Contributions to the Morphology and Physiology of Pulpy Fruits.

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With Plates **XXV** and **XXVI**.

NOTWITHSTANDING the activity which has, for more than half a century, been manifested in almost all departments of botanical research, the morphology and development of the pulp of succulent fruits still remains an almost untouched field, and the only writer¹ who, so far as I am aware, has dealt especially with this subject, has left very much to be desired as regards the completeness of his results.

Under the term *Pulp*, I include all the tissues, of whatever character, which become succulent in the mature fruit, for it is quite impossible to draw any clear distinction between those usually described as fleshy, as in the apple for instance, and those which are pulpy in the more common acceptation of the term, as in the grape; the one extreme passes quite gradually into the other.

The Botanists of the older school, in describing and classifying the different kinds of fruits, were guided chiefly by the characters presented by mature structures without reference in all cases to the precise origin of the various tissues, and hence it is that the present terminology, which has come down to us with hardly any material alteration, from the days of Mirbel and Jussieu, sometimes fails to convey correct impressions of individual fruits, although, regarded as a whole, its utility

¹ P. Lampe, Zur Kenntniss d. Baues u. d. Entwick. saftiger Früchte; Zeitschr. für Naturw. Halle, Bd. LIX.

[Annals of Botany, Vol. III. No. XI. August 1889.]

cannot be questioned. Still there does exist a number of fruits which do not correspond in all points to the definitions of any single group, but appear rather to share the peculiarities which characterise more than one class; and others, whilst they conform generally to certain types, are irregular in minor respects. Thus the fruit of *Daphne Mezereum* is commonly described as a berry—a term applied to that class of fruits whose succulent tissue is derived from the pericarp; but in the berry of *Daphne* not only is the pericarp fleshy, but also the outer integument of the seed, whilst the hard seed-coat is formed from the outer layer of cells of the inner integument. Instances of this kind might be multiplied, and in the course of a series of papers which I hope to publish on this subject, I shall have opportunities of describing some of the principal modifications which the various kinds of fruits may present.

It is a fact worthy of notice, that, whilst pulpy fruits are very common in certain natural orders, so much so as to constitute one of the ordinal characters, the morphological nature of the pulp itself may vary considerably within a very narrow circle of affinity. Amongst the British plants, the Caprifoliaceae afford perhaps the best examples of this fact; thus in *Lonicera Periclymenum* not only the pericarp and placenta become fleshy, but also the bracts and axis of the inflorescence; in the nearly allied *L. caprifolium*, however, the succulent tissue is derived from the placenta and pericarp alone. A further modification of the type as represented by *Lonicera* occurs in *Sambucus nigra*, in that here the pulp is reduced to the mesocarp, the internal layers of the pericarp being devoted to the formation of the stony endocarp, and the reduction is carried out with still greater completeness in *Cornus sanguinea*. Similar instances are also furnished by the orders Rosaceae and Urticaceae; but the above is sufficient to indicate the difficulty of arriving at a satisfactory classification of fruits whose chief distinctive feature is subject to so many variations which pass quite gradually one into the other. Of course the significance of

pulp is purely physiological, and hence more than one morphological member may be expected to be called into requisition to furnish it, just as the physiological organs of attachment and absorption may be represented by members other than roots in the true morphological sense of the word; and just as in the latter case, an accurate perception of the morphological nature of the organ which happens to function as a root-like body is indispensable, from a scientific and philosophical standpoint, to the formation of a correct appreciation of the body in question, so also in the case of the class of fruits under discussion: it is impossible that they can be properly understood unless the real nature of the pulp-forming tissue is clearly apprehended.

Besides the extreme case of the Honeysuckle, already mentioned, and the more common forms of berries and drupes, there are some plants, as the Rose and Strawberry, where the entire pulp is derived from the torus; in others the floral envelopes contribute the chief portion, as in *Hippophae* and *Morus*. In *Citrus* again it owes its presence to hairs which spring into the ovarian cavities, and which become distended with liquid. Another, and more irregular source of pulp is found in the aril, which makes its appearance after fertilization in some fruits: an example of this class is afforded by *Taxus*¹. Even in berries the relative parts played by the placenta and the pericarp show great variety in different plants. Thus in *Vitis* each furnishes about half, in *Solanum Dulcamara* the placenta, and in *Ligustrum vulgare* the pericarp, provides almost the whole pulp.

