Observations on Latex and its Functions¹.

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With Plate XII.

DURING the year 1898 and the early part of 1899, while engaged in Ceylon as temporary scientific assistant to Mr. Willis, the Director of the Royal Botanic Gardens, Peradeniya, I was occupied in investigations on caoutchoucyielding trees, chiefly *Hevea brasiliensis*, Müll.-Arg., (Para Rubber), and *Castilloa Markhamiana*, Markham, (a Central American rubber-tree)². The principal results of this economic work are contained in one of the circulars³ of the Royal Botanic Gardens, Ceylon, which is intended primarily for those interested in rubber-cultivation.

¹ A short abstract of this paper was read to the British Association, Sec. K, Dover, 1899; see Ann. of Bot., Dec., 1899.

² The *Castilloa* trees introduced into Ceylon in 1876 have hitherto been considered to belong to the species *C. elastica*, the well-known Mexican rubber-tree. They have recently been shown to belong rather to a closely allied species perhaps hardly more than a variety of *C. elastica*—which is found in Panama and known as *C. Markhamiana*, Markham (not Collins). See Willis, Panama Rubber (*Castilloa*), R. B. G. Ceylon, April, 1899.

⁸ Caoutchouc or India-rubber, it origin, collection, and preparation for the market, &c. Circular, R. B. G. Ceylon, June, 1899, pp. 105-168.

Annals of Botany, Vol. XIV. No. LIV. June, 1900.]

The purpose of the present paper is to draw attention to some of these observations and experiments with regard to their general botanical interest; to describe other observations bearing on latex; and to conclude with a few remarks and suggestions on the origin and functions of laticiferous tissue.

A word of apology is perhaps needed for the somewhat disconnected nature of the observations, which are, as it were, the outcome of what was fundamentally an economic study of rubber-plants.

There was not time to carry out more detailed work on the function of latex on the spot, and many of the matters touched upon can no longer be prosecuted at home with the same ease.

All remarks, unless distinctly stated to the contrary, apply to rubber-plants growing in Ceylon. Some of these may seem not altogether to tally with observations made on these plants elsewhere, thus admitting the possibility of the latex changing its character when the plants are moved from their natural habitats.

The paper is divided into seven parts, each dealing with a more or less distinct feature relating to latex, and concludes with remarks on its functions:—

- I. Proteids and the coagulation of latex.
- II. Oxydases in latex.
- III. The carbohydrates of latex.
- IV. Difference in properties between the latex of young and old organs of the same plant.
- V. The effect of wounding on the flow of latex.
- VI. A peculiarity in the exudation of latex from the severed base of the petiole of *Hevea brasiliensis* and *Plumiera acutifolia*.
- VII. A special laticiferous system in the developing seed of *Hevea brasiliensis*.

Latex and its Functions.

I. PROTEIDS AND THE COAGULATION OF LATEX.

Coagulation of latex is now known to be brought about by the proteid contained in it passing from a soluble to an insoluble state, whereby the particles of caoutchouc, &c. in suspension are gathered together into clots; or, as Biffen graphically puts it in a paper ¹ on the subject, the coagulating proteid 'gathers up the rubber particles in the same way as the white of an egg gathers up particles in suspension when clotted for the purpose of clearing jellies.' Consequently the conditions of coagulation depend upon the kind of proteid present in the latex. If it be globulin or albumen, then clotting should be brought about readily by heating; if albuminate, by neutralization.

Hevea brasiliensis. The proteid of this latex is said to be albumen, as is assumed in Biffen's paper². Its coagulation has been studied in some detail in Ceylon, primarily for the purpose of devising the best means of preparing commercial indiarubber by the clotting method. The results suggest rather an albuminate than albumen as the particular proteid present.

The latex, such as is collected from incisions in the trunk of the tree, mixes in all proportions with water, and as it is too thick for experimental purposes when pure, it has usually been employed diluted ten times with water. This diluted latex is not clotted by heat—no change takes place in it after boiling for several minutes; it shows a great contrast in this respect to the latex of *Manihot Glaziovii*, Müll.-Arg. (Ceara Rubber), which in the diluted form clots readily when boiled, and fairly quickly in the cold. This latter latex contains a globulin.

