VIII. *The Caoutchouc-containing Cells of* Eucommia ulmoides, *Oliver.* *By* F. Ernest Weiss, *B.Sc., F.L.S.* (*From the Botanical Laboratory, University College, London.*)

(Plates LVII. & LVIII.)

Read 21st January, 1892.

Introduction.

Eucommia ulmoides, the "Tu chung" of the Chinese, was named and described by Professor D. Oliver in Hooker's 'Icones Plantarum'* from some dried material, including bark, leaves, and fruit, which had been sent to the Royal Gardens, Kew, through the instrumentality of Dr. A. Henry. Professor Oliver called attention at the time to the most singular feature about the plant—namely, the presence in its tissues of innumerable elastic threads of silvery sheen, which become apparent when the leaf, bark, or fruit is snapped across and the parts drawn asunder.

Some of the dried material was handed to me for the investigation of these threads and of the cells containing this elastic substance. But little could be made out, except that they occurred accompanying the vascular bundles of the leaf, and very abundantly in the secondary phloem and in the pericarp. I was therefore very pleased when I received from Professor Oliver a second lot of material, which had been brought to Kew through the kind offices of Dr. Henry. This material was preserved in spirit, and consisted of a large assortment of winter buds in various stages, some only just beginning to open, others provided with shoots showing distinct internodes, and with leaves about one half the size of the fully developed leaf. Many of these buds were attached to the end of the last year's branches, which were therefore entering upon their second year's growth. I have consequently been enabled to study not only the distribution and structure, but also the development of the cells containing the curious elastic threads, which are so characteristic of the tissues of *Eucommia*.

I was at first inclined to look upon these threads as of the nature of a hardened gum or resin. This, however, is not the case, as they are quite insoluble in alcohol, and both gums and resins are distinguished by their solubility in alcohol from viscin and caoutchouc.

Weinling † describes viscin as an intermediate substance between resin and caoutchouc, and mentions its occurrence in young parts of *Ficus elastica*, where it is later on replaced by caoutchouc. It has also been described in *Euphorbia helioscopia* by Ohlenschlaeger, who calls it a caoutchouc-like resin. But viscin differs from caoutchouc by its solubility in ether, whereas caoutchouc only swells up in that liquid.

* Hooker, 'Icones Plantarum,' 3rd series, vol. xx. (1890) t. 1950.

† Weinling, 'Pflanzenchemie,' 1839.

The threads of *Eucommia* consist therefore of caoutchouc, for they are insoluble in alcohol, acids, and alkalis, though they become soft when treated with ammonia. They dissolve in chloroform and turpentine, and swell up in ether. When heated they melt, and they burn with the characteristic smell of burning rubber.

It is still uncertain whether the many substances described as caoutchouc or india-rubber are always the same chemical body, but that these threads consist of a substance having the usual characteristics of caoutchouc is beyond doubt.

With certain colouring reagents these threads were, curiously enough, stained in the same manner and of the same colour as the cuticle covering the epidermal cells. Thus when treated with dilute iodine they rapidly assume a dark yellow or brown colour, while the remainder of the section is only faintly stained. Similarly, methyl green acidulated with acetic acid stains both the cuticle and the caoutchouc threads intensely violet, while the rest of the section is stained light green, the xylem vessels being somewhat darker, but not of a violet colour.

From the bark the rubber can very readily be extracted. If the bark be broken in pieces and pounded in a mortar, the mass can be roughly separated into two parts—one consisting of the tangled elastic threads, with small bits of broken bark adhering to them, the other chiefly of bits of bark containing, no doubt, smaller pieces of the threads. From both parts chloroform will dissolve out caoutchouc, a larger amount naturally from the portion which consists chiefly of the threads. Thus a sample of the threads and bark weighing 443 mg. gave as much as 25 mg. of caoutchouc, while the remaining bark, weighing 607 mg., yielded only 6 mg. Taking the two quantities together, the yield of caoutchouc was 3 per cent. of the weight of the dry bark, and the same figure was arrived at independently by Professor F. W. Oliver with another sample.

The threads are clear and homogeneous, and the only impurity in the chloroform extract seems to be a little resin, which can be washed out with alcohol.

Whether the bark can be made use of commercially I must leave to those who are more experienced in technical matters, but it is interesting to note that efforts are now being made to extract gutta-percha from the bark of trees which have been drained in the ordinary way of that product. The yield in these cases was 5·3 to 5·7 per cent. of the wet bark used.*

The threads themselves *in situ* in a section, both in longitudinal and transverse aspects, are highly doubly refractive, and remain so when swelled up with ether; but they lose this optical property when dissolved in turpentine or melted into an amorphous mass.

The distribution of the caoutchouc-containing cells I had been able to determine from the dry material which I first examined, and these observations were confirmed by the examination of the material preserved in alcohol. They occur in the inner portions of the cortex, very much in the position in which the latex cells of *Euphorbia* are found, but are even more frequent in the secondary phloem, where they run between the companion cells (figs. 14 & 15), and in both cases present the appearance of very long narrow cells, attaining such a length that one only occasionally finds their ends. The sieve tubes of the secondary phloem have their sieve plates on their lateral radial, not

* Bulletin of Miscell. Information, Kew, September 1891.

on their transverse walls, as is the case in the primary phloem, and we find regular alternating peripheral rows of sieve tubes and companion cells, very often two of the former to one of the latter, as will be seen in fig. 14. Between the companion cells the cut ends of the caoutchouc threads will be seen.