It is a point of some interest that considerable difference prevails amongst plants as to the time at which the characters which distinguish the mature fruit first come into prominence. Thus in *Hedera Helix* the main features are all apparent before the flower is over, subsequent changes consisting chiefly

¹ There is perhaps some doubt as to whether the structure commonly known as the aril in this plant should be really included under this name; but I have followed the ordinary usage as regards this case.

in extension and growth on the lines already laid down in the bud and flower, except in so far as the cell-secretions are concerned. In *Solanum Dulcamara* the characteristic structure is not reached until the fruit has attained to about one-third of its full size, and in *Rubus fruticosus* the peculiarities of the pulp do not become manifest until the time of maturity is approaching; the 'stone' of this fruit, as in others which possess this structure, is however formed very early, for reasons which will be considered later. It is not always possible to trace the cause of this variation, but there can be little doubt that it is to be sought for in the state of complexity and specialization which is finally reached, for these characters can have been acquired for the most part but comparatively recently; and so in accordance with general principles, they will be proportionately late in their appearance.

To pass on now to the special part of this work, I propose in this paper to deal only with three forms, taken purposely from plants of common occurrence, and which will illustrate some of the varieties which are found in the nature and formation of pulp; later on I shall have opportunity to speak of other anatomical and adaptive characters presented by numerous other forms.

Hedera Helix.—This plant, with its inferior ovary, furnishes an example of a fruit whose pulp is mainly derived from the tissue of the carpels, for though the torus is not altogether without a share in its formation, it plays but a subordinate part in this respect, as will be evident from what follows. If the flower-buds be examined at a time when the inflorescence is just emerging from the scaly bract, it will be seen that the four floral whorls are already laid down, and that the carpels stand at a lower level than the other three whorls. This is due to the fact that they are formed relatively late, and that the external members are early raised up by a zone of growth which is formed below the level of their insertions. The carpels appear as five protuberances within these, and their growth subsequently keeps pace with that of the outer part of the

flower, although, owing to abortion, some of them may remain as arrested forms, the place of these being filled up by the more fortunate survivors. In fact, the whole bud develops in essentially the same way as Goebel¹ has described for the epigynous flowers which he investigated. But from the very first, the tissue of the carpels is clearly marked off from the peripheral cells which owe their presence to the activity of the meristem just referred to, in that in these structures the cell-divisions occur irregularly and without any definite order, except in the few layers destined to form the parchment-like endocarp.

But though cell-division is comparatively irregular in the carpels, it is far otherwise in the four or five peripheral cell-layers which surround them, and which form the cup-like band from which the other floral structures arise. Here the succession of cell-divisions proceeds with great regularity, and chiefly in a direction transverse to the axis of growth, though radial divisions also occur with considerable frequency. So regularly are the transverse divisions formed, that in radial longitudinal sections the cells for a considerable distance can be referred to the original mother-cell (see Pl. XXV, Fig. 2), and form members of a filament somewhat resembling a confervoid alga. Transverse sections show that these filaments are arranged in a very orderly manner as concentric circles, each one cell in thickness (Pl. XXV, Figs. 4, 5). But in spite of the general regularity which the longitudinal and transverse arrangements of the cells exhibit, cases occur by no means unfrequently in which cells, or rather cell-filaments (if the expression may be permitted), do not all divide and grow at the same pace as their neighbours. Sometimes this results in a filament ceasing to elongate, while those in connection with it are still increasing in length, and then the lateral cohesion of the chains of cells with each other is sufficient at times to drag apart the cells of the row which has ceased to divide, and when this takes place the transverse line of

¹ Goebel, *Zur Entwick. d. Frunterständ. uchtknotten*, in *Bot. Zeit.* 1886.

separation is almost always at the junction of the ends of two older mother-cells, that is, of cells which have divided a number of times transversely, so as to have given rise to a number of daughter-cells. This fact has some bearing on the problems as to the nature of the causes which effect the separation of cells in general, and in this case the cause is probably to be looked for in the degeneration of the middle lamella, and this explains why the separation commonly occurs between the points of contact of older cells, since such degenerating changes have been longer in operation at these places. In Pl. XXV, Fig. 5, is seen an example of such a separation, and the appearance there represented is highly characteristic of all similar occurrences in this plant. A small drop of gelatinous-looking substance reaches from the tip of one cell to the other, exactly as one would expect on the explanation just advanced. But *Hedera* is not a very suitable object in which to study the phenomena of cell-separation, which is presented in a far clearer manner in *Crataegus Oxyacantha*. If half-ripe fruits of this plant be examined, the cell-walls are seen to be very thick, and even without staining a striking differentiation of the walls into layers is quite obvious. This is of such a nature that the portion of cell-wall which abuts on the cell-contents is clear and distinct, with shallow pits, and resembles that of ordinary parenchymatous elements; but the portion which lies between two contiguous cells is of a brownish colour, and resembles gum in some of its characters. It can hardly be termed mucilaginous, as it scarcely swells at all in water, though potash and strong acids cause a decided increase in bulk to take place. The whole layers of cell-wall are very clearly differentiated by staining with haematoxylin, Hanstein's violet or, best of all, with Schultz's solution. At a somewhat later stage irregular cracks appear in the gum-like middle lamella, and finally intercellular spaces of a large size are formed, and in many cases the slimy substance of the degenerating portion of the wall can be seen stretching across in strands which fuse with the mass lining the spaces (see Pl. XXV, Fig. 17). As degener-

