The Development *of* Articulated Laticiferous Vessels.

By D. H. Scott, B.A., Ph.D. (With Plate X.)

1. *Literature.*

The development of laticiferous vessels from cells was, as regards certain instances, known to the younger Moldenhawer[1] as early as the year 1812. At that time these organs were not yet clearly distinguished from the other forms of tissue which occur in the cortex; they were comprehended, together with the sieve-tubes and soft bast generally, under the common name of "Vasa propria."

The true laticiferous vessels investigated by Moldenhawer were those of Musa and Chelidonium, which he found to be composed of sacs which open into one another. He erroneously supposed that this also held good of the laticiferous cells of *Asclepias fruticosa.* The anatomical investigation of plants had not then made sufficient progress to render a systematic study of development possible, and we can only wonder that Moldenhawer came so near the truth.

Among the more modern phytotomists, Unger, in 1840, maintained that laticiferous vessels are formed by the fusion of cells, but the instance he chose was unfortunately *Ficus benghalensis,* where the laticiferous tubes are now known to be inarticulated. As Unger's view was not till much later supported by any trustworthy observations, it is not surprising to find that a different theory, although wholly without foundation, was long accepted by many botanists. This view, according to which the laticiferous vessels are simply intercellular spaces which only obtain a membrane of their own in the later stages of their development, was first expressed by Schleiden,[2] though not with any great confidence, and afterwards, in 1846, maintained at length by an anonymous authoress.[3] This intercellular theory made a great impression on botanists, which is quite intelligible considering that it was then the only view supported by researches which were really diligent and careful, although wrongly interpreted. Even Mohl[4] received the new theory

[1] 'Beiträge zur Anatomie der Pflanzen,' Kiel, 1812, pp. 136, 140, 146, 151. Compare also Sachs, 'Geschichte der Botanik,' p. 305.

[2] 'Grundzüge der wissenschaftlichen Botanik,' 2nd edition, 1845, part I, pp. 213, 254.

[3] 'Botanische Zeitung,' 1846.

[4] See his 'Anatomy and Physiology of the Vegetable Cell,' 1852, p. 2.

with favour, and it was still defended by writers of repute as late as the year 1860.[1]

The investigations in question were chiefly carried out by means of longitudinal sections through the growing point, and embraced a large number of the plants which produce latex, among which the Apocyneæ, Asclepiadeæ, Urticaceæ, Euphorbiaceæ, Papaveraceæ, and Cichoriaceæ were represented.

Even the case of *Chelidonium majus*, where the remains of the cross walls persist, as is well known, during the life of the plant, seems at first not to have suggested any doubts as to the correctness of the intercellular theory. The question which was chiefly regarded in the researches of this period was, whether the laticiferous vessels do or do not possess a proper membrane from their first origin. It was supposed at that time that two distinct lamellæ of cell-wall must exist between each two neighbouring cells of any tissue, and when a double wall could not be detected between a laticiferous canal and the neighbouring parenchymatous cells, it was considered a necessary inference that the former had no cell-wall of its own at all. As soon as Mohl, only a few years later, had shown that the original wall between two neighbouring cells of a tissue is regularly a single lamella, this ground for the intercellular theory disappeared of itself.

In the mean time Schacht,[2] in 1851, brought forward an entirely new theory, according to which the laticiferous vessels generally are "laticiferous bast-cells, which are frequently branched." He thus refused to regard these vessels as forming an independent system, and wished to include them as a subdivision in the Bast-cell group. And here it must be remembered that Schacht and some other phytotomists of that time were in the habit of giving the name Bast to cells of the most different kind, if thick-walled, long or branched, without any regard to their position, just as in more recent times Schwendener has extended the name Bast to elements of the most various kinds which agree only in contributing to the mechanical strength of the organs to which they belong. Schacht's first researches extended to Euphorbia, Hoya, Rhizophora, Chelidonium, Lactuca, &c. His view had the one advantage over the intercellular theory, that he once more recognised the cellular nature of the elements of which the

[1] As, for example by Henfrey, 'Micrographic Dictionary,' art. "Laticiferous Tissue," 2nd ed.