If a trace of acid be added to the hot *Hevea* latex, clotting takes place immediately; on the other hand small quantities of alkalies postpone the coagulation indefinitely. It is not, however, necessary to add the acid to the hot latex; it brings

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² loc. cit., p. 170.

¹ Biffen, Annals of Botany, xii, June, 1898, p. 170.

about the coagulation quite as completely, but not so quickly, in the cold. The approximate weight of acid required to completely coagulate 100 cubic centimetres of pure latex has been worked out for the following acids :—

Sulphuric acid	0.1 g	ram	clots 100	c.c. late	ex.
Hydrochloric acid	0.1	"	,,	"	
Nitric acid	0.3	,,	,,	"	
Acetic acid	0.95	"	,,	,,	
Oxalic acid	0.2	"	>>	,,	
Tartaric acid	0.25	;9	,,	,,	
Citric acid	0.5	"	,,	"	

The first two are thus seen to be the strongest coagulators, while acetic acid is the weakest, nearly ten times as much being required.

Two special points are to be noticed regarding this acid coagulation.

In the first place, the quantity of acid needed depends only on the amount of pure latex present in the liquid to be clotted. A certain weight of acid is required to completely coagulate 100 cubic centimetres of latex, no matter whether this be diluted to five or ten times its bulk. In other words, doubling the dilution halves the acid for a given volume, e.g., 100 c.c. of liquid containing 5 c.c. of pure latex requires half the amount of acid necessary for 100 c.c. of liquid containing 10 c.c. of latex. The latex can be diluted to any extent, and yet its particles of caoutchouc are capable of being collected together into clots by the addition of the necessary quantity of acid. This was even done for latex diluted 2,000 times.

In the second place, if the acid be added to excess, above a certain amount, coagulation ceases to be complete. By complete coagulation is meant the removal from suspension of all the globules of caoutchouc, so as to leave the liquid quite clear. The range for complete or nearly complete coagulation is very small with all the acids employed, except acetic. With sulphuric acid, for example, the amount can

hardly be doubled without interfering with the coagulation, whereas with acetic it can be increased some four times, before the residual liquid shows turbidity.

The following reasons are suggested for this behaviour of *Hevea* latex towards acids. The latex is slightly alkaline. The proteid is of such a nature as to be insoluble in neutral solution, but soluble in alkaline or acid media, i.e. it is an alkali-albumen. When the alkalinity is neutralized by the necessary amount of acid, the proteid comes out of solution and produces with the globules of caoutchouc the clots of rubber. If excess of acid be added, then the proteid remains in solution, being now in an acid medium. The acid required for coagulation bears a definite ratio to the quantity of pure latex only, no matter what its dilution may be, because the alkalinity is not altered in amount by this dilution. Acetic, being a weaker acid than the others, does not bring about the changes so rapidly.

The effect on this latex of several saline solutions has also been tested, viz .- sodium chloride, alum, ammonium sulphate, magnesium sulphate and mercuric chloride (corrosive sublimate). The last-mentioned has the strongest and most complete coagulating power on the latex. With 0.3 grams and upwards per 100 c.c. of pure latex, all the caoutchouc is separated by it from the diluted latex. This is what might be expected, since this salt is one of the strongest precipitants for proteids. Magnesium sulphate is the next best coagulator. A one per cent. solution brings about a fairly complete coagulation. Ammonium sulphate has to be added until as much as 5 per cent. is present, before coagulation is anything like complete. Sodium chloride never brought about a complete coagulation; whatever its strength the residual liquid was always quite milky. Alum was more effective. With an amount between 1.5 per cent. and 3 per cent., nearly complete coagulation was brought about, but above and below this the process was incomplete.

The amount of proteid present in this *Hevea* latex is considerable. By analyses kindly made for me by Mr. Kelway Bamber, resident in Ceylon, by means of Kjeldahl's wet method, the amount of nitrogen found calculated out to about 2 per cent. of proteid.

Castilloa. The proteid of the latex of *Castilloa elastica* has also been investigated to some extent by Biffen¹. He found that the latex gives an acid reaction, and that on the addition of a little alkali it is coagulated. This he considered to be due to the nature of the proteid which exists as acid-albumen in the latex; on neutralization it comes out of solution and gathers together the caoutchouc particles into clots.