ation proceeds, the cells of the pulp become rounded off, and only remain in contact at points to which the change has not extended. These spots are especially those which appear in younger fruits as pits, and the pit membrane resists the pressures tending to split it apart, and thus are produced the 'glove-finger'-like extensions of the walls of the cells at these places when the rest of the middle lamella around them is swelling in thickness as degeneration proceeds. The presence of these sound parts of the cell-wall is interesting, since, as will be seen later, essentially the same thing occurs in *Hedera*. The (now) free surfaces of the cells which bound the inter-cellular spaces are seen to be coated with a brown mass, which is somewhat rugose on the surface—exactly the appearance one would expect to find from the manner in which the cells become isolated.

It will be seen that while the final results, namely cell-separation, are the same both in *Hedera* and *Crataegus*, the latter differs from *Hedera* in the great completeness with which the whole process can be followed out. It is probable that the nature of the process is really identical in the two cases, only that in the latter plant the thinness of the walls makes accurate observation difficult. There is, however, in *Hedera* a true mucilaginous degeneration of the cell-wall, which occurs later, and which will be described in its proper place, mention being made of it here for the purpose of avoiding confusion, as its visible occurrence is subsequent to, and could not be traced as a condition of, cell-separation.

But there is a further cause of irregularity in the cell-arrangement of the peripheral layers of the fruit, and this cause consists, not in the arrest, but in the increased activity of growth in individual filaments. Hence, owing to the strong tendency of the other cells to preserve their chain-like arrangement, the growing cell-row pushes its end in between¹ the rows of already formed and still growing rows, and drives them apart. The intruding portions may either be the ends

¹ Cf. Krabbe, Das gleitende Wachstum b. d. Gewebebildung d. Gefäßpflanzen. 1886.

of a cell-chain, or they may arise by the lateral bulging-out of a cell, and the subsequent separation of the protruding portion, by a cell-wall. The new 'apex' just formed then grows independently (see Pl. XXV, Figs. 3, 6, 7) between the cell-rows on all sides of it. It may, however, be urged that the appearance which I have described is simply due to a tangential division extending through a number of cells or through one cell which has then grown *pari passu* with its mother-cells and as a twin filament, but this suggestion is shown to be inadequate by a study of a series of transverse sections in which such an occurrence is taking place (Pl. XXV, Figs. 4, 5). Moreover, I have been able to observe karyokinesis in the terminal cell of one of these intruding rows at an early stage in its formation, and at a time when the surrounding cells exhibited no evidence of continued growth. This observation is not, of course, to be regarded as very weighty by itself, but it is perhaps deserving of mention taken in connection with others, all tending to establish the same conclusion. Another argument in favour of the belief that the filaments are actually intrusive, is to be found in the fact that immediately in front of a cell-row of this character it is very common to find a small triangular splitting, just as would be caused by forcing a wedge of wood into a piece of timber in the direction of the grain (Pl. XXV, Fig. 7).

This intrusion of younger between older cell-rows is by no means restricted to the peripheral layers, it occurs also in the central tissue (Pl. XXV, Fig. 2), which forms the pith in the lower end of the flower, and indeed it is a feature by no means uncommonly to be met with in organs which are growing in any one direction in such a way as to ensure a rapid multiplication of cells in a straight line. Roots, for instance, and some stems, particularly of such plants as Selaginellas, show the phenomenon remarkably clearly. It is true that I have not succeeded in tracing an intercalated row beyond a short distance from its point of origin; this may be partly due to the sinuous course which such rows probably in all cases take, but in any case it is not likely that they reach

to any great distance, as the increasing pressure they would necessarily encounter would certainly prove a serious check to their progress. Still the fact of their occurrence is not without interest in connection with the so-called pseudo-parenchyma of fungi, and other tissues of a similar nature.

