

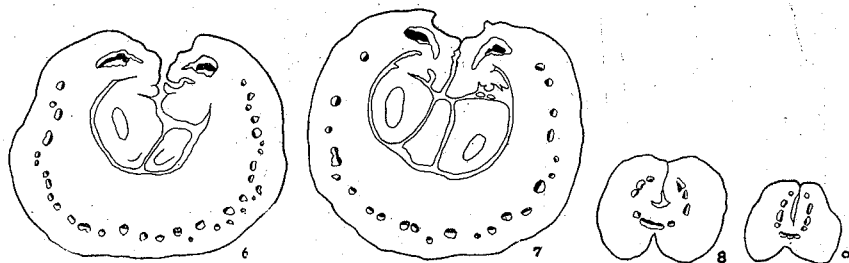
The present author, however, is inclined to think that in arriving at such a conclusion the structure and magnitude of carpellary margins have not been adequately assessed. What have been described as margins are in fact only parts of margins. Margins of carpels, unlike those of a foliage leaf, are generally well developed and have prominent vascular supplies (*cf.* Thomas, 1931; Arber, 1931; etc.). They may be as thick as, or sometimes even thicker than, the main body of the carpel (*cf.* condition in Leguminosae, Ranunculaceae, etc.). Being generally so well developed they can be distinguished to have: (1) an *outer face*, frequently a part of the dorsal surface; (2) an *inner face*, a part of the ventral surface that is usually fertile and bears ovules; and (3) a *lateral face* that represents thickness of the margins and is involved in fusion of margins whenever it occurs. The occurrence of a more or less distinct *lateral face*, that is usually sterile, is an important structural feature that seems to have been completely ignored or misinterpreted so far in a discussion of carpel morphology.

It appears to us that in the formulation and elaboration of the conduplicate concept, this lateral face of the carpellary margins has been mistaken for ventral surface of the carpel, and on that account the placentae are described as laminar instead of marginal. That this is so seems to be borne out by a consideration of the orientation of the ventral bundles of carpels and of the funiculi of ovules. It is common knowledge that in a carpel, as also in a foliage leaf, the *ventral (marginal) bundle in transverse section always stands parallel to the lateral face, xylem and phloem being in line with it, and at right angles to the ventral surface. The funiculi of ovules also show the same orientation* (*cf.* Text-Figs. 22-24). These features, which have been observed by the author in a large number of families including Ranunculaceae (Text-Figs. 1-9), Anonaceae, Magnoliaceae (Text-Figs. 10-11), Rosaceae, Crassulaceae, Leguminosae (Text-Figs. 12-16), etc., appear to be sound architectural criteria for distinguishing the *lateral face* from the *ventral surface*.

If we apply these tests to the illustrations of Periasamy and Swamy (1956), Bailey and Nast (1943) and Bailey and Smith (1942) we find that the surface in question is actually the lateral face of the carpellary margins as the ventral bundle stands parallel to it and the funiculus in line with it rather than at right angles, as it is to the ventral surface. The condition in *Cananga odorata* is very clear in so far as the orientation of the ventral bundles and the ovules is concerned (*cf.* Text-Fig. 17). The same is the condition in certain species of *Drimys* (Text-Fig. 18). In *Degeneria*, however, the lateral face of the carpellary



TEXT-FIGS. 1-5. T.S. of carpel of *Caltha palustris* from base upward, the lateral faces being closely appressed.

