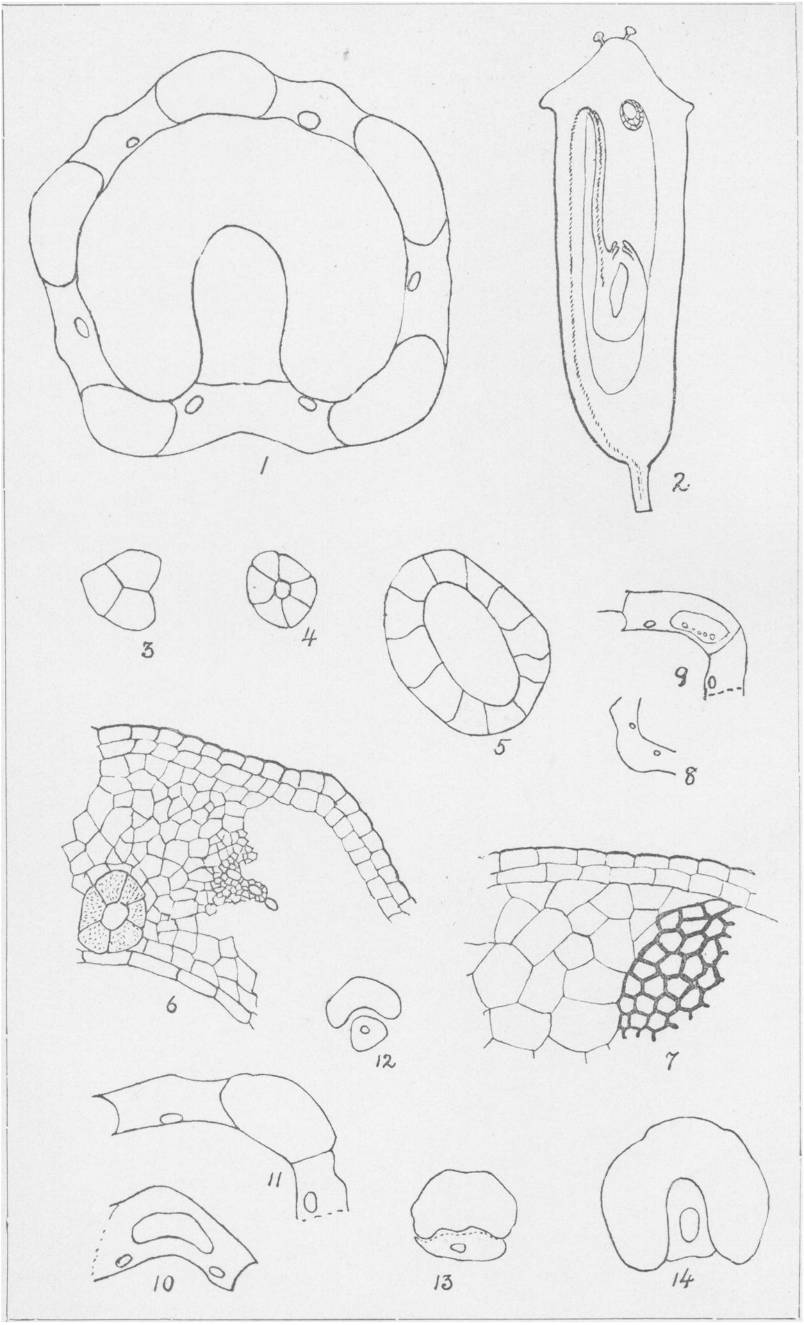

COULTER and ROSE on DEVELOPMENT OF THE UMBELLIFER FRUIT.

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Development of the Umbellifer Fruit.[1]

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(WITH PLATE XIV.)

In no family of plants does the fruit furnish more certain diagnostic characters than in the Umbelliferæ. So definite are they that the fruit alone can be made to determine the genus, and in most cases the species, while in every case it is an essential part of the description. This indicates at once an unusual amount of differentiation in the fruit structures, and a great diversity in its display. During the past year we have been making a critical examination of all our Umbelliferæ east of the 100th meridian, and this has directed our special attention to the minute structure of the fruit of all our species. This study has shown that while the grouping of these structures is very diverse, and hence available for diagnostic purposes, the structures themselves are simple and few in number.

It was a matter of interest to study the development of these peculiar structures, and for this purpose the common Chærophyllum procumbens was selected as a type, as its fruit contains all the structures found in the family. Beginning with ovary wall composed of undifferentiated parenchyma, supported by simple fibro-vascular elements, the changes wrought in the maturing ovary and then in the ripening fruit were traced.