At the period when the pedicels of the separate flowers begin to lengthen, the compact mass of tissue of which the carpels are composed suffers a change in appearance, due to the extensive formation of intercellular spaces. Of course the carpels are not composed exclusively of parenchyma, for besides the vascular bundles, there are numerous secretion passages present which are similar to those found in the rest of the plant ; since, however, their presence does not materially influence or contribute to the pulp they may be dismissed from further consideration. I have already mentioned the regularity which characterises the cell-divisions taking place in the peripheral layers or rind of the fruit ; and it may be regarded as certain that to the rapid radial division, and consequent tangential extension, of this rind is due the early splitting apart of the internal cells of the young ovary. Certainly the cells referred to are subjected to a strain tending to make them occupy a larger space than they normally would do, for besides the fact that cell-multiplication is not very active as yet in this region, growth in size is also very limited, and yet the ovary as a whole is increasing very largely in bulk. The cellular tissue splits up, then, to allow of this increase, but it is rather a passive, than an active process like that in *Crataegus*, and the cell-walls are still very thin, no clear middle lamella being visible until specially looked for, nor have I as yet succeeded in tracing any connection between the splitting and a degeneration of the cell-wall in this inner mass of cells. But the walls are so exceedingly thin that it might easily escape even careful observation, and the formation of mucilage already hinted at, and which will shortly be described, renders it quite probable that such a connection does exist. The cells which eventually separate do not however become completely isolated, but remain united with each other by their ends, so as to form

contorted and convoluted ribands of one or more cells in thickness, which anastomose freely with each other, while their free ends project into the meshes of the rude mesh-work of intercellular spaces, of which they themselves form the boundaries.

The cell-rows which together constitute the rind remain united chiefly by their radial walls, and separation, when it occurs, is mainly restricted to the tangential walls. In the latter may be seen indications of the same process which I have described for *Crataegus*, and also for those cell-rows of the rind which are separating, as seen in longitudinal sections of flowers and young fruits. A well-developed middle lamella is commonly traceable before the commencement of the changes which ultimately result in the separation of the cell-rows (Pl. XXV, Fig. 10).

After the flower has withered, rapid multiplication of cells takes place in the vicinity of the ovaries whose ovules have been fertilized, and this is especially noticeable in the lax tissue of the carpels; any one cell may elongate in almost any direction, and then by division give rise to the rudiment of a fresh riband of cells, which grows in the meshes formed by the older cells. Sometimes single cells divide into four daughter-cells, each of which becomes a new centre of cell-formation, and indeed the whole process reminds one somewhat of the budding of yeast. Beautiful karyokinetic figures are seen during the process, showing the activity with which division is proceeding, and in this way the interior of the fruit again becomes more firm as the large production of fresh tissue takes place.

I have said nothing hitherto of the formation of the endocarp in this fruit. It is due to the three or four layers of cells which line the ovarian cavities, but it is very slightly developed, and it is perhaps best left for consideration in connection with other forms in which a greater degree of completeness is reached.

If the young fruits gathered about the end of January be examined, the cell-walls which bound the intercellular

spaces are found to be covered with a substance of mucilaginous or gelatinous nature, and which is obviously related to the cell-wall itself. The substance is very transparent and homogeneous, and may readily escape observation altogether unless staining reagents are employed, and these have to be used with some care, because if water be applied to the sections previous to staining, it rapidly swells up and disappears. Haematoxylin, Bismarck brown, and Hanstein's violet all gave fair results, but the two former reagents were by far the most satisfactory. If the section of material which has been preserved in alcohol be rapidly washed with water, and then stained with Kleinenberg's haematoxylin, the mucilage appears as a glairy substance lying in the intercellular spaces and around the edges of the section; but if the sections are stained at once without rinsing with water the mucilage is seen in its unswollen condition. In this state (e.g. after staining) it refuses to swell up, owing perhaps to the alum in the reagent, and the same is true of chromic acid material.

It is found either lining the cell-wall or aggregated in little drops, and in the latter state the drops most frequently occur at places where two cell-walls meet. As the fruit grows older the mucilage becomes more and more apparent, and when sections of alcohol material which is almost ripe are placed in water, a very rapid separation of the cell-layers is seen to take place, due to the expansion and swelling of the intercellular mucilage. It is best studied in alcohol material, since if fresh fruits are cut the protoplasm also issues from the cut cells and interferes with the observations, as it is itself of a glairy consistence, and is so abundant as to mask everything else in sections of younger fruits. It appeared possible that the entire mucilage might be derived from this source, but the contracted primordial utricles, which are present in alcohol material, showed no trace of the substance in their interior, nor was it present in the space left between them and their cell-walls. Still, the extremely sharp line of demarcation which exists between the non-swollen part of the cell-wall and its mucilaginous investment gives at first some support to the idea that

the latter might be of the nature of a secretion, which spreads over the free portions of the cell-walls which line the intercellular spaces. Reference, however, to *Crataegus* and other similar forms shows that this point has but little weight, and besides this, it is not likely that cells engaged in rapidly dividing would be also employed at the same time in actively secreting mucilage. Thus, although the actual steps resulting in its formation are difficult to follow, there can remain but little room for doubt that the substance in question owes its origin to degenerative changes which are going on in the outer layers of the cell-walls, and which only become evident at a period subsequent to the splitting apart of the cells, which results in the formation of the intercellular spaces referred to. And indeed it has already been pointed out that the cells of the interior of the fruit are obliged to split, in order to admit of the radial extension of the whole, since the peripheral cells divide, at first, in such a way as necessitates either such an expansion, or a throwing of the surface into folds, and in this way it is possible that the result may become manifest before the cause which effected it.