Now the latex of the *Castilloa* introduced into Ceylon (*C. Markhamiana*) does not behave like this. On the very gradual addition of alkali to the latex or to the filtrate² of the latex no coagulation or precipitation occurs. Alcohol causes a coagulation of the latex and a copious precipitate in the filtrate, which is quite soluble again in water. Proteid is present in considerable quantity, about 4 per cent. being indicated by analysis. Coagulation is brought about neither by acids nor by boiling. Thus it looks as if the proteid belongs to the class of albumoses. At any rate the type of *Castilloa* introduced into Ceylon differs in this respect strikingly from that of the true *Castilloa elastica* examined by Biffen.

When the latex of *Castilloa* is mixed with water and allowed to stand, in the course of an hour or two the caoutchouc particles have all floated to the top in the form of a thick cream. The diluted latex of *Hevea*, on the contrary, shows no sign of creaming, even when submitted to a low temperature. The difference is most likely due to the larger size of the caoutchouc globule in the case of *Castilloa* as compared with that of *Hevea*.

The presence in latex of these most important plastic substances, proteids, is perhaps one of the strongest facts in support of the view that the laticiferous system takes part

¹ Biffen, loc. cit.

² The liquid part of the latex without the globules of caoutchouc.

in nutritive functions, either as a conductor or a storer of albuminous matter¹. A thorough study of the proteids of latex is much needed. Such interesting work as that of Green², done on latices which had been kept for some time, has not the same value as examinations of milk freshly drawn from the tree, owing to the liability of these complex nitrogenous bodies to change. It is a piece of research peculiarly fitted for the tropics, where laticiferous trees, which freely yield their milk, abound. The few laticiferous plants of temperate climes are mostly herbs, consequently the collection of their milk for chemical purposes is very tedious and unsatisfactory.

The latex of *Hura crepitans*, L. (Sandbox tree) is one well worth attention. It exudes copiously from a wound in the trunk and appears to contain abundant proteid, which seems to be largely globulin.

II. OXYDASES IN LATEX.

Several latices, which are pure white when they first issue from a wound in the plant, rapidly darken on exposure to the air. This is due to the presence of an oxidizing ferment or oxydase, which, with the aid of the oxygen of the air, acts on some constituent of the latex, changing it to a deep brown colouring matter.

The latex of *Castilloa* is a good example. It rapidly darkens on exposure and dries to an almost black rubber. By creaming the caoutchouc particles can be separated from the dark beer-like liquid and made into a sheet of nearly colourless rubber. By quickly heating the collected latex, the darkening is arrested, owing to the destruction of the enzyme.

The latex of *Hevea* collected from the tree-trunk does not darken at all on exposure to the air, and provided that moulds and putrifactive organisms are kept away, rubber

¹ Sachs, Physiology of Plants, p. 362. Pfeffer, Physiology of Plants, p. 581.

² Green, Proc. Roy. Soc., 1886, No. 242.

prepared from it remains indefinitely of a light colour. On the other hand, the latex from the wall of the unripe capsule (fruit) changes on exposure, from milk-white to black. The darkening is wholly prevented, if the latex is quickly subjected to heat. No doubt there is an oxydase present in Sometimes, but by no means the latex of the capsule. always, the changing latex from the capsule shows an intermediate brick-red colour, before the blackening sets in. peculiarity of this reddish colour is that it disappears on heating, whereas the black colour is permanent. The latex made to exude from young shoots sometimes blackens, but not always, whereas the blackening of the latex from the capsule is without exception in my experience. Oxydases, as a rule, show their presence more often in young organs than in mature ones.

III. THE CARBOHYDRATES OF LATEX.

Sugar in variable proportions has been shown to be of frequent occurrence in latex. The little—0.3 to 0.7 per cent.—found in the trunk-latex of *Hevea* seems at all times to be cane-sugar. Examinations made at different periods of the year, thirteen in all, showed no reduction of Fehling's cupric reagent, till after heating with an acid. The latex of *Manihot Glaziovii*, examined on three separate occasions, behaved similarly. Tannin is absent from both of these latices.