[2] 'Botanische Zeitung,' 1851, p. 513.

laticiferous vessels are composed. In other respects, however, his theory was directly at variance with the facts. The fact especially that all laticiferous vessels, both the articulated and the inarticulated, form continuous open tubes which may traverse the whole plant, was ignored, and, indeed, expressly denied by Schacht, who asserts that these "bast-cells" are never connected with one another. Thus, not only the development but even the anatomy was completely misunderstood.

In 1855, Unger[1] came forward again as the representative of the cell-fusion theory. In the work cited all laticiferous vessels are described under the heading cell-fusions. The author expresses his view as follows:—"As the result of many researches, carried out according to this method,[2] it has been established that the elements of the laticiferous vessels are always cells of peculiar fluid contents. These cells appear as short or long, simple or repeatedly branched cylindrical sacs, the ends and branches of which frequently inosculate, so that a system of communicating tubes proceeds from them." The mode of development is not described more in detail; Unger had probably traced it only in the case of some plants with really articulated laticiferous vessels, such as Chelidonium and Sanguinaria,[3] and then assumed that the results of his researches also applied to the inarticulated latex-cells, an error which is the more excusable as the distinction between the two categories of laticiferous canals had not yet been detected.

In 1856, the first minute investigations of the development of articulated laticiferous vessels were published by Schacht,[4] who, however, only actually traced the process in one plant, *Carica papaya.* The remarkable latex vessels of this genus form, as is well known, a much branched system, which here, unlike most other cases, is developed on the inner side of the cambium. They form concentric circles in the xylem, tracheæ and laticiferous vessels being produced alternately by the cambial layer. The cross-walls and also portions of the side-walls are, according to Schacht, soon absorbed. The main trunks of the vessels also send out numerous branches, which are sometimes extremely thin, and these can either inosculate with other

[1] 'Anatomie und Physiologie der Pflanzen,' p. 157.

[2] Maceration and boiling with potash.

[3] The latex-sacs of Sanguinaria are not in communication, and are, therefore, of course no longer reckoned among laticiferous vessels; but this was not known in Unger's time.

[4] 'Monatsberichte der Berliner Akademie,' 1856, 2, p. 515.

vessels or end blind. These fine ramifications, termed capillary tubes by Schacht, are said to traverse the intercellular spaces. Connecting tubes are also formed in the parenchyma of the medullary rays, which are said to arise from the fusion of cells, and to establish a communication between all the vessels. In the cortex only lateral branches from the main trunks are said to occur.

Schacht's observations also extended to various other plants, of which Sonchus has most interest for us. In this case Schacht has not much to say about the actual development. His words are,[1] "The process of the fusion of cells to form the laticiferous vessels seems to be the same here as in Carica, with the one difference that the parenchyma cells of the medullary rays take part in the process much more rarely here than in the other case," &c. It is scarcely to be inferred from this that Schacht had really traced the development, nor do the figures which he gives[2] show anything of the origin from cells. On the other hand, the mode of lateral union between the vessels is correctly represented. They here send out lateral protrusions which meet those of other vessels, and establish a connection in a way similar to the process of conjugation in Spirogyra, &c.

There can be no doubt that this work of Schacht's marks an important advance in our knowledge of these organs. Schacht himself still struggled to save his Bast-cell theory, asserting that true bast-cells also undergo fusion,[3] but his position could no longer be regarded as tenable.

During the next few years comparatively little of interest was published on the laticiferous organs. In 1862 Hartig[4] recognised for the first time the distinction between articulated and inarticulated laticiferous vessels. Among the former he mentions the Cichoriaceæ and Papaveraceæ, as well as the Acerineæ, which are no longer considered as possessing true laticiferous vessels. Those of the Euphorbiaceæ are described as inarticulated. The distinction thus rightly introduced was not generally accepted till much later.