In the leaf a group of caoutchouc-containing cells accompanies the ramifying fibro-vascular bundles, running just below the phloem, while in the petiole and all along the bundle of the midrib they form two groups at the side of the bundle, and do not run below it. A few cells are scattered through the parenchyma, which forms the cushion on the underside of the midrib, and a good many are found in the parenchyma of the petiole.

The pericarp of *Eucommia*, which resembles in appearance that of the Elm, is especially rich in these caoutchouc-containing cells. Below the epidermis of the pericarp we find a few layers of large chlorophyll-containing cortical cells, which become very much compressed in the dry fruit. Within these are the fibro-vascular bundles, the main trunks running longitudinally, and connected by branching and anastomosing lesser bundles. The longitudinal bundles have a strong group of caoutchouc-containing cells accompanying them on their inner side, and immediately beneath them we find a large mass of circularly running cells of the same nature, forming quite a dense coat of hyphæ-like thin-walled cells, showing their cell-walls very distinctly when the caoutchouc has been dissolved out by chloroform.

Further within we find a group of thicker-walled cells very similar to and running in the same direction as the caoutchouc-containing cells, but with curious, almost black, granules and contents. The innermost layer of the pericarp consists of sclerenchymatous cells.

The caoutchouc-containing cells reminded me in many ways of the latex cells of the Euphorbiaceæ and Apocyneæ, in spite of their remaining unbranched and containing their caoutchouc in a consolidated mass. But the main difference between these cells and the latex cells became apparent when I began to study their development, and found that they can originate anew in all the secondary growths, both in the secondary phloem and also in all new organs, whether stem or leaf; whereas all true latex cells, according to Chauveaud's latest embryonic researches *, arise from a limited number of initial cells, which can be distinguished at an early stage in the development of the embryos of Euphorbiaceæ, Urticaceæ, Apocyneæ, and Asclepiadæ.

Schmalhausen †, it is true, had previously affirmed this embryonic origin of latex cells for a large number of cases, but his observations did not include the latex cells which are found in the secondary phloem in *Ficus*, *Morus*, *Broussonetia*, *Maclura*, and *Nerium*. These, however, according to Chauveaud, are also formed from the specialized cells of the embryo mentioned above, for, as he says (p. 151) :—

"Dans les cas où la plante acquiert des formations secondaires, ces formations sont parcourues par des tubes laticifères issus des branches voisines des assises génératrices

* Chauveaud, G., in Annales des Sciences naturelles, série vii. tome xiv. (1891) pp. 1–160.

† Schmalhausen, in Mém. de l'Acad. de St. Pétersbourg, 7e série, vol. xxiv. (1877) no. 2.

et appartenantes au système laticifère primitif. On ne constate jamais l'apparition de nouvelles initiales après les premiers stades du développement embryonnaire."

In *Eucommia*, however, the caoutchouc-containing cells, whether they exist in the embryo or not, are continuously formed anew in all new secondary growths. In the very young buds and in the youngest parts of older shoots, *i. e.* therefore in all meristematic regions, no trace of these cells will be found. They first make their appearance in the cortex of a rapidly growing internode. The cortical tissue growing very rapidly here, we find a large number of transverse divisions to each initial cortical cell, the lateral walls of which have already attained some considerable thickness, and the tissue presents the appearance of a number of cells divided up by thin transverse walls (see figs. 1, 5, 8).

This appearance of young tissues is figured by Sachs in his text-book in the case of the hypocotyledonary portion of the stem of the Sunflower (fig. 56), and in fig. 94 of his Lectures for the rapid tangential growth of the cortical cells.

In the cortical cells at this stage longitudinal divisions take place in cells which are noticeable by their very granular protoplasm, which completely fills the cells, whereas the surrounding cortical cells have large vacuoles at this stage (fig. 1). The cortical cells also contain several plastids, which are absent in the cells referred to. These initial cells occur most frequently about midway between the epidermis and the fibrovascular bundles, in a region where the cortical cells are loosely packed and intercellular spaces abound, and are of considerable size; they may, however, occur only three cells beneath the epidermis, where the intercellular spaces are much smaller.

The longitudinal division of these cortical cells may take place either by radial or tangential walls. In radial longitudinal section, such as those from which figs. 1 & 4 are drawn, the two daughter cells have arisen by tangential division of the mother cell.

Fig. 6 is a drawing of a transverse section of an internode at a somewhat later stage of development, but it shows two young stages of division before any further elongation has taken place, or, at any rate, that part of the cell which has not elongated, and therefore they have the same appearance as a young stage. They are characterized by the larger diameter of the cells, by the presence of nuclei, and by the straight dividing wall. In the case in which this wall is anticlinal, I could not but compare the appearance of the daughter cells at this age with Chauveaud's figures of transverse sections of some embryos of *Euphorbia*. The figures in question are those of *Euphorbia exigua* (pl. i. fig. 2), of *Euphorbia Peplus* (pl. ii. figs. 6 & 7), and of *Broussonetia papyrifera* (pl. vii. fig. 8). In all these cases the initial cells, which develop into the latex cells, occur in groups of two, and suggest an origin (by longitudinal division of a mother cell) similar to that of the caoutchouc-containing cells of *Eucommia*.

A number of other species of *Euphorbia* (*E. falcata*, *E. helioscopia*, *E. Lathyris*) are figured by Chauveaud with a ring of latex-cell initials, and these too may have been derived in pairs from a mother cell.