Whilst the mucilage is apparent at an early period it becomes far more pronounced as the time of maturity draws near. The number of cells of which the pulp is composed is at this time very large, but the riband-like arrangement is still easily discernible, especially near the periphery; in consequence, however, of the increase in the absolute size of the cells in the internal part of the fruit, the bands become forced into close juxtaposition, and the intercellular spaces form a proportionately smaller part of the entire volume of the fruit. Hence in sections taken through mature specimens the process of swelling can be readily followed out, as the addition of water to the preparation effects a great displacement of the cell-ribands, which were originally almost in contact.

The cell-contents do not present any features of striking interest as long as the fruit continues to grow in size. Chlorophyll is present, especially in the peripheral layers of cells, and

starch is also in some cases distinguishable, though only in very small quantities. Crystals of oxalate of lime are not uncommon, especially near the vascular bundles; but the most interesting of the cell-contents is the oil which is present in minute quantities in the protoplasm of all the cells. This substance is often only detected with difficulty until the fruit is ripe, but careful staining, especially with osmic acid, generally succeeds in making it apparent. As the fruits ripen, on the other hand, the volume of oil in the cells increases very largely; it forms aggregates of spherical drops of a considerable size, which are surrounded by a delicate pellicle of protoplasm, which serves to keep the several drops asunder. When it is being secreted at this late stage of the development of the fruit, it is seen to appear in the first instance as a number of excessively small brightly refracting globules, which are embedded in the substance¹ of the comparatively thin primordial utricle. The globules increase rapidly in size and run together so as to form larger and larger drops, though each drop is, at least temporarily, provided with a membrane which serves to separate it from the rest in its immediate vicinity. This limiting membrane must disappear between the points of contact of drops about to fuse, in much the same way as two soap bubbles behave when placed in such a position that their cavities are about to unite, for, although I have not actually seen the process in operation, it must occur, since the number of drops grow less as the actual size gets larger. But besides the increase in size caused by running together of the drops, there is the active process of secretion going on in the protoplasm, and by virtue of which its own substance is gradually used up. The larger drops now project into the cell vacuole and soon fill it, while the protoplasm only remains as a thin layer lining the cell-wall, and the now large oil drops. Addition of potash, especially on warming, causes the oil to run into

¹ Cf. Wakker, Studien ü. d. Inhaltskörper d. Pflanzenzelle; Prings. Jahrb. XIX. Bd. 1888. I have not been able to trace any structures resembling elaioplasts in *Hedera*, but it is perhaps a significant fact that the chlorophyll-granules are still intact during the oil-secretion.

one or two large globules, by effecting the disappearance of the membrane; no saponification takes place at all, the oil is quite unaltered by potash, even when treated with it for a considerable time. It is, however, easily dissolved by ether, chloroform, or turpentine, and from these solutions it may readily be recovered by distillation. Osmic acid stains it quickly, and proved a most useful reagent in aiding the watching of its formation, but fair results were also obtained by lengthy treatment with solutions of iodine.

The oil-forming tissue is found chiefly in the inner part of the fruit. The cells of the rind, though they contained it in small quantities, are for the most part filled with the red sap to which so many dark-coloured fruits owe their characteristic appearance. Still, these may also be regarded as forming, together with the carpels, the pulp of the fruit which is thus derived from the whole mass of the ovary, with the exception of the few cells which are devoted to form the soft parchment-like endocarp. I do not propose to deal with this structure here, but to reserve it until it is met with in a better developed form in other types. Still, although it is feebly represented, it has as much claim to regard, from a taxonomic standpoint, as that in *Sambucus* or *Prunus*; and I think it is a pity that all these fruits are not included under the common term drupe, instead of artificially restricting this term to a one-seeded form. For they all agree in the essential feature of the endocarp, and fall quite naturally into the same category, whereas under the present system both *Hedera* and *Sambucus* are removed from their obvious alliance with forms like *Prunus*, and placed in the same class with *Vitis* and *Daphne Mezereum*.

Rubus fruticosus.—This fruit gives us an example of the drupaceous type, in which a portion of the pericarp only is devoted to the formation of pulp, the remainder undergoing modification to enable it to meet other and special requirements. If the walls of the ovaries are examined in the young state, shortly before the unfolding of the flower-bud, the cells of the middle and outer regions are seen to be arranged in irregular radial rows, each containing about eight to ten cells.