In the following year (1863) the knowledge of our subject was further extended by the publication of Vogl's[5] researches on the laticiferous vessels of two plants belonging to the Cichoriaceæ. He observed the development of

[1] Loc. cit., p. 524.
[2] Loc. cit., figs. 11—13.
[3] Loc. cit. p. 530.
[4] 'Botan. Zeitung,' 1862, p. 97.
[5] 'Sitzungsberichte der Wiener Akademie,' vol. 43 B, p. 668.

these vessels in the cambium of *Taraxacum officinale* and Podospermum. He gives figures of stages in which the cross-walls are still present, and also makes the interesting statement that the communication between the vessels by means of lateral branches is established before the cross-walls are absorbed. He sums up his results in the following words :—"The laticiferous vessels of both plants arise from the fusion of cambiform or sieve-cells,[1] which are situated one over the other or side by side; the fusion is determined by the conversion of the membranes of the cells undergoing amalgamation into pectose." Vogl, as shown by his fig. 4, plate ii, confused the young laticiferous vessels with sieve-tubes.

The statement of Trécul (to whose researches I shall return below) that a communication exists between the laticiferous vessels and the tracheæ called forth a renewed investigation of these tissue forms. Hanstein's prize essay[2] (1864) contains a very full treatment of the subject, in which, however, the distribution and other anatomical conditions are chiefly regarded. As regards the development, Hanstein was an unconditional supporter of the theory of cell-fusion. But he also failed to observe directly the successive stages of development. With special reference to the laticiferous vessels of the Cichoriaceæ, Campanulaceæ, and Lobeliaceæ, he says that "the fusion of these cells generally takes place at such an early stage that, owing to the delicacy of the parts which still prevails, it escapes direct observation."[3] He adds, however: "The arrangement of the sac-shaped trunks of the vessels corresponds exactly to that of the neighbouring cells, while the length of the latter can often be recognised in the still distinguishable joints of the sacs." A little further on he gives the grounds of his opinion still more clearly. He says:[4] "On the other hand, the origin of these vessels from chains of cells finds its repeated proof, on the one side, in the comparison with those of Carica, and on the other in the Papaveraceæ," &c. We thus see that Hanstein's view, like that of Unger, is supported rather by analogy than by direct observation. The argument from analogy had become, of course, much stronger since the publication of Schacht's observations on Carica. How incomplete the researches

[1] Vogl also uses the term "Leitzellen."

[2] 'Die Milchsaftgefässe und verwandten Organe der Rinde,' Berlin, 1864.

[3] Loc. cit., p. 14.

[4] Loc. cit., p. 15.

were on which the theory of cell-fusion was at this time based is manifest from the fact that Hanstein still extends this theory to the inarticulated latex-cells.

Dippel's work[1] (1865), which also received a prize from the Paris Academy, agrees with Hanstein's as regards the main results. He finds that all laticiferous vessels consist at first of cells arranged in rows, and those which do not form a network are said by him to admit of being broken up into their elements by means of maceration. Dippel, not content with simply extending these results to the inarticulated latex-tubes, claims to have actually seen the cross-walls in these also. This statement has been refuted by De Bary[2] and Schmalhausen, who have shown that the cross-walls seen by him did not belong to the laticiferous cells at all, but to other cells lying above or below them. The same observers have also proved the incorrectness of his conception of these vessels as modified sieve-tubes.

Trécul published, between the years 1857 and 1868, a long series of papers on the laticiferous vessels and allied organs, which are remarkable for the great number of species investigated. I will pass over his theory of circulation, according to which the laticiferous vessels correspond to the veins and the tracheæ to the arteries of animals, and only touch slightly on a few points, which are of interest with reference to the development.

Among the Papaveraceæ Trecul[3] observed the origin of these vessels from cells in Argemone. Here, as in other cases, the latex is said to be formed before the cross-walls are absorbed. And here, too, communication exists between neighbouring vessels by means of protrusions, as is the case with so many of the articulated latex vessels.

Among the Cichoriaceæ[4] the development is described as follows:—The laticiferous vessels arise from cells which are fused into continuous tubes. The latter are all in communication with one another, so as to form a network. The communication between the cells comes about in three different ways—1. By the fusion of cells which stand one above the other. 2. By the more or less frequent absorption of the side walls at the points where two cells or vessels are in immediate contact. 3. When the vessels are at a distance

[1] As the work itself was not at my disposal, I had to use De Bary's report in the 'Bot. Zeitung,' 1867, p. 333, as well as references in the 'Vergleichende Anatomie,' &c.