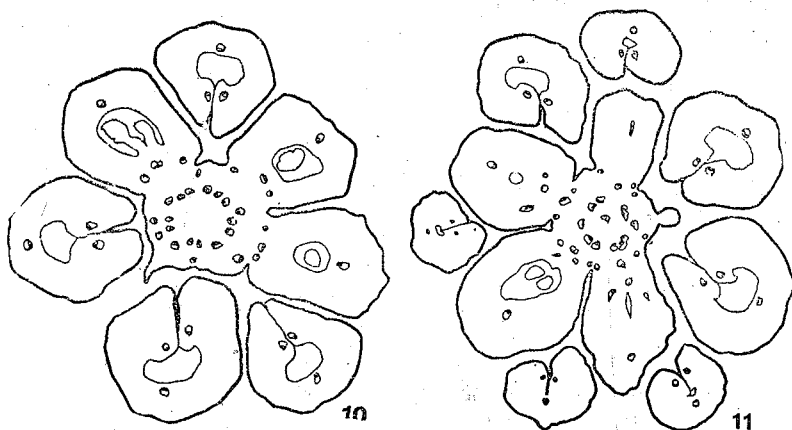


TEXT-FIGS. 6-9. T.S. of carpel of *Paeonia emodi* from base upward. Note the ventral bundles oriented parallel to the surface of the lateral face.

margins has become rather extensive and tends to flare apart externally forming a crest-shaped stigma (Text-Fig. 19). But there is little doubt that the situation is basically the same as in the last two species. Thus by accepting the concept of *lateral face* the ovules in all these cases can be interpreted as borne marginally and not superficially as suggested by the authors of the conduplicate concept.

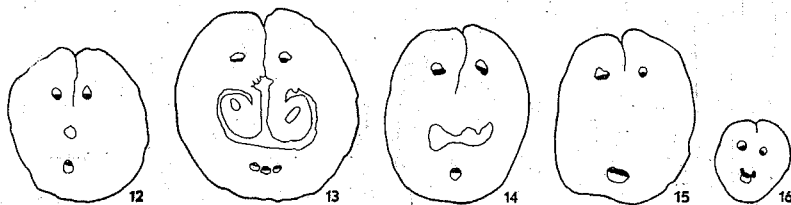
Vascularization of ovules.—As a rule, ovules receive their vascular supply from the ventral bundles or their fusion products, the placental strands (see Puri, 1952). Supporters of the classical concept of the carpel consider it as an important structural feature which ordinarily indicates the marginal (or sub-marginal) position of the placentae. In some cases, however, as in certain species of the Winteraceae (Bailey and Nast, 1943), Nymphaeaceae (Saunders, 1936), etc., dorsal bundles also have been known to contribute ovular traces. This has been cited as an evidence supporting the contention that the placentae are superficial on the ventral side and not marginal. True that in some cases as in the Nymphaeaceae, Butomaceae, etc., placentation is laminar rather than marginal and that the supporters of the classical concept of the carpel find it difficult to offer a satisfactory explanation

of it (see Puri, 1952; Parkin, 1955). But, as has already been stated, this fact does not lend any support whatsoever to *conduplicate folding* of the carpel.



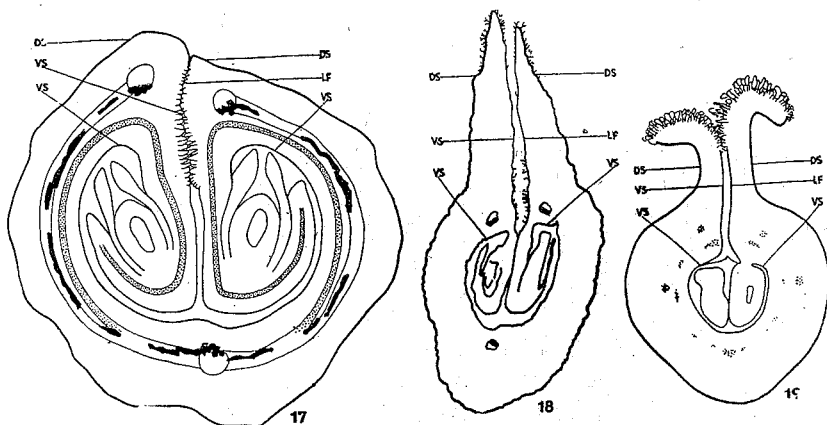
TEXT-FIGS. 10-11. T.S. of young gynoecium of *Michelia* sp. from base upward. The 'solid' style in the lower side in Fig. 11 gives the false impression of conduplicate folding.