The same origin of the caoutchouc-containing cells of *Eucommia* occurs in the cells of the pith (fig. 3), but takes place here in somewhat older internodes, therefore at a later period than in the cortex. The caoutchouc-containing cells in the pith are of very much rarer occurrence than the similar cells in the cortex, which fact may be connected with the splitting away of the pith cells a little later on, so that a hollow stem is formed, with septa made up of very much stretched cells of the original pith, in which septa the caoutchouc cells can be made out. But the origin of the cells is the same, and the pith at that early stage has a structure quite like that of the loosely built cortex (fig. 3).

I was also able to observe a similar origin of the caoutchouc-containing cells in the parenchymatous tissue surrounding the vascular bundle of the petiole (fig. 2). Here too they arise by a longitudinal division of a cell of this tissue, which, however, here consists of more elongate cells more closely set than those of the cortex or pith, both of which are tissues with considerable intercellular spaces.

In the secondary phloem I was not able to observe the actual origin of these cells, as the phloem cells are at their commencement more elongate than the cortical tissue, and there would be little difference between them and the caoutchouc-containing cells either in size or contents at so early a period. I cannot therefore state whether a cambium cell divides into two daughter cells, each of which grows out into a caoutchouc-containing cell, or whether these cells are each the result of differentiation of a single cambium cell. But from the young stages which I was able to observe in the secondary phloem, which contained a nucleus, and in which the caoutchouc was only in part formed, I can definitely conclude that these caoutchouc-containing cells do originate in the secondary phloem, and do not make their way there, as the latex cells of *Broussonetia* and *Ficus* for example do, according to Chauveaud.

After the longitudinal division has taken place, the cells begin to grow out, and force their ends upwards and downwards through the intercellular spaces of the tissue in which they arise. This can be seen from fig. 3 in the case of the pith, and from fig. 4 in the case of the cortex. In fig. 4 growth has as yet commenced only at one extremity, but from the later stages it will be seen that the cell grows rapidly at both ends (fig. 5). The protoplasm, being now distributed over a larger area, becomes much clearer, and at the same time a vacuole makes its appearance in the cell, and enables the protoplasm to remain applied to the increasing surface. The origin of this vacuole is seen in fig. 4, and it is also seen in the more elongate cells of fig. 5. Here, however, it is only indicated in the wider part of the cell near the nucleus, as in the outgrowing parts the superficial view is drawn in order to show the appearance of the larger granules of caoutchouc. The lighter protoplasm enables us to see more clearly the large nucleus, which remains more or less in its initial position, and indicates the original position of the cell. I have never been able to find two nuclei in any of these cells, any appearance of two being attributable to some other cell, usually the sister cell lying below the cell under observation.

To whatever length therefore these cells may grow, we must at present assume that all growth and other functions are regulated by this single nucleus. This would probably account for the fact that these caoutchouc-containing cells never branch like the latex cells of the Euphorbiaceæ, which cells Treub *, Schmidt †, Haberlandt ‡, and other

* M. Treub, in Comptes rendus (1879); and in Archives Néerlandaises, t. xv. (1880) pp. 39–60.

† E. Schmidt und Fr. Schmitz, in Sitzb. d. niedrh. Ges. für Natur- und Heilkunde zu Bonn (1879). (E. Schmidt, Bot. Zeit. (1882) p. 594).

‡ G. Haberlandt, 'Function und Lage des Zellkerns,' 1886.

observers, have shown to contain numerous nuclei. The unbranching character of the cell would not, however, preclude the existence of several nuclei, as Treub has shown that many unbranched bast-fibres have several nuclei. Though therefore a ramifying cell, such as a latex cell, requires several nuclei for its continuous growth, which seems to last during the entire life of the plant, an unbranched but very extensive cell may also have several nuclei, and it is no doubt the presence of several nuclei which has enabled the branching cell to be evolved from the non-branching one.

The caoutchouc-containing cells of *Eucommia* are therefore simpler in structure than the latex cells of the Euphorbiaceæ, and would also appear to be more primitive than the multinucleate fibres described by Treub.

The nucleus of the caoutchouc-containing cells in the early stages is elliptical or round, usually containing one large nucleolus, but in later stages it becomes spindle-shaped, and often, in fact, generally, possesses two large nucleoli. The fact that the nucleus remains in its initial position, and is of considerable size, almost touching the cell-wall on either side, is an additional support to the purely negative evidence, which has led me to the conclusion that only a single nucleus is present in these cells.

As the ends of the initial cells grow out, they make their way upwards and downwards along the path of least resistance, *i. e.* along the intercellular spaces. As these are, however, large and numerous, the course of the cells is fairly straight (fig. 8). But usually the two sister cells become separated by the obstacles they meet on their course, and even at so early a stage as that represented in fig. 6, though the caoutchouc-containing cells run in pairs, yet most sister cells are separated by considerable intervals. They can, however, usually be matched in couples. This becomes more difficult in the later stages, as is apparent from fig. 7.

The growing end of the cell is often curiously dilated into a bulbous termination, similar to those described by Schmalhausen for the ends of the latex cells in the root of *Euphorbia* embryos. But Schmalhausen speaks of a tapering end behind which the actual dilatation occurs, whereas those of the caoutchouc-containing cells of *Eucommia* terminate bluntly with the bulb. Schmalhausen's observations gave him the impression as though it were only with difficulty that the latex cell could find room, between the cells, to push in its apex, and that it endeavours by extension to fill up all possible cavities.