[2] 'Vergleichende Anatomie,' p. 205.

[3] 'Comptes Rendus,' t. 60, 1865, p. 522.

[4] Ibid., t. 61, 1865, p. 787.

each sends out branches towards the other, which arise as protrusions. They grow between or even through the cells of the intermediate tissue until they meet and inosculate. In *Tragopogon pratensis* Trécul observed branches of this kind, which attained a length of 1·15 mm.

Among the Aroideæ[1] Trécul seems to have observed both the absorption of the cross-walls and the communication by means of lateral branches in various species of Caladium.

In another passage[2] Trécul calls attention to the fact that in the Euphorbiæ no trace of the origin from cells is to be perceived, and is thus the first after Hartig to observe the distinction between the articulated and inarticulated vessels.

More detailed accounts of the development are not to be found in Trécul's treatises.

The next work of importance on this subject, that by David (1872), is occupied with the inarticulated latex-cells. To him belongs the credit of finally establishing the distinction between the two classes of laticiferous organs, although he failed to discover the true mode of development of those which are inarticulated. He supposed that new latex-cells are constantly being formed in the meristem of the growing point, and, consequently, that a great number of these cells, which have been developed successively, exist in the mature plant. It is now known that the latex-cells are formed, once for all, in the embryo, and in very small numbers (in some cases six), and that the whole laticiferous system of the plant consists exclusively of the abundant ramifications of these few original cells. This discovery was first made by Schmalhausen[3] (1877), and afterwards confirmed by the researches of Weber in the Würzburg Laboratory.

Schmalhausen's work is also of great value as regards the development of the articulated laticiferous vessels. His observations on the mode of origin of these organs in the Cichoriaceæ seem to me to be by far the most accurate that we possess. In describing my own observations I shall often have occasion to refer to his statements, so that only his main results need be mentioned here. Schmalhausen investigated the embryos of Tragopogon and Scorzonera. He found that the rudiments of the laticiferous vessels exist in the embryo of the ripe seed, and that they are converted

[1] 'Comptes Rendus,' t. 61, p. 1163.

[2] Ibid., t. 60, p. 1349.

[3] 'Beiträge zur Kenntniss der Milchsaftbehälter der Pflanzen,' St. Petersburg, 1877.

into actual vessels during germination by means of the absorption of the cross-walls and portions of the side-walls. This process is said to begin at the root end and thence to advance to the opposite end of the embryo. The distribution of the laticiferous organs in the embryo resembles that among the Euphorbiaceæ. In both cases they form two systems, one of which belongs to the Periblem the other to the Plerome. The laticiferous vessels have nothing in common with the sieve-tubes either as regards development or structure. I reserve details for the second part of the paper.

The 'Vergleichende Anatomie' of De Bary contains, in addition to valuable original observations, a summary of the results of all researches on the subject previous to 1877. This may be regarded as pretty exactly representing the present state of the question, as very little new information has been gained since that year. The conclusion at which one must arrive is that the development of the articulated latex-vessels by cell-fusion may be regarded as established with approximate certainty, but nevertheless, that the process has only been directly observed in very few cases.[1]

Since 1877 only one work has appeared which requires to be noticed here. This is E. Faivre's[2] investigation of *Tragopogon porrifolius*. The author asserts that the ripe embryo of this plant consists essentially of parenchyma containing abundant protoplasm, neither tracheæ nor laticiferous vessels being as yet developed. The former are said to show themselves first, but even they only after the root has protruded from the envelopes of the seed. The laticiferous vessels he finds to be developed by the fusion of rows of cells, and this mode of origin could often be detected subsequently by means of the evident articulations. The latex-vessels were found in the greatest numbers in the cotyledons. Faivre also has observed the two ways in which neighbouring vessels are connected, by the fusion of transverse rows of cells, and by outgrowths. As regards the distribution, Faivre finds that an intimate relation exists between the tracheæ and the laticiferous vessels, although they are never in communication. The latex itself is said not to appear until the root has attained a length of several millimètres. I shall soon have an opportunity of showing how far I have been able to confirm Faivre's statements by my own observation.