Periasamy and Swamy (1956) have brought out a very interesting situation in *Cananga odorata* where although the ventral bundles occur very close to the placentae yet they do not furnish any ovular traces directly. It is, on the other hand, the dorsal bundle, situated quite far away on the opposite side, that gives off branches which divide far to furnish ovular traces. This means that in this species ovules receive their vascular supply from bundles farther away from them and not from those which are nearer to them. Such a situation renders the vascular bundles obviously ineffective, unless, of course, we believe in migration of the ovules from dorsal position to marginal position, in determining the position of the ovules, for even if the ovules were marginal they would still get their vascular supply from the dorsal bundle irrespective of their position.



TEXT-FIGS. 12-16. T.S. of carpel of *Acacia arabica* from base upward showing orientation of the ventral bundles and the ovules.

The form of young carpels, carpelloses and styles.—In some cases very young carpels, carpelloses and styles, in transverse sections, appear to assume a form which is very similar to conduplicate folding. All such cases have been used to support the conduplicate concept. It is stated, for instance, that "During the earlier stages of the ontogenetic development of primitive carpels (as of conduplicate leaves) the sides of the folded lamina, as seen in transverse sections, are approximately parallel" (Bailey and Swamy, 1951). It is also asserted that "in the sterile carpels of male flowers of Lardizabalaceae and other families this unmodified conduplicate form may be retained at anthesis." Further on, certain styles, in transverse section, are also described to show conduplicate folding.