May not some of the sugar contained in the collected latex come from the surrounding injured tissues, and not be originally present in the laticiferous tubes? I have noticed that in certain species of *Ficus*, the first two or three drops of latex from an incision in the stem taste much sweeter than those which exude later. A few experiments regarding this point were made on the latex of *Hevea*. From each incision the first latex exuded was collected separately from the next and so on. The sugar was then estimated in these different portions. Time did not allow of these experiments being more thoroughly carried out, but in such as were done the

results indicated most sugar in the latex which first trickled from the wounds, suggesting that the latex in oozing out had carried with it saccharine sap from the surrounding injured cells.

Biffen¹ has shown that the amount of sugar in latex is more in that collected from the plant in the late afternoon than in that in the early morning, the inference being that the laticiferous tubes receive the sugar arising from assimilation. Considering that the quantity is small, on an average about 1.5 grams of glucose per 100 c.c. of latex, it is quite possible that a considerable portion may have come from the adjacent injured tissues, such as the parenchyma and phloem-elements.

One of the most peculiar features connected with latex is the occurrence of the well-known rods of starch in the laticiferous tubes of *Euphorbia* and allied genera. Does it mean that these tubes serve as channels for the conduction in a solid form of the carbohydrate elaborated in the leaf?

It is an attractive view, and one which received a certain amount of support from the work of Treub² some years ago. He found that after darkening portions of the stems of succulent species of *Euphorbia*, the starch-rods had wholly or largely disappeared from the darkened areas. His results, however, are somewhat vitiated by the long duration of the darkening—three to five weeks.

Schimper's³ experiments, on the other hand, show that the laticiferous tubes are not depleted of their starch in the dark. He found that the darkening of the leaves of *Euphorbia Peplus*, *E. Lathyris*, and *E. heterophylla* made, as a rule, no appreciable difference in the starch in the milk-tubes, whereas the starch disappeared wholly from the mesophyll of the leaf. He also incidentally mentions the fact that the dead leaves of *E. Lathyris* and *E. Myrsinites* have their tubes still full of starch.

¹ Biffen, Annals of Botany, xi, 1897, p. 338.

- ² Treub, Ann. du Jardin Bot. de Buitenzorg, iii, 1883, p. 39.
- ³ Schimper, Bot. Zeit., 1885, pp. 771-779.

Groom ¹ confirms Schimper's work, that darkening does not make the starch disappear from the laticiferous tubes, and mentions that in *Euphorbia Peplus* the tubes contain starch till the death of the plant.

I find that these starch-rods are still present in the yellow and fallen leaves of such of these plants as have been examined, viz. Euphorbia pulcherrima, E. Bojeri, E. Rothiana, Pedilanthus tithymaloides, Hura crepitans, Excoecaria bicolor, Sapium biglandulosum; and appear to be here as numerous as in the mature green leaves. Since my return to England I have investigated the dead and withered leaves of Euphorbia Lathyris and E. graeca, and find the starch-rods quite evident in them.

It looks then as if it is a general rule for the starch to be left in the laticiferous tubes of the dying leaves. On this account, as well as from the fact that these starch-rods are well formed in leaves not yet mature, it appears as if they are produced once for all in the tubes as these differentiate, and exist throughout the life of the organ, having nothing directly to do with carbon-assimilation.

It is worth mentioning here that starch often remains in the guard-cells of the stomata as well as in the laticiferous tubes of dead leaves, whereas the rest of the leaf-tissue is, as a rule, free of starch : hence it might be argued that, as no doubt the starch is used by the guard-cells and reformed again and again, the starch of the laticiferous tube is also used and reformed again. This of course may possibly be the case. The point to emphasize, however, is that the starch seems to have no direct connexion with assimilation, and that the tubes can hardly be considered as starch conductors or storers. If it has any nutritive value, then it is for the use of the tubes themselves.

¹ Groom, Annals of Botany, iii, 1889.

IV. DIFFERENCE IN PROPERTIES BETWEEN THE LATEX OF YOUNG AND OLD ORGANS OF THE SAME PLANT.

While investigating the latex from young stems and leaves of certain indiarubber trees, with the object of testing the feasibility of extracting commercial rubber from them, it was found that in several instances the 'rubber' obtained was quite different from that got from the trunk and main branches. This is an important point relative to the production of caoutchouc from young organs.