The dilatations I have observed in many cases, however, could have no such cause, as they were found in the middle of wide intercellular spaces (fig. 10). Immediately behind the apex, the walls, usually thin and delicate, are considerably thickened (fig. 10). In some of the bulbous terminations the contents were still of a granular nature, and had not yet coalesced into a solid mass, characteristic of their final state. In these cases the bulbous terminations contained a certain amount of substance, staining deeply with protoplasmic stains, and there is no reason to suppose that these cells were unable to continue to grow. In others, however, the contents were already fused into a solid mass of homogeneous caoutchouc, and little or no protoplasm could be observed, so that a considerable difficulty would lie in the way of our considering these as actively growing ends. I would suggest, therefore, that these dilatations, when they occur in such positions as that figured in fig. 10, indicate that the limit of growth of one of these cells has been reached, which may be due either to the nucleus having come to the end of its functional power, or, as seems more likely, to the nucleus having been cut off from communication with the growing point of the cell by a blocking up of its lumen with caoutchouc. For in many cases in which the end-bulb still contained protoplasmic substance, or at least a substance staining like protoplasm, but containing also a large amount of caoutchouc granules, the thinner portion of the cell behind the end-bulb was entirely filled with a solid mass of caoutchouc, between which and the cell-wall I could not demonstrate any protoplasm.

I searched diligently for a nucleus in these end-bulbs, which at first seemed to me likely places for additional nuclei, but could in no case discover any.

Other dilatations occur occasionally in places where growth has been hindered by some obstruction, and here, too, a thickening of the cell-wall takes place (fig. 11). It is such an irregular growth in which we get a short horizontal extension, that appears as a long cell in the transverse section (fig. 7).

The bulbous dilatations occur in the most striking manner in the teeth of the developing leaves, where they may be seen in large numbers, especially after swelling up the ordinary tissues with sulphuric acid (fig. 12). Here they are very irregular in appearance, and here they would seem to indicate that the growth of the caoutchouc-containing cells had become impeded by the slowness of the development of the leaf. Here, therefore, the cells should still be in a growing condition, and yet in many cells the contents are already clear, indicating that the caoutchouc has become set into a solid mass.

In longitudinal section (fig. 13) the bulbs will be seen arching over the end of the vessel and terminating but a few cells behind the meristematic cells of the tooth.

The Contents of the Cells (fig. 9, *a*, *b*, *c*, & *d*).

During the early stages of growth of the cells above described, the protoplasm contains a number of smaller and some very much larger granules (figs. 5 and 9 *a*). These latter and some of the smaller are of the nature of caoutchouc, and can best be identified by the intense blue or violet colour which they assume with acidulated methyl green. Their solubility in chloroform is another test. These granules appear also in many of the cells of the primary phloem, in which no caoutchouc-containing cells occur (fig. 9 *d*). Nor do these phloem cells become stored with caoutchouc, but the granules seem to be re-absorbed, for in older internodes of the same shoot no such granules are seen.

In the caoutchouc-containing cells, the large granules become more numerous till the cells are densely packed with granules (fig. 9 *b*), and finally they become welded into a solid mass, which at first shows its origin from a granular matrix by numerous lines indicating splits and cracks in the contents (fig. 9 *c*). Ultimately, however, the contents become quite homogeneous, as mentioned at the commencement of this paper, and form elastic threads, which are observed on breaking asunder a bit of bark or a leaf. The contents are then drawn out of the cells and show themselves to be very elastic. If a young developing leaf be treated in this way, the contents may be pulled out before the complete fusion of the granules has taken place, and threads will be seen presenting a jagged outline owing to the granules protruding along the side of the thread. By the time the fusion has taken place it is impossible to demonstrate any protoplasmic contents to the cells, and we must assume that all further growth ceases.

Concluding Remarks.

From the foregoing description of the caoutchouc-containing-cells of *Eucommia*, it will be seen that, while reminding one in many particulars of the latex cells of the Euphorbiaceæ, yet in some very essential points they differ from them.

They agree with the latex cells in their occurrence in the inner portion of the cortex, in the secondary phloem, and to some extent in the pith. They elongate enormously, and make their way by a sliding growth into the growing regions and largely into the leaves. They contain at the commencement numerous large caoutchouc granules in their protoplasm, though these granules afterwards become welded into a homogeneous mass of caoutchouc. They differ, however, chiefly from latex cells—

(1) In remaining unbranched and containing only a single nucleus.

(2) In arising *de novo* in all secondary growths, such as the secondary phloem and in new shoots and leaves.

As far as this secondary difference is concerned they would in this agree with the latex cells of the Cannabineæ, of *Urtica*, and of *Vinca*, in which the latex cells do not arise from specialized cells of the embryo, as they do in the Euphorbieæ.

Chauveaud has, therefore, also distinguished the latter, as "tubes continus primitifs," from those of *Urtica*, which he calls "tubes continus ultérieurs." So, too, they might be called in *Eucommia*, were it not for the fact that their contents, except possibly at a very early stage, are very different indeed from what is usually termed latex. They seem to contain only the one substance, which I have taken to be caoutchouc, and never present fats, oils, or starch. I have, accordingly, preferred to call them merely what they seem to me to be, *i. e.* caoutchouc-containing cells.