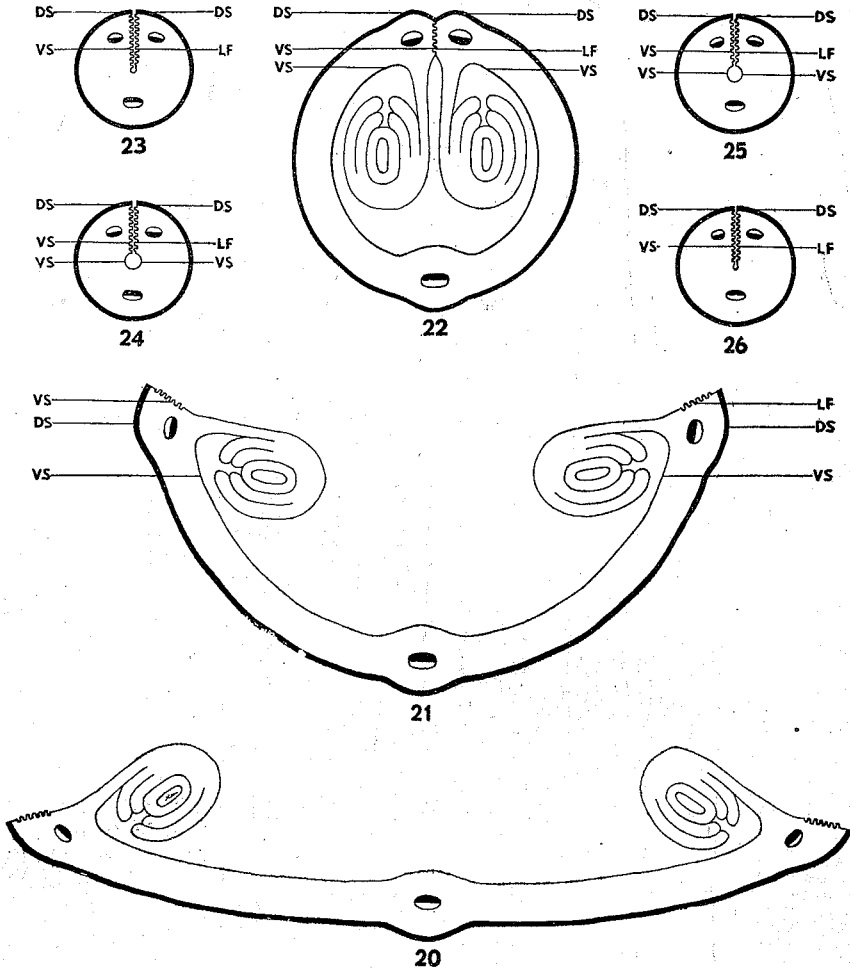


TEXT-FIG. 17-19. T.S. of carpel of *Cananga odorata* (modified after Periasamy and Swamy, 1956). Fig. 18. Same of *Drimys granadensis* (modified after Bailey and Nast, 1943). Fig. 19. Same of *Degeneria vitiensis* (modified after Bailey and Smith, 1942). Their explanation according to the present author is given on the right and that according to conduplicate concept on the left.

(DS = Dorsal surface; VS = Ventral surface; LF = Lateral face.)

The present author is inclined to think that these instances can be interpreted in a different way. It appears to him that these are cases in which the *functional* ventral surface which encloses the locule has not yet developed, as in very young carpels and carpelloses (cf. Fig. 23), or it has become more or less obliterated along with the locule, as in 'solid' styles (Text-Fig. 26). What has been interpreted as ventral surface in such cases is, according to the present author, the lateral face of the carpellary margins which have been brought together as a result of *involution* (cf. Text-Figs. 20-22 and 24-25). Such a suggestion, beside getting support from the orientation of the ventral bundles, is also borne out by the fact that the carpel and all its parts, as a general rule, follow a centripetal mode of development. In a young primordium of a closed carpel the first thing to differentiate is the dorsal surface covering a peg-like outgrowth, then the lateral faces of the carpellary margins and finally the inner ventral surface

with placentae and ovules. Such a sequence of events is very clearly seen in the numerous photomicrographs of cross-sections of young carpels reproduced by Grégoire (1938). Illustrations of Tepfer (1953), Periasamy and Swamy (1956) and Tucker (1959) also show the same thing, although these authors have interpreted them differently.



TEXT-FIGS. 20-26. Schematic representation to illustrate the difference of opinion between the present author (right side legend) and the supporters of conduplicate concept (left side legend). Fig. 23. Diagrammatic representation of a T.S. of young carpel in 'solid' state showing differentiation of lateral face. Fig. 24. Shows a later stage of the same with differentiation of locule. Figs. 25-26. Diagrammatic representation of transverse sections showing solidification of style. The appearances in Figs. 23 and 26 have been erroneously interpreted as representing conduplicate folding, the condition actually having been obtained through involution and solidification. In Text-Figs. 23-24 young and old stages have been overlapped together for convenience.

(DS = Dorsal surface; VS = Ventral surface; LF = Lateral face.)

Similarly in a sterile carpel, if there is no locule, and consequently no functional ventral surface, the adjacent lateral faces of the carpellary margins, if they are free, give the false appearance of conduplicate folding. Styles also may present the same deceptive appearance in transverse section after they have lost the locule and the functional ventral surface (Text-Fig. 26). Like a very young carpel or a carpellode they are solid inasmuch as they lack locules and the functional ventral surface. The occurrence of solid¹ young carpels, solid¹ carpellodes and solid¹ styles, therefore, does not lend any support to conduplicate folding, rather it supports the concept of involute folding of the carpellary margins.

More recently Periasamy and Swamy (1956) have cited some ontogenetic evidence in support of the conduplicate concept. This evidence in our understanding is conditioned by a basic assumption that the margins represent the last products of the marginal meristem. While this is largely so it is not all truth, for in cases where the margins are thick and well developed certain parts of them, particularly their outer edges, may show marginal activity for longer periods. Obviously these outer edges will be the last products of the marginal meristems and they are not equal to the whole margins.