In the case of *Hevea*, the rubber collected from the young stems and leaves, as well as from the unripe capsules, is somewhat adhesive, and has less elasticity and strength than that from the trunk.

In the *Castilloa* introduced into Ceylon, the latex from the stems bearing leaves, as well as from the leaves themselves, moulds between the finger and thumb into a very sticky substance, wholly unlike the caoutchouc-containing latex of the trunk. It dries to a brittle material, which becomes viscous when warmed. The quality of the rubber from stems of this *Castilloa*, 12.5 to 25 c.m. in circumference, was likewise tested; it seemed to have properties intermediate between that of the shoots and the trunk, being slightly sticky and somewhat deficient in elasticity. From all that I have heard, the true *Castilloa elastica* does not exhibit this distinction between the shoot and trunk.

The climbing rubber-plants Landolphia Kirkii and Urceola esculenta show a similar difference between the latex from the shoot and that from thick stems.

Ficus elastica also exhibits this peculiarity¹. Attention was called to this in *Ficus* as far back as 1839 by Weinlung. He called the substance 'viscin,' and considered it intermediate between resin and caoutchouc.

Perhaps in the foregoing plants the laticiferous tubes

¹ See Weiss, Trans. Linn. Soc. iii, 1892, p. 243; also Seeligman, Le Caoutchouc et la Gutta-percha, 1896, p. 91. formed in primary growth have their globules in suspension in the latex, of a different composition from those arising in the secondary tissues.

In many plants this so-called viscin seems to occur throughout the laticiferous system, e.g. the common breadfruit (*Artocarpus incisa*) and jak (*A. integrifolia*)—trees of the tropics.

Most likely there are bodies which do not come within the categories of caoutchoucs and guttas, and yet are hydrocarbons with the same percentage composition. Probably some of these viscous substances are such. Also it appears probable that all caoutchoucs are not identical, and that when prepared as pure as possible from the latex, as by the ingenious centrifugal method of Biffen, it may be found, for example, that the caoutchouc of *Hevea* has slightly different properties from that of *Castilloa*.

V. EFFECT OF PREVIOUS WOUNDING ON THE FLOW OF LATEX.

An important fact connected with the tapping of *Hevea* trees, and a remarkable one from a botanical point of view, is that wounding the bark causes a greater flow of latex from subsequent injuries.

Mr. Willis¹, in his experiments on the yield of these trees, found that the weight of rubber obtained from the second tapping of a series of trunks was about double that obtained from the first incisions. Further experiments have shown that this increase in weight is due to a much greater flow of latex, from fresh wounds in a tree recently tapped, than in one hitherto intact.

One of our experiments indicated that it is possible to increase the quantity of latex to as much as seven times that obtained at the first tapping, using the same number and kind of incisions on each occasion. This fact we have found

¹ Willis, Rubber Cultivation in Ceylon. Circular R. B. G. Ceylon, Jan. 27, 1898.

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subsequently to be well known among the rubber-tappers of the Amazon valley, the home of *Hevea brasiliensis*. However, it seems, up to this, hardly to have been mentioned in the literature on the subject of rubber-tapping, although it is one of the most important points connected with the yield of caoutchouc from *Hevea*.

The increased quantity of latex from a new incision in the bark made 10 to 15 centimetres distant from an old one, can hardly be due to the formation of new milk-vessels, since the wound-response and increase in question may be recognizable after the lapse of a single day.

This response to wounding seems an important point relative to the function of latex, and a very practical one regarding the tapping of Para rubber-trees; and it needs further investigation. It will also be interesting to see whether other rubber-trees, such as *Manihot Glaziovii* (Ceara rubber), behave in a similar manner.

Full details respecting the practical results of experiments on this wound-response are to be found in the Circular mentioned at the beginning of this paper.

VI. A PECULIARITY IN THE EXUDATION OF LATEX FROM THE SEVERED BASE OF THE PETIOLE OF HEVEA BRASI-LIENSIS, Müll.-Arg., AND PLUMIERA ACUTIFOLIA, Poir.

Hevea brasiliensis. The leaf is trifoliate, with a long petiole, slightly swollen where it joins the stem. The large lanceolate leaflets are attached by very short stalks to the petiole.