Externally these are bounded by the epidermis, but internally they pass into an inner zone of tissue, which lines the cavity of the ovary, and which consists of very small cells which form a somewhat misty-looking layer. It is from the last-mentioned tissue that the stony endocarp is formed which renders the examination of all but very immature fruits a matter of considerable difficulty. The number of cells does not increase greatly, the divisions which do occur are mainly transverse to the long axis of the fruit; tangential divisions are very rare, except in the peripheral cells, which ultimately form the epicarp, although even here they are by no means of common occurrence.

As the drupes increase in size after the flower has withered, they are unable to expand equally in all directions owing to the mutual pressure consequent on their crowded condition, and hence each is broadest at its upper portion (Pl. XXV, Fig. 20). When differentiation begins in the pericarp, those cells which finally give rise to the endocarp are the first to become specialized. These cells consist of fibres so elongated that a chain of such fibres running round the fruit cavity resembles a segmented ring or hoop. Owing to the regularity with which the cells fit into one another, this appearance is rendered most strikingly prominent, and the whole of the interior of the ovary appears to be bounded by these 'rings,' which run in a transverse direction round it. Only a part of the endocarp, however, forms these transversal rings, the rest consists of fibres, also regularly arranged, but whose longest axis runs in a direction at right angles to that of the cells just described. The result of this arrangement is that the ovarian cavity is protected by a band of tissue, of which one half is fitted to stand strains and stresses in one direction, while the other half is equally well capable of resisting similar strains and stresses in a direction at right angles with the first. The regularity of the two systems is somewhat broken by subsequent changes due to growth, but the general formation is sufficiently obvious even in ripe fruits. The endocarp, when differentiated, rapidly increases in thickness in the way I have

already described for *Sambucus nigra*¹, only that here the 'slipping' takes place to a far greater extent, and the later addition, so remarkable in *Sambucus*, is entirely wanting in *Rubus*. Lignification sets in very early in the cells of the endocarp, and results in the conversion of the entire tissue into the well-known hard shell which encloses the seed of so many drupes. Markings of a pitted character may be detected in these fibres, whose walls thicken to such a degree as to almost obliterate the cell-lumen; but as we shall see later, many other fruits exhibit these markings in a state of much greater perfection.

At a stage subsequent to that at which the endocarp has become clearly recognisable, the character of the cells at the periphery of the fruit begins to change and the limits of the epicarp are defined. I have already mentioned the fact that exclusive of the endocarp, the cells are roughly arranged in radial rows, each containing about eight to ten cells. The outer four or five of these become gradually flattened radially, and consequently extended tangentially, whilst their walls also are thickened as the process of distortion takes place. The cells which are thus displaced from their originally regular position, form an interlocking mass of a very tough texture, and this mass represents the removeable skin which encloses the softer portions of the fruit. Internally the cells pass by a somewhat sudden transition into the pulp, which must now be considered. At the inner boundary of the epicarp, which consists, as I have said, of flattened elements, there is a layer of cells which are of an approximately isodiametric shape, and whose walls, unlike those of the cells of the epicarp, are exceedingly thin. This layer forms the outer boundary of the mesocarp or pulp proper.

As would be expected from the conditions under which the separate drupelets are placed, the mesocarp does not surround the endocarp as a layer of equal thickness throughout, but is developed to the greatest extent on the free portions where

¹ Ann. Bot. vol. ii. p. 389.

the pressure caused by mutual contact does not exist. The cells, two or three deep, which lie internally to the thin-walled elements above mentioned, undergo a remarkable change of shape shortly before the fruit reaches maturity. They suffer an enormous extension in the radial direction, so much so that they can be compared to nothing so well as to cylinders whose ends are rounded. Intercellular spaces make their appearance during this alteration which separates one cylindrical row from the others around it, and serve to bring out the striking individuality of these cells into yet sharper relief. It is owing to the presence of these cells, whose thin walls bear so small a proportion to the bulk of fluid which they contain, that the interior of the fruit appears to be filled with nothing but juice. If the walls had been a little thicker, and the cells greater in number and consequently smaller, a fruit would have been produced which would have occupied a position intermediate between such forms as the blackberry and the more fleshy types which are represented by members of the other end of the series.

The cylindrical cells pass quite abruptly into a tissue composed of small and crowded cells, which forms an ill-defined layer outside the endocarp. It is not easy to say whether they should also be referred to the mesocarp, and yet they certainly do not belong to the endocarp, but they form rather a neutral ground between these layers, and serve merely to establish continuity between the inner and middle zones of the fruit.