The investigations which I am now about to describe

[1] See De Bary, loc. cit., pp. 199 and 203.

[2] 'Comptes Rendus,' t. 88, 1879, p. 269.

were undertaken at the suggestion of Professor Sachs, with the object of investigating the development of the laticiferous vessels in certain instances somewhat more closely, and as far as possible by direct observation. I have endeavoured to avoid mere conclusions from analogy with reference to the development, such as are so frequent in most of the former investigations, except those of Schmalhausen and De Bary, and to rely only on successful thin sections. The following statement, therefore, refer exclusively to quite clear and unmistakeable objects, such as only thin sections can afford.

2. *Original Observations.*

I will first describe the development of the laticiferous vessels in the germ plant of *Tragopogon eriospermus*, as I have investigated this object more minutely than any other, and germ plants generally have hitherto been examined by very few observers with reference to this question. It will first be necessary to describe shortly the distribution of these vessels in the seedling.

In the root of the seedling there are two distinct systems of laticiferous vessels. First, scattered and not very numerous vessels traverse the cortical parenchyma. They lie pretty close to the surface, commonly in the fourth or fifth layer of cells. Secondly, the axial cylinder possesses a number of latex-vessels, which belong to the phloem, and, as corresponds to the diarchic structure of the root, form two large opposite groups, each of which occupies about a quarter of the circumference. In the hypocotyl the laticiferous vessels preserve the same general arrangement (fig. 1). Here, however, the hypodermal vessels are much more numerous than in the root. They lie still closer under the epidermis, from which they are frequently separated only by a single layer of cells. These vessels may be either isolated or lie two or more together. The latex-vessels of the fibro-vascular system assume a distribution corresponding to the stem structure. Here, namely, they lie chiefly on the outer (phloem) side of each bundle, though they also occur in the interfascicular tissue.

In the node the fibro-vascular bundles and the latex-vessels belonging to them bend outwards into the cotyledon so that they come to lie nearer the surface in the cotyledodonary sheath than in the hypocotyl. The hypodermal vessels, on the contrary, preserve a direct course in entering the cotyledons. At the point where the fibro-vascular bundles enter the cotyledonary sheath their latex-vessels are invariably connected with the hypodermal vessels by means of cross branches. Similar connections occur repeatedly in other parts of the sheath. In the cotyledons the latex-vessels usually accompany the fibro-vascular bundles, which are here much ramified, though here also isolated latex-vessels occur. I have never been able to trace these vessels into the growing point of the germ-stem above the youngest leaves, but have always found them continued into the young leaves themselves. It appears, therefore, that the laticiferous vessels, like the fibro-vascular bundles, are never cauline (stammeigene in Nägeli's sense).

The arrangement just described exists very evidently in germ plants with the root protruding about five millimètres from the seminal envelopes. The first question to be settled is at what stage the differentiation of the organs in question first begins. With reference to this point I have investigated the like embryo in the dry seed. In a cross-section (through the cotyledonary sheath, for example) (fig. 2), in the position where the hypodermal vessels are always found at a later stage, cells are here and there to be detected which are immediately distinguishable from their neighbours by their smaller size. In the radial direction they are only half as wide as the ordinary parenchyma cells. Seen in cross-section they always appear two together, and are commonly separated from the epidermis by a single layer of cells. In a longitudinal section (fig. 3) we find that these cells form longitudinal rows, and have evidently been formed by the division of cells of the third layer from the surface by means of tangential walls. It is the outer of these two narrower rows of cells from which the hypodermal latex-vessels are developed. Even at this early stage a differentiation of the cell-contents appeared to me to be perceptible, as the cells in question contain only a few small aleurone grains, while the latter are present in great abundance in the parenchyma cells.[1]

The rudiments of the fibro-vascular bundles also exist in the embryo. Here, however, I was not able to distinguish the latex-vessels in their earliest stage of development from the other cells of the procambium.[2] It was for this reason that, in studying the first origin of the former, I turned my atten-

[1] This deficiency in aleurone grains extends more or less to the sister-cells of the rudimentary latex-vessels. Where this is the case it is possible that two latex-vessels were to be formed side by side, which is not at all unusual.