Yet, morphologically, they may be equivalent to the cells usually termed latex cells, but are less specialized and less elaborate in structure than these, and I think we may therefore venture to assume that latex cells of a more organized type may have been derived from cells similar to those of *Eucommia*, and possibly our conclusions may support the views of some observers who have dealt with the relationship of the various forms of laticiferous tissues.

Pax *, in his paper on the Anatomy of the Euphorbiaceæ as affecting their classification, takes the separate closed sacs containing latex which are found in some of the Ricinocarpeæ and in the Acalypheæ as the starting-point in the evolution of the latex cells of Euphorbiaceæ. In the group of the Johannesiæ the individual cells of the articulated sacs are of different length, some of considerable length, and if, as Pax

* Engler's Botanische Jahrbücher (1884), pp. 384–421.

suggests, we consider the number of these cells reduced to one, and that one endowed from its first formation with a very pronounced power of elongation, we arrive at the ordinary latex cell, such as we find it in the group of the Euphorbieæ.

Chauveaud * inverts this order and considers the long, branching, but undivided cells of the Euphorbieæ as the most primitive form of latex tissue (" tubes continus primitifs "), just as the unicellular or non-cellular Siphoneæ represent a more primitive form than the multicellular plants. The fact, also, that the latex cells of the Euphorbieæ arise in the embryo itself seems also to strengthen Chauveaud in his conclusion, and he lays great stress on three cases in which the embryo presents the continuous latex cells, whereas in the adult plant the laticiferous system is represented by a series of closed sacs, though he has no direct observations to show that the latter have arisen by a dividing of the continuous cells of the embryo. The plants alluded to are *Aleurites triloba, Jatropha Curcas*, and *Jatropha multifida*.

My own observations on *Eucommia* tend in no way to support Chauveaud's theory of the relationship of the different forms of laticiferous tissues, but illustrate, I think, another step in the series of forms through which Pax would lead us to the highly specialized inarticulated laticiferous tubes. Pax's suggestions have been provisionally accepted by Dr. Scott †, in his valuable paper read before this Society, in which he shows how, starting from the same primitive condition of closed laticiferous sacs, we might also derive the articulated laticiferous vessels of *Manihot* and *Hevea*. The fact that these two different systems, the non-articulated cells of the Euphorbieæ proper and the articulated vessels of *Manihot* and *Hevea*, can be derived from the closed secretory sacs, such as those found in the Ricinocarpeæ, by a development towards the same end, namely, towards continuity, seems to me to be a strong claim for the correctness of Pax's suggestion; whereas, according to Chauveaud, the " tubes continus primitifs " become discontinuous by dividing into a number of separate cells, such as are found in *Cnesmone* and *Dalechampia*, only to become continuous again in the case of the articulated vessels of *Hevea* and *Manihot*.

It is not, however, my object in this paper to discuss the origin of the articulated vessels, as in *Eucommia*; my observations bear only on non-articulated cells.

I consider that we are dealing here with a primitive, though not the most primitive, form of a latex cell. The caoutchouc-containing cells of *Eucommia* are, I think, similar to the closed latex sacs described by Pax in the group of the Johannesieæ, but are somewhat more specialized, and therefore, in some respects, more like the latex cells of the Euphorbieæ proper. Their specialization shows itself in the fact that the initial cell divides into two before elongation takes place, so that we have always two daughter cells in the place of the primitive mother cell. This division of the initial cell into two reminds one, as I have stated previously, of the appearance of the initial cells figured in some of the Euphorbian embryos by Chauveaud, so that I do not regard it as improbable that this division into two may have been a step in the evolution of the non-articulated latex cells of Euphorbia.

* Annales des Sciences naturelles, Série vii. tome xiv. (1891) pp. 1–160.

† Journal of the Linnean Society, vol. xxi. (1885) pp. 566–573.

The caoutchouc-containing cells of *Eucommia* are unbranched and still contain only one nucleus, but it is easy to conceive that a division of this nucleus into several younger nuclei, a division which might become necessary by the dimensions of the cells, would enable the cell under certain conditions to branch out in other directions, as it has become normal for the latex cells of the Euphorbiaceæ.

But the faculty of branching having been acquired, and their powers of growth having been increased by their multinucleate condition, the number of these cells might very naturally become reduced. Such reductions are of frequent occurrence in the vegetable kingdom. I need only cite the reduction which takes place from multisporangiate leaves to unisporangiate forms among the Cryptogams, and the reduction of the number of archegonia which has taken place in the phylogeny of the Gymnosperms and Angiosperms.

There is also, both in the vegetable and in the animal kingdom, the well-known tendency of "anticipation," which for example, in the group of vascular Cryptogams, has caused the differentiation of sexes to be anticipated by the heterosporous forms in the sporangium, while the more primitive homosporous forms do not show that differentiation until the prothallium is developed.

This same tendency has, I think, in the evolution of the laticiferous cells, caused the embryo to produce these laticiferous cells, and their formation from cells in older tissues has become unnecessary, by reason of their excessive growth and vitality, very much as Pax suggests.

The occurrence of closed latex sacs in the adult plant in *Aleurites* and *Jatropha*, for which Chauveaud has described non-articulated latex cells in the embryo, may indicate merely the retention of the older form of laticiferous tissue by the adult plant, while the latex cells which are to supersede the closed sacs are found already starting, and at least supplying the embryo.