It is manifest that a considerable difference exists, both as regards the origin and mode of development of the pulp in the two cases we have hitherto considered; for whilst in *Heaera*, in addition to the carpels, the raised up portion of the torus also enters in part into its formation, in *Rubus* the whole is formed from a limited portion of the tissue of the carpels. Again, whilst in *Hedera* all the characters, apart from those which are the result of secretional activity, could be predicted from the structure of the bud, in *Rubus* it is not until the approach of maturity that the most striking features of the fruit

become visible. A further point worthy of note is the difference in the endocarp of the two plants, and while this perhaps finds its explanation partly in the fact that the ripe seeds of the blackberry require more protection than those of the ivy, I think this is by no means the whole explanation. If the mode of growth which prevails in the two cases be compared, it will be seen that they are fundamentally different. In *Rubus* the peripheral cells do not divide, or only to a slight extent, but suffer flattening by the expansion of the cells interior to them. The effect of this is of course to produce considerable pressure on the interior cells, and it is conceivable that this pressure might exert a prejudicial influence upon the delicate ovule which, but for the presence of the resistant endocarp, would be exposed to the full influence of this force of compression. As it is, however, owing to the remarkable manner in which growth takes place in the cells of the endocarp, the effect of such a pressure on the ovule is entirely obviated, and it is able to develop in a free and unconstrained manner. In *Hedera*, on the other hand, the cells of the rind are rapidly dividing, and, as we have seen, the internal tissue is unable to keep pace with the extension, and its cells are rent apart. Consequently the ovules in this plant are not in the least subjected to the action of a force like that obtaining in *Rubus*, and hence the early development of a means of protection would be superfluous. That the tensions and pressures really exist may be easily shown by cutting the fruit across and noticing the way in which curvatures take place. *Sambucus nigra* affords a particularly good example of a fruit whose ovule would require protection, since if a longitudinal section of moderate thickness be cut through the fruit when about half ripe, and if then the hoop which is formed by the endocarp be divided at one end, the free ends thus formed at once cross over each other and reduce the size of the fruit cavity.

Rubus Idaeus presents essentially the same structure as *R. fruticosus*, except that in this plant the epidermal cells grow out into long hairs.

Solanum Dulcamara.—In the fruit of this plant we meet with a case in which the pulp owes its origin to two sources, being derived partly from the wall of the superior ovary, and partly from the tissue of the placenta. The carpels at the time of flowering are somewhat thin structures, containing a number of vascular bundles which run at a distance of about eight cells from the epidermis, and even at this period there is a difference perceptible between the cells which lie outside, and those which lie inside, the zone of vascular bundles. The former already show a flattening of their cavities like those which correspond to them in *Rubus*, and this appearance is accompanied by a slight thickening of their walls. The cells of the interior, on the other hand, are fairly isodiametric and thin-walled; they are much distended with cell-sap, and their protoplasmic contents become reduced to a thin primordial utricle, as may be easily shown by plasmolysing. Those cells which immediately bound the cavities of the ovaries are somewhat smaller than the rest, but they show no marked irregularity of size.

At the flowering time, the ovules stand out from the placenta into the cavities of the bilocular ovary and do not touch the carpel-walls, but if fertilization is effected this state of things is soon altered. Radial and tangential divisions arise in the layers of cells lying beneath the inner limiting layer (epidermis) of the carpels, and this process causes an ingrowth of the tissue of these bodies into the space left between the ovules. At the same time the cells of the placenta also multiply and grow larger, though the limit of possible expansion of this structure is of course determined by the size of the fruit-cavities. The placenta, however, takes advantage of all the spare room left between the ovules, and by growing out between them, causes them to appear as if they were sunk in its substance (Pl. XXVI, Fig. 30). Those processes grow outwards, enclosing the ovules, until they finally meet with the similar ingrowths of the carpels, which likewise penetrate between the separate ovules. The two surfaces then become pressed together, and the line of demarcation between them is

gradually obliterated, and complete union takes place. In this way the ovules become entirely enclosed in the pulpy tissue, even long before the fruit is ripe, and it is impossible to distinguish that portion whose origin is carpellary from that which is derived from the placenta. The changes which take place in the outer cells of the pericarp, and which result in the formation of an epicarp, have already been adverted to, and need not be further described, as they are essentially similar to those occurring in *Rubus*, except that here the epicarp is somewhat thicker, and separates with greater ease from the inner tissues.