The following points may be noted regarding the flow of latex :---

1. When the petiole of a *mature* foliage leaf is cut or broken sharply across at its base (Plate XII, line A-B, Fig. 1), no latex exudes from the injured surface attached to the stem, whereas the surface of the detached petiole is immediately suffused with latex.

2. When the severance is made quite close to the stem

(line C-D in the diagram) the reverse takes place, and latex oozes out only from the stem side.

3. On cutting through the leaf-stalk higher up (such as E-F in the diagram), latex exudes freely from both surfaces.

4. By making the incision follow as closely as possible the place where the absciss-layer will eventually be formed (indicated by the broken line in the diagram), it is almost possible to sever the base of the petiole without any exudation of latex appearing on either surface.

5. In a leaf which has not yet reached maturity, these peculiarities are not observable; latex exudes from both surfaces alike, when the petiole is cut across at the base (such as A-B in the diagram).

6. When the base of the short stalk (petiolule) of the leaflet of a mature leaf is cut through, latex appears on both surfaces. These leaflets are disarticulated by means of absciss-layers just as the petiole is, but do not resemble the latter in the peculiarity of the exudation of latex.

These observations point to an obliteration of the cavities of the laticiferous vessels at the region of the petiolar base, on the leaf attaining maturity. Since the place of interruption to the flow of latex appears to correspond with the position of the absciss-layer, the idea naturally suggests itself that the special cells composing this layer are formed on the maturity of the leaf, and cause the closure of the laticiferous vessels at this point. A microscopic examination, however, shows no definite layer of cells at all in this position. The abscisslayer only seems to be formed about the time that the leaf changes colour previous to its fall.

There are two marked differences between the microscopic appearances of the young and mature leaf-base. As the leaf assumes its adult condition, certain cells making a more or less broken layer across the base of the petiole become sclerosed to form 'stone' cells; there is also a marked deposition of cluster-crystals right across this region. Such structural changes suggest a closure of the laticiferous vessels

at this point, due to the pressure upon them of these altering cells.

About one hundred laticiferous plants have been tested regarding the flow of latex from the cut petiolar base, and in only one other plant, *Plumiera acutifolia*, has a case been found at all as striking as that of *Hevea*.

Plumiera acutifolia. The flow of latex from the cut petiole takes place precisely as in *Hevea.* Unlike it, however, a microscopic examination reveals no special structural changes in the base of the petiole on the leaf attaining maturity. There is no formation of ' stone' cells or deposition of crystals, the only difference being that the laticiferous tubes are less marked in the adult than in the young leaf.

Plumiera rubra behaves similarly, but *P. obtusa* does not exhibit this peculiarity; latex issues from both surfaces when the base of the petiole is cut across.

Contrasting the two cases of *Hevea* and *Plumiera* it looks as if the interference with the flow of latex, at the base of the petiole, may be brought about, not by any special form of cellular tissue closing the tubes, but rather by the pressure of the ordinary parenchyma at a region destined to be that of the absciss-layer.

Microscopic examinations have failed to show any definite obliteration of the cavities of the laticiferous vessels, crossing from the leaf to the stem. They seem, however, to be more crushed here than elsewhere in the petiole.

The severing experiments are difficult of explanation on any other supposition than that of the obliteration of the cavities of the tubes, unless it be that the block occurs in the tubes themselves, as by a coagulum forming in the latex, or by an ingrowth of the walls of the tubes.

Since this phenomenon is so exceptional amongst laticiferous plants, it may perhaps be looked upon as merely accidental, and an extreme case of the general tendency for laticiferous tubes to be somewhat crushed in mature tissues.

Nevertheless, it seems to me that this peculiarity affords to some extent an argument against the view that the latici-

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ferous tubes act as agents for the conveyance from the leaf of plastic substances formed in the mesophyll, at least as far as these two plants are concerned.

VII. A SPECIAL LATICIFEROUS SYSTEM IN THE YOUNG SEED OF HEVEA BRASILIENSIS, Müll.-Arg.

If laticiferous tubes have the function of conducting foodmaterials to growing organs, one might expect to find a rich development in the fibrovascular bundles going from the placenta to the ovule. On this account I was led to examine the developing seeds of *Hevea*.