Whether *Eucommia* has initial cells in its embryo similar to those of Euphorbia or not we have no means at present of ascertaining, but I would like again to mention that these cells in *Euphorbia* often occur in pairs, and then present all the appearances of the initial cells in the cortex of *Eucommia*. I incline to the belief that the embryo of *Eucommia* has no such cells, first on the ground that they would be unnecessary to a plant which is so well provided with other cells in its new organs, and, secondly, because these caoutchouc-containing cells do not arise in meristematic regions, but in a secondary manner, in tissues which are far progressed towards maturity.

The function of the caoutchouc-containing cells, as far as the preceding observations go, cannot be in any way connected with the conduction of food substances; for they are closed cells filled with a solid mass of caoutchouc, which would prevent the passage of food substances as effectually as a callus plug. Their presence in large number in the leaves might suggest the idea that they conduct away substances formed in the leaf, but they terminate not so much in the assimilating layer as at the margin of the leaf, which would be much more suggestive of some sort of protection against insects or other animals, to which the caoutchouc might prove distasteful. Their occurrence, too, in the middle of the pericarpal wall in such large numbers would support this theory. If the

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But the faculty of branching having been acquired, and their powers of growth having been increased by their multinucleate condition, the number of these cells might very naturally become reduced. Such reductions are of frequent occurrence in the vegetable kingdom. I need only cite the reduction which takes place from multisporangiate leaves to unisporangiate forms among the Cryptogams, and the reduction of the number of archegonia which has taken place in the phylogeny of the Gymnosperms and Angiosperms.

There is also, both in the vegetable and in the animal kingdom, the well-known tendency of "anticipation," which for example, in the group of vascular Cryptogams, has caused the differentiation of sexes to be anticipated by the heterosporous forms in the sporangium, while the more primitive homosporous forms do not show that differentiation until the prothallium is developed.

This same tendency has, I think, in the evolution of the laticiferous cells, caused the embryo to produce these laticiferous cells, and their formation from cells in older tissues has become unnecessary, by reason of their excessive growth and vitality, very much as Pax suggests.

The occurrence of closed latex sacs in the adult plant in *Aleurites* and *Jatropha*, for which Chauveaud has described non-articulated latex cells in the embryo, may indicate merely the retention of the older form of laticiferous tissue by the adult plant, while the latex cells which are to supersede the closed sacs are found already starting, and at least supplying the embryo.

Whether *Eucommia* has initial cells in its embryo similar to those of Euphorbia or not we have no means at present of ascertaining, but I would like again to mention that these cells in *Euphorbia* often occur in pairs, and then present all the appearances of the initial cells in the cortex of *Eucommia*. I incline to the belief that the embryo of *Eucommia* has no such cells, first on the ground that they would be unnecessary to a plant which is so well provided with other cells in its new organs, and, secondly, because these caoutchouc-containing cells do not arise in meristematic regions, but in a secondary manner, in tissues which are far progressed towards maturity.

The function of the caoutchouc-containing cells, as far as the preceding observations go, cannot be in any way connected with the conduction of food substances; for they are closed cells filled with a solid mass of caoutchouc, which would prevent the passage of food substances as effectually as a callus plug. Their presence in large number in the leaves might suggest the idea that they conduct away substances formed in the leaf, but they terminate not so much in the assimilating layer as at the margin of the leaf, which would be much more suggestive of some sort of protection against insects or other animals, to which the caoutchouc might prove distasteful. Their occurrence, too, in the middle of the pericarpal wall in such large numbers would support this theory. If the latex cells have been derived from such cells as have been described, it would seem that their primary function was to store up the waste products, or, at all events, to secrete some substance which would render the leaves distasteful, and, therefore, more or less immune. When the laticiferous system, however, was elaborated to form a continuous system throughout the plant, whether as articulated vessels or non-articulated cells, the secondary function of food conduction may have been added to their first and primary function of protection.

How do the foregoing observations affect the systematic position of *Eucommia*? Professor Oliver, from the scanty material with which he had to deal, especially owing to the absence of flowers, did not definitely assign *Eucommia* to any natural order, but suggested that it might have affinities with the Euphorbiaceæ, and perhaps more especially with the Phyllanthoideæ. If the cells described have any morphological affinity with the latex cells of Euphorbiaceæ, they would tend to support Professor Oliver's suggestion that this plant might be associated with the Euphorbiaceæ.

The Phyllanthoideæ, however, according to Pax *, are devoid of laticiferous tissues; we should therefore have to include *Eucommia* among the Crotonoideæ, which have some laticiferous tissue, however elementary, and if we were to lay as much stress on the anatomical character of the laticiferous tissue as Pax does in his paper in Engler's 'Jahrbuch' we might place it either in a group at the side of the Johannesieæ, or between the Johannesieæ and the Hippomaneæ.

As, however, no flowers are to hand, these suggestions are merely speculative, and at present practically valueless; for, if we adopt Chauveaud's classification of the laticiferous tissues, we might associate *Eucommia*, as possessing "tubes continus ultérieurs," with either *Cannabis*, *Urtica*, or *Vinca*. The value of these anatomical characters in classification can only be secondary. Still, as they have their function as secondary characters, it may be as well to mention that in *Eucommia* we find no medullary phloem groups, and that the secondary phloem presents distinct masses, hard bast elements alternating with the soft bast.

In conclusion, I take this opportunity of thanking the Director of the Royal Gardens of Kew for putting this interesting material at my disposal, and I wish also to acknowledge the help and suggestions I received during my investigations from Professor F. W. Oliver.