[2] Cf. Schmalhausen, loc. cit., p. 23.

tion to the hypodermal vessels, for as regards these no confusion is possible.

I have not succeeded in every case in demonstrating the presence of rudimentary laticiferous vessels in the embryo of the ripe seed. The stage of development at which the embryo enters upon its resting state in the dry seed is known to be more or less accidental. There are probably individual ripe seeds in which the cell-divisions in question have not yet taken place, and only occur at the commencement of germination. On the other hand, the rudimentary fibro-vascular bundles can invariably be distinguished with certainty. It follows that Faivre's assertions, according to which the ripe embryo consists essentially of parenchyma, in which neither tracheæ nor laticiferous vessels are "developed," give a very inaccurate representation of the real state of the case. On the other hand, Schmalhausen's results agree fully with my own.

The latex-vessels in process of formation are much easier to distinguish as soon as germination has once begun. In seeds which had lain twenty-four hours in earth, but showed no external signs of germination, I found the rudimentary hypodermal vessels pretty clearly differentiated (fig. 4). They appear as longitudinal rows of somewhat elongated cells, which are as a rule about half as wide and double as long as the parenchyma cells. It is still easy to see that they have been formed by the division of cells belonging to the third, and in some cases to the fourth layer from the surface. The sister cells, which lie on the inside, remain smaller than the other parenchyma cells, and have evidently undergone further cross-divisions, which are passed over in the cells of the laticiferous vessels. As regards the cell-contents, the differentiation is now very conspicuous. Both the epidermis and the parenchyma cells still contain a quantity of aleurone grains. The latter are entirely absent from the young laticiferous vessels. These have uniform finely granular contents, with a darker spot, which may possibly indicate the position of the nucleus.

In germinating seeds with the root just beginning to show itself, the hypodermal laticiferous vessels are a little further developed. Their contents now begin to assume the characteristic appearance of latex, and can be distinguished at once by their colour from those of all the other cells. The cross-walls, however, are still completely preserved.

In seedlings with the root protruding three to four mm. from the seminal envelopes, the laticiferous vessels can be clearly recognised in almost every part. It is at about this time that the first indications of the absorption of the cross-walls are usually to be observed. At this stage of development the condition of these vessels is as follows:

In the root the hypodermal vessels are already in a fairly advanced state; they contain latex, and here and there it can be seen that the cross-walls are perforated, at any rate in the middle. The other system, that which belongs to the axial cylinder, is more backward in its development. The contents of the cells are not visibly different from those of the other procambial cells; and all their walls are still unaltered.

The same conditions prevail to a certain extent in the hypocotyl. Here, however, the development of the two systems is more nearly equal.

At the base of the cotyledons the connecting branches between the axial and the hypodermal latex-vessels are as far advanced as the main trunks themselves. They already contain some latex. In this region one occasionally finds cross-walls which are already perforated. In the upper part of the cotyledons the development is not so far advanced. The cross-walls are everywhere present, though sometimes slightly swollen. Towards the apex of the cotyledons no latex can be detected in the vessels.

The laticiferous vessels in the cotyledons already form a complex network. The connection between the main trunk is always formed by cross rows of cells, which afterwards undergo fusion. In these germ plants I have never observed union by conjugating outgrowths, which is so common elsewhere.

Cases not unfrequently occur in which one or more cells of a row are divided into two by longitudinal walls. Both the cells so formed take part in the formation of the vessel. Here a subsequent bi-partition has evidently taken place in some of the cells which already constitute the young latex-vessel, while the other cells remain undivided as usual.

In germ plants, where the root has attained a length of about six mm., all stages in the development of the laticiferous vessels can be observed. I will follow the same order as before, and begin with the hypodermal vessels of the root. These are now almost in the mature state. The cross-walls are all perforated, and it is sometimes difficult to find any traces of them. The articulations are very long, generally twice as long as the parenchyma cells, which are themselves much elongated. Thus the same relative length is still maintained as exists in the earliest stages of development. The laticiferous vessels of the axial cylinder, on the other hand, are by no means so far advanced. The absorption of the cross-walls is here only beginning, and some of them are still perfect. The side-walls also are still without perforation.