Whilst the changes above detailed are proceeding, modification is going on in the outermost layer of the ovular integument, which results in the formation of a protective shell, which takes the place of the endocarp in other fruits. The thickening substance, which soon becomes strongly lignified, is deposited on the inner or central wall, and extends partially up the lateral or radial ones, but, as in many other cases, it is not complete, and hence a section of the young seed shows these walls as spike-like projections which terminate in thin membranes. The outer, or peripheral, wall is not thickened at all, but its more external layers undergo mucilaginous change (Pl. XXVI, Figs. 31, 32) at a very early period. This mucilage may perhaps be regarded as part of the pulp, as it fills the interspaces left between the ovules and the surrounding tissues as a somewhat viscous mass. It is of extremely common occurrence in fruits, and owes its origin to the most varied sources; we have seen it in *Hedera*, and in *Ribes* it is also met with, being derived from the placental cells; and besides these instances it occurs in a great number of fruits, as *Linum* (where it is produced from the seed-coat as in *Solanum*), whose ovaries do not become pulpy at all.

As the fruit ripens the green colour changes to the well-known bright red, so characteristic of the berries when mature; the change is due to the appearance of a great number of orange-red chromoplastids, which are, in part at least, derived

from the chlorophyll granules¹, and fruits such as those of the Bittersweet afford fine examples for studying the development of these structures. Unfortunately most of my material was preserved in alcohol, so that I was unable to follow all the steps of the process, which can of course only be done in perfectly fresh specimens. As the colour of the ripening fruit begins to change, the starch, which previously filled the cells, slowly begins to disappear, and no trace of this substance can be detected at maturity, its place being taken by sugar, which is dissolved in the cell-sap.

I cannot bring this paper to a close without recording my warmest thanks to Professor Bayley Balfour, at whose suggestion this investigation was undertaken, for the kindly help and advice which he has given me during its progress.

¹ See Schimper, Ueber die Entw. d. Chlorophyllkörner u. Farbkörper, Bot. Zeit. 1883; also in Pringsheim's Jahrb. Bd. xvi. p. 131.

EXPLANATION OF FIGURES IN PLATES XXV AND XXVI.

Illustrating Mr. Farmer's paper on the Morphology and Physiology of Pulpy Fruits.

Figs. 1-14. *Hedera Helix*.

Fig. 1. Longitudinal section through young bud. The shaded part represents the tissue of the carpel. *v*, vascular bundle.

Fig. 2. Longitudinal section through elongating portion of pith, just below carpels, shows two cell rows pushed apart by intruding filament, *F*.

Fig. 3. Longitudinal section of part of the rind: two cell rows growing past each other.

Figs. 4, 5. Successive sections (transverse) through young fruit rind. *aa*, sections through the same intruding filament.

Figs. 6, 7. Longitudinal section through rind. *E*, epidermis.

Fig. 8. Transverse section through carpellary portion of half-ripe fruit. *m*, inter-cellular mucilage.

Figs. 9, 10, 11. Transverse sections through parts of older fruits (Haematoxylin).

Figs. 12, 13, 14. Cells with oil contents from almost ripe fruits.

Figs. 15-18. *Crataegus Oxyacantha*. Middle lamella, coloured yellow.

Fig. 15. Transverse section of $\frac{1}{2}$ -ripe mesocarp. The well-differentiated middle lamella as seen when mounted in water.

Fig. 16. The same in potash.

Figs. 17, 18. Somewhat older, mounted in Schultz solution.

Figs. 19-23. *Rubus fruticosus*.

Fig. 19. Diagrammatic transverse section, young fruit, showing layers of the endocarp.

Fig. 20. Same in longitudinal section.

Fig. 21. Transverse section of ovary in the bud.

Fig. 22. Same sometime after flowering.

Fig. 23. Same when almost ripe.

Figs. 24-32. *Solanum Dulcamara*.

Fig. 24. Longitudinal section, ovary in flower.

Fig. 25. Same shortly after flower has withered.

Fig. 26. Transverse section of ovary in same style as in Fig. 25.

Fig. 27. Transverse section, young epicarp.

Fig. 28. The same much more advanced, part of the mesocarp also shown. *E* = epidermis.

Fig. 29. Transverse section of inner portion of pericarp in same stage as Fig. 25; some of the cells are dividing tangentially, to form the inner ovular protuberances. *I*. *E*. inner epidermis or limiting layer.

Fig. 30. Shows the pericarp (*Pe*), meeting placental (*Pl*) outgrowth, round two ovules (*o*).

Fig. 31. Transverse section through ovule, showing mucilaginous layer (*m*).

Fig. 32. Mucilaginous layer (*m*) in later stage; *s*, the thickening seed-coat.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 6.

Fig. 7.

Fig. 15.

Fig. 14.

Fig. 18.

Fig. 19.

Fig. 21.

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Fig. 4.

Fig. 5.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 13.

Fig. 16.

Fig. 17.

Fig. 17.

Fig. 22.

Fig. 20.

Fig. 23.

Fig. 24.

Fig. 29.

Fig. 27.

Fig. 28.

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Fig. 25.

Fig. 26.

Fig. 32.

Fig. 30.

Pe.

Fig. 28.

Fig. 31.