* F. Pax in Engler's Bot. Jahrb. (1884) p. 404, and in 'Engler's Natürliche Pflanzenfamilien,' vol. iii. p. 5.

DESCRIPTION OF THE PLATES.

Plate LVII.

Fig. 1. Longitudinal section through the cortex of a young internode, showing two initial cells with dense protoplasm surrounded by the loose cortical cells. These latter possess a vacuole and plastids, which are not present in the initial cells.

Fig. 2. Two initial cells in the more closely packed cells of the petiole of a young leaf.

Fig. 3. Initial cells in the pith of *Eucommia*, showing commencement of elongation.

Fig. 4. Initial cells in the cortex beginning to elongate at one extremity, and showing the formation of the vacuole.

Fig. 5. A group of very young caoutchouc-containing cells, showing their elongation in two directions. The larger granules in these cells are grains of caoutchouc, the smaller ones protoplasmic granules. The two lower cells have been derived from one mother cell.

Fig. 6. Transverse section of a young internode. The cortical tissue has large intercellular spaces, in which the young caoutchouc-containing cells can be seen in pairs. The larger cells are those which have been cut through in the region of the nucleus.

Fig. 7. Transverse section through an older internode, in which the caoutchouc-containing cells have become more separated one from the other, and show clearer contents owing to the consolidation of the caoutchouc granules into a homogeneous mass.

Fig. 8. Longitudinal section through an older internode, showing the course of the caoutchouc cells through the very loosely packed cortex.

Plate LVIII.

Fig. 9 *a*, *b*, & *c*. Different stages in the consolidation of the caoutchouc granules. In *a* the granules are not very numerous; in *b* they almost fill the cell; and in *c* they have become fused into a single mass.

Fig. 9 *d*. Cell from the phloem of a young internode, in which large grains of caoutchouc make their appearance within the primordial utricle.

Fig. 10. Bulbous dilatation by which many of the caoutchouc cells terminate in the cortical and other tissues.

Fig. 11. Bulbous dilatation which is not terminal.

Fig. 12. Tooth of a young leaf after treatment with sulphuric acid. The leaf is rendered transparent, and shows the irregular bulbous terminations of the caoutchouc cells.

Fig. 13. Longitudinal section of tooth of young leaf, showing the termination of two caoutchouc cells.

Fig. 14. Transverse section of the secondary phloem of *Eucommia*. The caoutchouc cells are seen running between the sieve tubes and the companion cells. The sieve tubes have their sieve plates on the radial walls. *m.r.* median ray; *s.p.* sieve plate; *c.c.* caoutchouc cell.

Fig. 15. Longitudinal section of the secondary phloem, showing the course of the caoutchouc cells. Sieve plates are seen in surface over and in section.

(Figs. 14 and 15 have been drawn from preparations made from dried material.)

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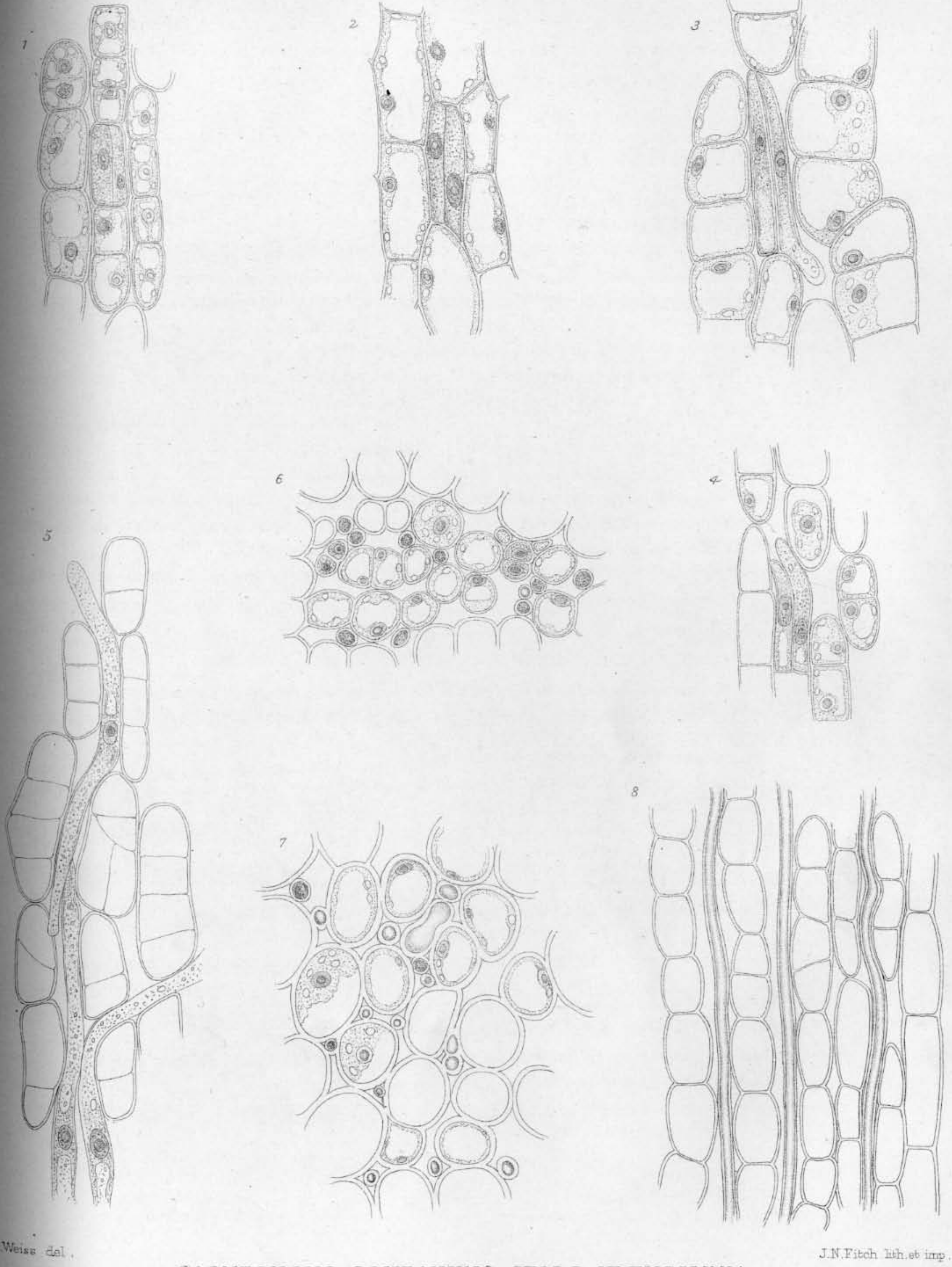