A description of the structure of the mature fruit of Umbellifers in general will make plainer the questions to be answered by a study of its development. The two carpels face each other, and are in contact at first by their commissural or ventral faces, but eventually separate. The fruit is compressed laterally (at right angles to the plane of the commissural faces) or dorsally (parallel with the commissural plane), or not at all. As the two carpels are but repetitions of each other, a description of structure may be confined to a single one. The surface of the carpel is usually marked by five ribs or wings longitudinally placed. The two nearest the commissure are the laterals; a single dorsal one occurs on

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the back of the carpel, while the pair between the dorsal and the laterals are the intermediates. In addition to these five primary ribs or wings secondary ones may appear (as in Hydrocotyle Asiatica), and even become more prominent than the primary ones (as in Daucus and Trepocarpus); or occasionally even all external indications of ribs may be lacking (as in Sanicula). The presence of these ribs or wings, their varying size and structure, furnish good diagnostic characters. At the summit of each carpel a stylopodium may be developed, of various appearance, from prominently thick conical to a flat or depressed cushion.

The general structure of the pericarp wall well represents the typical leaf structure, with under and upper (that is, outer and inner) epidermal layers bounding a more or less developed mesophyll (figs. 6, 7). It is in the mesophyll region that the characteristic fruit structures are developed. The constant occurrence in the outer epidermal region of the two distinct layers of epidermal cells suggests that the outer layer represents the connate calyx, while the inner is the true epidermis of the pericarp. The mesophyll region of the pericarp is naturally separated into three structures: (1) oil-ducts, (2) strengthening cells, and (3) undifferentiated parenchyma.

I. Oil-ducts.—These occur in varying number, size and position in the different genera, and are of such constancy as to furnish most valuable characters. By far the most common position for oil-ducts is in the intervals between the ribs, where they occur singly or in groups. In this position they may occur close against the inner epidermal layer, or centrally in the pericarp section, while in Cryptotænia and Erigenia they seem to be developed in the inner epidermal layer itself. In Æthusa, Cœlopleurum and Cryptotænia oil-ducts occur both in the intervals and beneath the ribs. In some cases, as in Polytænia, there are two sets of oil-ducts, one forming almost a continuous layer about the seed-cavity, the other composed of smaller ducts, and scattered through the very thick pericarp. In Zizia there are also smaller accessory ducts in the ribs. In Conium there is no development of oil-ducts, but the whole inner epidermal layer of the pericarp becomes a secreting layer. In Hydrocotyle, on the other hand, in the absence of oil-ducts groups of secreting cells occur just beneath the outer epidermis of the pericarp, and in some species eventually break through it, forming superficial oil vesicles. Anthriscus and some Bupleurums have neither oil-ducts nor secreting cells. In Osmorhiza the mature fruit usually gives no trace of oil-ducts, while the immature fruit may show groups of four to six oil-ducts in the intervals and one to three in the ribs themselves. The obliteration of oil-ducts on approach to maturity would seem to make them represent aborted organs in this case, and may account for the discrepancy of opinion concerning the oil-ducts of certain genera. It is an interesting fact that this suppression of oil-ducts seems to involve the formation of an oily layer. In Osmorhiza the mature fruit has an oily layer about the seed, a region occupied in the immature fruit by a distinct line of oil-ducts. In Hydrocotyle, however, the isolated groups of secreting cells are such as always precede the formation of oil-ducts. In Hydrocotyle, therefore, the oil-ducts could be called rudimentary; in most Umbellifers they are oil-ducts proper; in Conium a secreting layer has been developed; while the development of the Osmorhiza fruit gives us distinctly all three phases. Hence, to summarize: (1) most genera have distinctly developed oil-ducts, variously placed, (2) a few have a layer of secreting cells, (3) some have groups of secreting cells, and (4) others have neither oil-ducts nor secreting cells, in fact, without any representation of this one of the three structures of the mesophyll.