Carpel primordium of *Cananga odorata*, according to Periasamy and Swamy, arises as a peg-like projection which appears as a solid structure in transverse section. Somewhat later, marked activity of the two masses of marginal meristems along the adaxial side "brings about the formation of a median longitudinal furrow" which deepens further. This stage, which is marked by the cessation of activity of the marginal meristem, is believed to indicate completion of laminal differentiation of the carpel. Since this is attained before the inception of placental ridges, it is asserted that it rules out any suggestion of involution of carpellary margins.

The present author believes that in these early stages the lateral faces of the carpellary margins have been misinterpreted as ventral surface of the carpel. The longitudinal furrow referred to above is actually formed by these lateral faces only and not by adaxial (ventral) surface of the carpel as is suggested by Periasamy and Swamy. These have been brought together through the so-called pylogenetic involution. The orientation of the ventral bundles and of the funiculi of the ovules bear strong testimony to such an inference. Thus the ontogenetic data recorded by Periasamy and Swamy appear to be satisfactorily explained in terms of the classical concept and there appears to be no necessity of propounding a new concept.

A natural corollary of the conduplicate concept is that the primitive stigma is believed to be crest-shaped extending laterally along the whole length of the ovary as in *Drimys piperita*. The present author is inclined

¹ This term refers to the condition lacking locule. Miss E. R. Saunders used the same expression in a different sense.

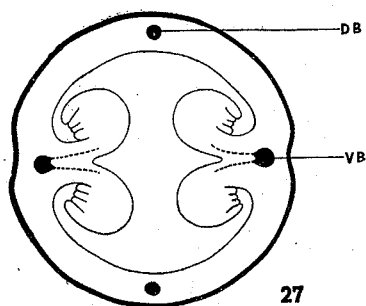
to suggest that in the primitive Ranales there might have been several attempts, in different directions, towards the formation of a stigma for receiving the pollen. Only one of these attempts, which resulted in a terminal stigma, was successful, while the others must have been more or less abortive. One such abortive attempt, if the author be permitted to indulge in such a speculation, may have been towards the formation of a crest-shaped stigma. Here the lateral faces of the carpellary margins might have extended outward quite extensively. This appears to be a more plausible interpretation of the conditions seen in *Degeneria*, *Drimys* and others, and following this the crest-shaped stigma in these species no longer remains a primitive structure but it represents the culmination of an evolutionary line that perhaps ended blindly, being apparently not very successful.

This brief analysis of the conduplicate concept reveals that the case of conduplicate folding is far from being proved. The data used to support this can still be explained, and perhaps more satisfactorily, on the basis of the classical concept of the carpel. Besides, a carpel is essentially an ovule-bearing organ and it is difficult for us to visualize how such a structure could show conduplicate folding in its ontogeny, unless of course we assume that ovule-bearing for carpels is a secondary innovation. In fact we cannot justifiably designate the structure as carpel before the inception of ovule.

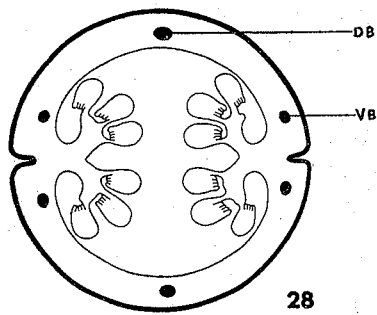
Regarding laminar placentation, it has been generally admitted that it occurs in a few cases, e.g., Nymphaeaceae, Butomaceae, etc., and that it has not been satisfactorily explained so far by the supporters of the classical concept (cf. Parkin, 1955). But the cases cited by the exponents of the conduplicate concept do not, in the opinion of the author, conform to this type. *Degeneria*, *Drimys*, *Cananga*, etc., all seem to have marginally attached ovules, and have already been satisfactorily explained on the basis of the classical concept of carpel. In these cases the ovules appear to be superficial only because the surface representing the thickness of the carpellary margins has been mis-interpreted as the ventral surface of the carpel.