In the hypocotyl the hypodermal vessels are just as far advanced as in the root. The cross-walls are absorbed, and a vessel may often be traced a considerable distance without finding any signs of them. The latex-vessels of the fibro-vascular bundles are further advanced than the corresponding ones in the root, but not so far as the hypodermal vessels. The cross-walls are perforated, and much larger openings are present in the side-walls. The latter fact, which I have often observed, agrees with Smalhausen's statement, that the absorption of the side-walls precedes that of the cross-walls, though other observations lead me to doubt whether this is an invariable rule.

In the cotyledons the perforations are smaller than in the hypocotyl. Here all the laticiferous vessels, whether belonging to the fibro-vascular system or not, show the same stage of development. Their articulations are comparatively short, corresponding to the slow growth of this part.

The absorption of the cross-walls in the cotyledons continues to make but slow progress. Even in seedlings, with the root about one cm. in length, the process is by no means completed (fig. 5). When two vessels are in contact large perforations already exist in the side-walls. The cross-walls, however, are only partly absorbed, and in some places the openings are still quite small.

As regards the order in which these vessels are developed in the different parts of the seedling, it appears to me that two rules are followed. In the first place the principle holds good that the latex-vessels reach maturity soonest in the parts where growth first takes place. Accordingly the hypodermal vessels of the root are completed very early, because the base of the root is the part which has the most energetic growth when germination begins. The corresponding vessels in the hypocotyl are little if at all more backward, for here also elongation begins very early. On the other hand, the cotyledons scarcely grow at all for a long time, and here too the development of the laticiferous vessels goes on very slowly, and is not completed till very late.

As mentioned above, Schmalhausen called attention to these facts. But, secondly, I have often had occasion to observe that the latex-vessels of the plerome are very backward in their development compared to the hypodermal vessels. This is particularly conspicuous in the root, but also holds good of the hypocotyl — at any rate in its lower part. The hypodermal vessels contain latex when no signs of it are to be found in those of the plerome. And, further, the fusion of the cells is far advanced in the former at a time when it has scarcely begun in the latter. This distinction, however, does not hold good in the cotyledons. Here the development is uniform at all parts of the same cross-section.

With reference to the actual process of cell fusion I have obtained the following results:—The wall which is to be absorbed first appears somewhat swollen; the swelling, however, is not very marked. Then the membrane begins to dissolve gradually at some one point. Probably a middle lamella is present which resists solution longest, for stages are often found where the perforation is still closed by an extremly thin membrane. The opening is at first very small; it often, but by no means always, occupies the centre of the cross-wall. It increases gradually in size, and before the cross-wall has quite disappeared the contents of the two cells become continuous. As regards the lateral perforations I have only to confirm Schmalhausen's statement, that they are habitually formed in the neighbourhood of a cross-wall.

The observations on Tragopogon which I have just described were partly repeated on *Scorzonera hispanica*.

Here also the rudiments of the laticiferous vessels can be recognised in the ripe seed. The process of their development is essentially the same as in Tragopogon. Even before the cross-walls are absorbed the cells become distinguishable from the others by their contents, and no doubt already contain latex. The distribution is somewhat different in the two plants. In the seedling of Scorzonera almost all the laticiferous vessels belong to the phloem part of the fibro-vascular bundle, only in the cotyledons some are found isolated in the cortical parenchyma near the epidermis. In one other point Scorzonera differs from Tragopogon; in the former the outgrowths from the latex vessels, which afterwards establish communication between the main trunks, are formed at an early stage of germination. We have already seen that these outgrowths appear to be wanting in the seedling of Tragopogon. This mode of connection between the latex-vessels is best observed in the neighbourhood of the growing point of the stem in older plants of Scorzonera, and especially in their young leaves. Here it is easy to find vessels in which the articulations are still clearly distinguishable (fig. 8). These young vessels send out lateral protrusions, which penetrate between the parenchyma cells. In a great many cases they end blind. The points at which they are formed appear to be determined by the pressure due to the turgescence of the surrounding cells, that is to say, they are formed where the resistance to their growth is least.