II. Strengthening cells.—Under this name we would define certain groups of cells, which are unlike enough in structure, but seem to serve the common purpose of strengthening the pericarp wall or its ribs. They usually occur beneath each rib, and are normally developed about the simple fibro-vascular elements of the pericarp wall (fig. 6). These fibro-vascular elements may eventually become obliterated. The group of strengthening cells may consist of fibrous tissue, sclerenchyma, sclerenchymatous parenchyma, or small-celled parenchyma. It may be well marked off from the surrounding tissues, as in the distinct thick-walled groups of Osmorhiza, Cryptotænia, Conium and Chærophyllum (figs. 1 and 7); or it may gradually merge into the surrounding tissue, as in Angelica, Thaspium, etc. In Hydrocotyle, Pastinaca and Heracleum the strengthening cells are developed in a broad continuous band about the seed-cavity; while in Sanicula, Conioselinum and Æthusa they seem to be entirely wanting. In the last named genus they may be found in the very tips of the prominent ribs, the position usually held by strengthening cells being occupied by large and loose parenchyma, the other structures remaining normal. Strengthening cells are thus unlike in elements and position, are in groups of varying size and distinctness, or in bands, or may be wanting entirely. From these facts important characters may be obtained for generic grouping.

III. UNDIFFERENTIATED PARENCHYMA.—This has merely the negative character of not being transformed into either strengthening or secreting cells. Its abundance is dependent upon the development of the strengthening cells. It will be seen, however, that although it furnishes no diagnostic characters, it is probably most concerned in the growth of the pericarp.

Each carpel primarily contains two ovules, one of which soon becomes aborted (fig. 2), although it is developed sufficiently to display its nucellus and integuments, as well as its anatropous character. The other ovule eventually occupies the whole space of the ovarian cavity.

The fibro-vascular connection of the ovules with the plant axis is as follows: A fibro-vascular bundle enters each carpel at its base, thus making it a lateral out-growth from the axis, while the axis itself continues its growth in the carpophore. The carpellary bundle almost at once subdivides into five branches, and these branches ascend the carpellary wall beneath the five primary ribs.

The two lateral bundles (that is, those beneath the lateral ribs) are the largest, as they contain the fibro-vascular elements to be distributed to the ovules. These lateral bundles pass in the carpellary wall to the very summit of the carpel, and then send a branch inwards and downwards into the funiculus of the anatropous ovule (fig. 2). The remaining elements of the fibro-vascular bundle pass on to the floral organs and stylopodium. It will be seen that in this case, as in Compositæ, the ovules are lateral outgrowths. A point or two in the development of the ovule may be mentioned in this connection. At first both ovules lie at the summit of the ovarian cavity, but soon, by the development of the funiculus, one is thrust toward the bottom, with the micropyle near the center of the cavity (fig. 2). It is in this position that the pollen tubes are seen to enter the micropyle, and subsequently the ovule develops so as to fill the ovarian cavity. The aborted ovule is retained at the summit of the cavity, its funiculus never developing, and its micropyle out of reach of the pollen-tubes, even if its nucellar structures were developed to receive them.

To recur now to the mature seed, it will be found to consist mainly of a much developed embryo-sac, filled with endosperm and a small embryo. The embryo-sac never entirely replaces the nucellus, more or less of the nucellar tissues being found on the commissural side, either pressed against the flat or concave face of the embryo-sac or embraced in its infolding (figs. 12, 13, 14). Important characters have been obtained from the commissural face of the seed, based upon the fact that it may be convex, plane, concave, or more or less involute. Great care should be exercised, however, to obtain seed of perfect maturity, or a comparison on this basis will amount to nothing. All seeds at first have a convex or plane face, and the amount of concavity or infolding will depend upon the development of the embryo-sac. In some cases the embryo-sac, instead of developing uniformly, develops strongly towards the commissure on the two sides, resulting in a concave or involute seed-face. This variation may occur in the mature fruits of a single species (as in Eulophus), so that there may be found plane or concave seed-faces in one and the same plant.

Having described the structures to be found in the mature fruit in general, it remains to describe the method of their development in Chærophyllum procumbens.

I. Development of oil-ducts.—In very young buds groups of 3 or 4 parenchyma cells of the pericarp, next the inner epidermis, begin to be set apart for the formation of oil-ducts (fig. 3). The first indication of this is in the fact that they become secreting cells, and are discolored by the characteristic oily contents, and also become larger than the surrounding parenchyma cells. The 3 or 4 secreting cells then begin to divide radially, so that, at about the time of anthesis, the resulting intercellular space becomes an oil-duct of small caliber, with 6 to 8 secreting cells (fig. 4).

This radial division continues as the fruit matures, thus gradually enlarging the caliber of the duct, until it reaches its full size, with a dozen or so secreting cells (fig. 5). The ducts are thus enlarged intercellular spaces, developed by the radial division of the surrounding secreting cells, and simply act as reservoirs.