The gynoecium is of the typical Euphorbaceous type, consisting of three carpels united into a trilocular ovary with a single suspended anatropous ovule in each loculus. After fertilization the ovary wall becomes differentiated into two parts, an inner portion composed of cells, which lengthen greatly in the radial direction, and lignify to form the hard wall of the capsule, and an outer layer which retains its parenchymatous condition and in which a rich laticiferous system is developed. The laticiferous tubes are not so extensive in the septa and central column bearing the placentas. The funicle and raphe of the developing seed are almost devoid of laticiferous tubes. A number of ovules and seeds have been examined in various stages of development, and only very occasionally has a laticiferous element been seen in these regions. The main fibrovascular bundle passing through the funicle and raphe to the chalaza is thus, as a rule, not accompanied by laticiferous vessels, at any rate by tubes containing caoutchouc and similar substances.

While examining the developing seed, a somewhat singular development of laticiferous elements was discovered just beneath the inner limiting layer of cells of the inner integument. These are absent from the ovule at the flowering stage, and only arise sometime after, when the capsule has reached a considerable size.

Figures 2 and 3 show the situation and general arrangement

of this laticiferous system in a seed, which has nearly reached its full size, but which is still far from maturity. A sheath, as it were, of laticiferous tissue forms around the nucellus, extending right from the chalaza to within a short distance from the micropyle. This is marked in thick irregular lines in the figures, one of which represents a median longitudinal, and the other a transverse section of the young seed.

The *Hevea* trees in the Peradeniya Gardens from which the material was collected, flower during April. Some capsules taken on May 5, which had grown to the size of large peas, showed no sign of this laticiferous system in the inner integument. The system at this early stage had not commenced to be differentiated.

A second lot obtained on May 13, with young seeds 5 to 6 millimetres long, revealed the commencement of this laticiferous system. Groups of parenchymatous cells situated, as a rule, about one or two rows of cells external to the inner limiting layer of the inner integument, increase considerably in size—to four or five times that of the neighbouring cells. Their walls thicken somewhat and their contents assume a more coarsely granular condition (Fig. 4). These, the laticiferous cells, appear first about the chalaza and develop more rapidly in the half of the seed along which the raphe runs ; indeed the production seems finally to be greater in this half than in the other. The walls between groups or rows of these cells partially break down, and processes grow out from many of them.

At a later stage (middle of June) this laticiferous system had reached about its full development. The processes are now a conspicuous part of the system; they branch a little. When a young seed at this stage is cut across, latex oozes out around the nucellus, or rather around the developing endosperm, since the former is now much crushed.

This laticiferous system then of the inner integument consists of a number of cells communicating one with another, due to the partial dissolution of the intervening walls, and of unsegmented processes emitted from these cells (Figs. 5 and 6). Such a laticiferous system suggests a blending together on a small scale of the articulate and inarticulate types.

No such laticiferous tissue is developed in the young seed of the somewhat closely allied rubber-tree, *Manihot Glaziovii*. The developing seeds of three other members of the order have been examined, viz. *Croton tiglium*, *Jatropha multifida* and *Euphorbia Lathyris*, without finding any such system.

It will be instructive to extend the investigation to other genera of the laticiferous Euphorbiaceae, to ascertain whether any more cases like that of *Hevea* are to be found, likewise to see whether this laticiferous system of the seed-coat of *Hevea* may be considered as a new production or as vestigial in the evolution of the group, as well as to endeavour to discover what function, if any, it may perform here.

This laticiferous system just described is interesting from another point of view. Scott¹, who has investigated the laticiferous tissue of the vegetative parts of *Hevea brasiliensis* and *Manihot Glaziovii*, showed that the tubes are true vessels, formed by the breaking down of the septa of rows of cells, and that these do not give out conspicuous processes. On the other hand, in the young seed of this plant, it has just been pointed out that the processes or unsegmented outgrowths from the cells are an important item in the construction of this laticiferous system.

REMARKS ON THE ORIGIN AND FUNCTION OF LATICIFEROUS TISSUE.