As pointed out earlier, the supporters of the classical concept do not have any clear insight into superficial placentation. The present author has, however, suggested tentatively that it may be a function of unequal extension of the ventral surface of the carpellary margins and that of the rest of the carpellary leaf (Puri, 1960). Such an explanation gets support from the condition prevalent in certain members of the Gentianaceae, Orobanchaceae, etc., where half-placentae separate apart from their counterparts due to extension of the intervening regions of the carpellary margins (Text-Figs. 27-32). Thus conceived the superficial placentation renders itself easily explicable.

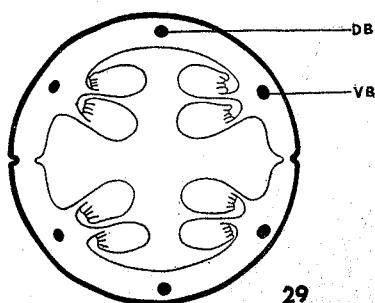
Professor W. Troll and his co-workers have brought to bear voluminous literature on the morphology of the carpel. Their work (Troll, 1939; Sprotte, 1940; etc.), is essentially ontogenetic and recognizes three forms of carpels: (1) *peltate* carpels with *manifest* peltation;



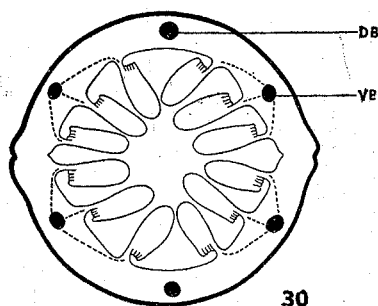
L. CRISTATUM



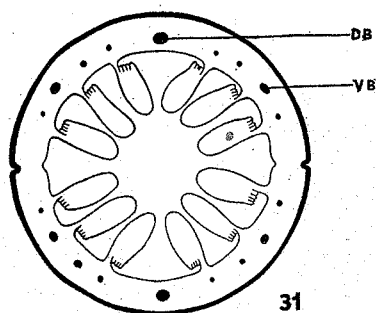
E. RAMOSISSIMA



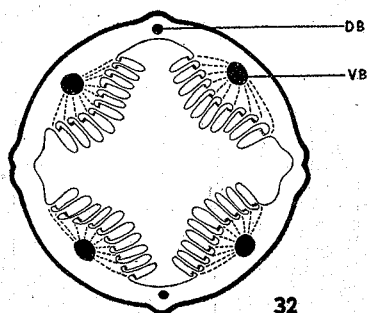
S. PANICULATA



G. PEDECILLATA



G. APRICA



G. CONTORTA

TEXT-FIGS. 27-32. T.S. of ovaries of certain genera (*Limnanthemum*, *Erythraea*, *Swertia* and *Gentiana*) of the gentianaceae showing gradual separation of half-placentae from their counterparts. By imagining an excessive extension of the marginal

regions that are fertile, and non-extension of the midrib regions that are sterile, one can visualize how the condition of superficial placentation could have been obtained.

(DB = Dorsal Bundle; VS = Ventral strand.)

(2) those with *latent* peltation and (3) those without any peltation or *epeltate*.

Carpels with manifest peltation have long stalks and ascidiform lamina whose free margins bear stigmatic papillae almost to the base (e.g., *Thalictrum*). Like the petiole, the stalk has unifacial anatomy and develops in ontogeny after the upper part of the lamina has appeared. The transition zone between the stalk and the lamina develops into what has been called the "cross-zone" (Querzone), which also takes part in the formation of the ascidium and in bearing ovules.

Carpels with latent peltation are comparable to leaves which show peltation in embryonic condition but not at maturity. A stalk may be present as in *Eranthus* or lacking, as in *Consolida ajacis* which has sessile carpels.

The epeltate carpels are characterized by complete absence of peltation at any stage of their development. They are horse-shoe-shaped from the very beginning and do not show any fusion of their margins at the base. They are believed to have been derived from peltate carpels through suppression of the "cross-zone" and the stalk.