In Hydrocotyle (in which there are only groups of secreting cells and no ducts developed) the absence of ducts seems to be explained by the lack of power of radial division in the secreting cells. In Osmorhiza this power is also poorly developed, so that while the ducts are at first outlined, they are presently encroached upon and obliterated by the development of contiguous cells, thus forming a continuous oily layer composed of obliterated ducts and intervening secreting cells. In Conium no ducts are developed, because groups of cells are not set apart as secreting cells, but only a single layer of cells, and there can thus be no development of intercellular spaces, although the power of radial division is retained. Hence Hydrocotyle has no oil-ducts because its secreting cells lack the power of radial division; Conium has none because its secreting cells are in a plane instead of in groups; while most Umbellifers have oil-ducts because their secreting cells are in groups, and also have the power of radial division. The only other phase is the entire absence of secreting cells, as in Anthriscus and certain Bupleurums.

II. Development of strengthening cells.—In young buds there is no setting apart of this region from the ordinary parenchyma of the pericarp wall (fig. 8). Upon approaching anthesis, however, the parenchyma cells surrounding each fibro-vascular bundle sub-divide (fig. 9), and at anthesis quite a distinct group of small parenchyma cells is discovered beneath each rib (fig. 10). This comparatively small size is due not only to cell division and moderate growth but also to the strong growth of the surrounding undifferentiated parenchyma. While the region is indicated before anthesis it does not become really a region of strengthening cells until the development of the fruit. It is then that the walls begin to thicken, until at maturity a group of strengthening cells is composed of firm, heavy-walled tissue (fig. 7). The contained fibro-vascular elements are encroached upon, and for the most part obliterated, as they are really functionless after anthesis. This differentiation proceeds centrifugally from the fibro-vascular elements as a center, at first a comparatively small area being included. The surrounding parenchyma is gradually invaded, until in some cases the whole thickness of the pericarp wall is concerned (figs. 1 and 11). The amount of primary parenchyma transformed into strengthening cells varies widely. In Chærophyllum this structure reaches probably its maximum development, occupying the whole thickness of the pericarp wall, separating the undifferentiated parenchyma into isolated patches, and also being very thick-walled. In certain genera the strengthening-cell groups of the mature fruit are in the same condition as those of Chærophyllum at anthesis, viz.: differing from the surrounding parenchyma only in smaller size, and never becoming thick-walled, as in Angelica. Continuous bands of strengthening cells, as in Hydrocotyle, are always developed next to the seed cavity, in the same position as the continuous secreting layers. Hence we find strengthening-cell structures developing in bands or groups, and when in groups they may become thick-walled or not. In certain genera this kind of differentiation is entirely lacking, while in Æthusa we find the anomalous feature of the strengthening-cell regions developing a large-celled and loose parenchyma.

III. Development of undifferentiated parenchyma.—This region, lying between the strengthening-cell groups, is chiefly concerned in the development of the pericarp wall in size. After anthesis there seems to be but little increase in the thickness of the pericarp wall, the growth being chiefly extension. This extension is effected by the radial division of the undifferentiated parenchyma cells, the amount of tangential cell division being comparatively small. The exception to this is found in ribs and wings, which represent regions of strong tangential cell division in the undifferentiated parenchyma.

In this way the three structures of the pericarp wall are built up, and in their endless, but simple and constant variations, we find a clew to the classification of a group of plants otherwise hopelessly confused.

Explanation of Plate XIV.—All the figures are from Chærophyllum procumbens Fig. 1, Cross section of mature carpel, showing large strengthening cell areas; small solitary oil-ducts in the intervals, two on the commissural side; and a deeply sulcate seed-face. Fig. 2, Longitudinal section of carpel at anthesis, showing abortive ovule; developing ovule thrust down into ovary cavity ready to receive pollen-tubes seen at summit of stylopodium, and which should have been represented as passing through the ovary cavity and entering the micropyle; and fibro-vascular connections of ovule. Figs. 3, 4 and 5, Development of the oil-duct. Fig. 6, Section of ovary wall at anthesis, showing beginning of a strengthening cell group about the simple fibro-vascular elements; a developing oil-duct; and inner and outer epidermal layers, the latter of two layers, probably indicating a connate calyx. Fig. 7, Mature strengthening cells, sharply marked off from surrounding parenchyma Figs. 8, 9, 10 and 11, Development of strengthening cell area, fig. 10 being taken at anthesis. Figs. 12, 13 and 14, Cross sections of developing seed.