F.E. Weiss del.

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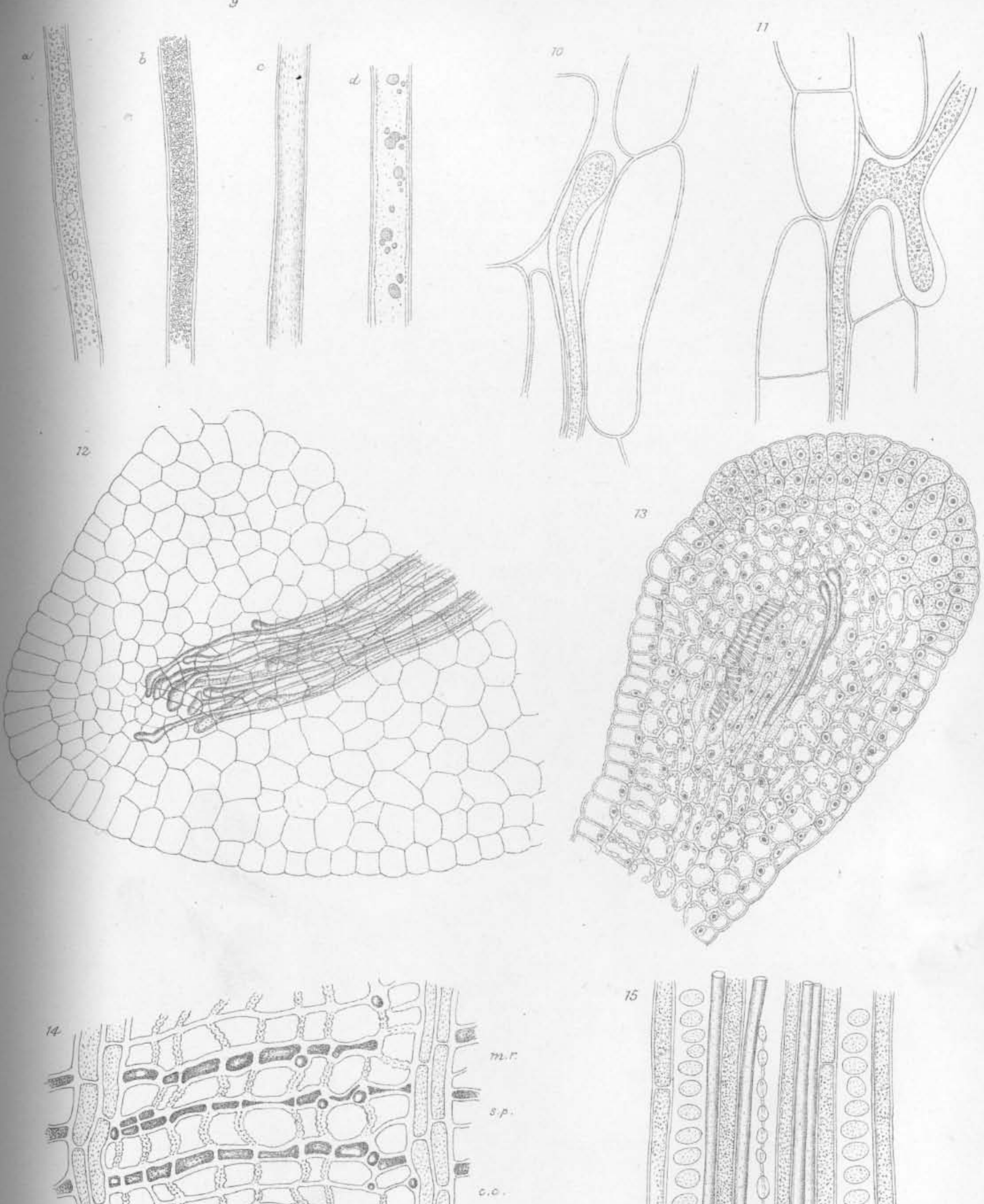
CAOUTCHOUC-CONTAINING CELLS OF EUCOMMIA.



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