When the branches formed in this way happen to meet the branches or trunks of other latex-vessels their walls are absorbed at the point of contact, and their contents become continuous. The appearance presented recalls the phenomena of conjugation among the algæ—a comparison which was already made by Schacht. An important difference between the two processes is, however, to be found in the fact that a laticiferous vessel produces these outgrowths quite independently of the presence of a neighbouring vessel.

The development of the laticiferous vessels in the embryonal tissue of older plants agrees, so far as my observations extend, with that in the seedling. The vessels very generally have a crooked course, which is partly explained by the fact that the cells which take part in the formation of one and the same vessel do not necessarily lie in the same longitudinal row. It is quite usual for cells situated in contiguous rows, and at somewhat different levels, to undergo fusion by absorption of that part of the side-wall which is common to both. In this case parts of the latex-vessel will lie in the same straight line with cells which belong to the parenchyma, the vessel itself having a broken course.

With reference to the subject of this paper, I further examined the secondary cortex of Scorzonera, Taraxacum, and Chelidonium. In the root of Scorzonera laticiferous vessels are formed from the cambium in great abundance. In cross-section they appear ranged in radial rows, which are not usually separated by more than six layers of parenchyma cells. As a rule each radial row is double. The latex-vessels are accompanied by sieve-tubes, which are fairly numerous. In a tangential section it can be seen that the portions of tissue containing the latex-vessels and sieve-tubes form a coarse network, the meshes being occupied by the cortical rays. Frequent anastomoses between the vessels occur, both in the radial and tangential direction, some being direct, while others are effected by means of outgrowths. The cross-walls are absorbed very early. It is only quite near to the true cambial layer that one finds them still present. The early stages of development are

parent, and for this reason it can here be easily demonstrated that each of the cells has a nucleus. Treated with hæmatoxylin these nuclei become just as clear as those of the parenchyma cells, which they resemble in every respect. They have a lenticular form, and are closely applied to one of the side-walls of the cell. Each has a fairly large nucleolus. The nuclei persist throughout life. I have found them in old latex-vessels which were beginning to become disorganised.

The parenchyma cells of the secondary cortex contain a quantity of compound starch grains, which are formed as soon as the cells have passed out of the cambial condition. In the young latex-vessels starch grains are entirely absent from the first, which makes it very easy to distinguish them at an early stage.

There is also one point in the distribution to which I will call attention. I have often convinced myself that laticiferous vessels also occur in the xylem of the root, and that not only in the medullary rays, but actually among the tracheæ. This is not invariably the case, but it is very frequent. I must therefore express my disagreement with Hanstein's assertion that in the Papaveraceæ "no true laticiferous vessels penetrate between the crowded cells and vessels of the xylem bundle."[1] Hanstein was of the opinion that the pitted vessels which are often found filled with latex had been mistaken for true laticiferous vessels. I have myself often seen pitted vessels in this condition. Their strongly thickened pitted walls bear no resemblance whatever to those of the real latex-vessels. In size and other characters they are also entirely different, so that confusion could hardly take place between them, even if the contents were "strongly coloured," which in the vessels in question was not the case. The latex-vessels are always much less numerous in the xylem than in the phloem. Sometimes, but extremely rarely, they are in immediate contact with the tracheæ.

The results of my very fragmentary observations may be summed up as follows:

1. It has been shown by direct observation that the laticiferous vessels of the plants investigated arise from rows of cells, of which the cross-walls, and, where two vessels are in contact, parts of the side-walls are gradually absorbed. The absorption takes place, as a rule, very early—in the seedling, for example, during the first stages of germination;

[1] Loc. cit., p. 77.

in the secondary cortex shortly after the cells are severed from the cambial layer.

2. The communication between vessels not in contact is effected in two ways; partly by means of cross rows of cells which undergo fusion, and partly by means of inosculating outgrowths, which form connecting canals, as in the Conjugatæ.

3. Even before the cross-walls are absorbed the cells are distinguishable by their contents, and probably already contain latex.

In conclusion, I must express my hearty thanks to Prof. Sachs for the constant aid which he has given me throughout my work.