Professor Troll and his school consider that in the mode of initiation, development, location and vasculature the carpels are essentially similar to foliage leaves. Their approach (*Gestalt*, as it is commonly known) to carpel morphology is inclusive, rather than exclusive, with the classical concept. The only difference, as we see it, is that they go only so far as their ontogenetic observations take them. In other words they are more realistic and less idealistic than a classical morphologist who goes further beyond to visualize to understand a peltate structure in terms of his *type* to which all the different forms are referable.

Thus conceived the involute carpels and the peltate carpels are not different types but different forms of the same type representing different lines of specialization. Just as a peltate leaf can be visualized in terms of an ordinary leaf, so also a peltate carpel.

An apparently very powerful attack on the classical concept of angiosperm carpel comes from Grégoire (1938) who asserts that the foliage leaf and the carpel are two morphologically irreducible categories or two distinct morphological types which are fundamentally different from one another. His view, which has been described as *sui generis* view, has been the subject of several excellent reviews during recent years (see Tepfer, 1953; Joshi, 1947; and the work of Professor Troll and his school). Without going into details of the subject, therefore, it may be pointed out that Grégoire was rather hasty in his conclusion and overemphasized the differences that he observed in

the morphogenesis of leaf and carpel. These differences according to most morphologists are differences of degree rather than of kind and are explicable in terms of their functional requirements.

The relationship between the carpel and the ovule is perhaps a most controversial aspect of carpel morphology. According to the classical concept the ovule is considered as a part and parcel of the carpel, being borne on its margin. But ever since the time of Schleiden (1849) someone has always believed that the ovules are axial structures and that the carpels just form sterile envelopes for them (*e.g.*, Hagerup, 1938, 1939; Barnard, 1957 *a*, 1957 *b*, 1958; Moeliono, 1959; etc.). Free central and basal placentations seem to fit in well with such a concept. But an obvious difficulty is experienced in dealing with parietal placentation. Hence some authors (*e.g.*, Lam, 1948) recognize both axial (Stachyospor) and carpellary (Phyllospor) ovules. Some others (*e.g.*, Hagerup, 1939) have explained the parietal placentation as a condition in which the central axial column bearing ovules splits into a number of segments that become fused parietally with the ovary wall, much in the same manner as the epipetalous stamens. Apparently Hagerup does not admit of any phyllosporous condition.

This view of treating the ovule as an independent structure does not get any support from anatomy. The placenta on which the ovules are borne is invariably a double structure, being composed of two halves (*see* Puri, 1952)—a fact borne out by its often clefted nature, double vascular supply and orientation of its ovules in two opposite directions (*see* Text-Figs. 27–32). If the placenta were equivalent to a stamen it should not have been a double structure.

In a brief but very thought-provoking article Fagerlind (1958) has focused pointed attention on this problem. I recognize with him the limitations of ontogenetic studies but I do not see any equivalence between the primordia of a carpel and its associated ovule on the one hand and that of a foliage leaf and its axillant branch on the other. No doubt in longitudinal sections, with which Fagerlind is dealing, the primordia of an ovule and of a vegetative axillary branch look very much alike. But it is not difficult to see that the ovule is seldom situated in a truly axillant position—opposite the midrib; most frequently in open carpels with parietal placentation it corresponds in position with the carpellary margin. In closed carpels too its position is quite different from that of an axillant branch. So I do not see much in common between the ovule-bearing placenta of angiosperm and an axillary branch of a vegetative shoot or for that matter the ovuliferous scale of gymnosperms. The position of the placenta, like its anatomy, is better explained on the basis of the classical concept.

Thus broadly speaking the classical concept of the angiosperm carpel still holds good and serves as a 'useful instrument of description'. It has the advantage of being simple and yet applicable to all the groups of angiosperms. As long as facts can be explained on this basis we would not like to accept any other interpretation.

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