The morphology of the laticiferous tissue of the Euphorbiaceae is of much interest. When De Bary published his Comparative Anatomy of the Phanerogams and Ferns, the Euphorbiaceae were considered as including only plants with the inarticulate type of laticiferous tube.

Scott² in 1884 and 1885 showed that *Manihot* and *Hevea*, members of this order, had, however, an articulate laticiferous

¹ Scott, Quart. Jour. Micro. Soc., Vol. xxiv, 1884, and Jour. Linn. Soc., Vol. xxi, 1885. ² Scott, loc. cit.

system, and put forward the view that laticiferous tissue has been evolved independently along two distinct lines in the Euphorbiaceae.

The elaborate work of Chauveaud¹ in 1891 further complicated the story of the origin of the laticiferous apparatus in the order. He finds in such genera as *Aleurites* and *fatropha*, an embryonic inarticulate system replaced by an articulate one, and was driven to the conclusion that in this group the inarticulate system is the more primitive.

There is still room for a considerable amount of anatomical work on the laticiferous elements of the Euphorbiaceae, in order that the origin and development of the two systems may be traced.

It seems to me possible that an articulate system may give place to an inarticulate one by the gradual substitution of elongation and branching of the laticiferous cells for previous fusion of them. On the other hand, it might be simpler to regard the two systems as of independent origin from simple laticiferous cells, if it were not that the results of the work of Chauveaud quoted, hardly allow of this.

The origin of laticiferous tubes from secretory sacs containing tannin, resin, &c., is strongly suggested by such groups as the Papaveraceae and Aroideae, where there is a gradual transition from secretory cells to true vessels. Again, laticiferous plants as a whole are devoid of other secretory reservoirs.

Assuming that secretion, or the holding of substances of no further nutritive value, is the primary function of laticiferous cells, why is it that in certain groups of plants these cells, either by great elongation and repeated branching, or by the formation of vessels, have been changed into a complicated system of communicating tubes? Surely to perform some additional function or functions.

A conducting function is the one which naturally suggests itself. Since extracted latex contains such valuable foodstuffs as proteids and carbohydrates, the view of the tubes

¹ Chauveaud, Thesis. Paris, 1891.

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being channels for the transport of these materials is one which has received much consideration. The early development of the system in the embryo and young organs, as well as its association with the sieve-tubes, are brought forward in favour of this theory. It has even been suggested that in certain plants they take the place of sieve-tubes, since these latter diminish in number as the laticiferous tubes increase.

Another hypothesis put forward is that latex functions as a protection to the plant, either by closing wounds or by checking the ravages of insects. No conclusive evidence has been brought forward to show the likelihood of the laticiferous system of any plant having been evolved for such reasons. These plants seem just as liable to insect pests and fungus-diseases as others. In a tree like *Hevea* with thick latex, no doubt an injury to the bark is effectually closed by a plug of rubber, thus preventing, we may suppose, the entrance of fungus-hyphae, but to conclude that the latex has been elaborated for such a purpose is another matter.

If the formation of laticiferous tubes has been called forth in all plants possessing them to perform a common function, then I am inclined to think the idea of their serving as channels for holding water in reserve as one of the most plausible. Laticiferous plants are markedly characteristic of tropical regions, where transpiration is great. The development of a system of tubes running throughout the plant to be filled with water during the wet season and then to be gradually drawn upon during times of drought, is intelligible.

Warming, in a paper in the Botanical Gazette for January, 1899, entitled 'Vegetation of Tropical America,' mentions lianas and other plants of tropical forest and scrub as often laticiferous, and says, 'most likely latex serves several purposes, and one of them, I suppose, is to supply water to the leaves in times of need when transpiration becomes too profuse.'

From our experiments in Ceylon we found that the quantity of latex extractable from incisions in the trunks of *Hevea* trees varied considerably with the time of year, and seemed

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to depend largely upon the available moisture in the soil. After heavy rain the exudation of latex is much more copious and thinner, looking as if the vessels had become surcharged with water.

As the necessity for a reserve of water increased, the laticiferous system would tend to become more extensive and more intimately associated with the surrounding tissues. The genus *Euphorbia* chiefly inhabits dry regions and is one of the richest in latex.

This view does not explain the proteid or starch grains of latex, yet, I think, it is one to be borne in mind in studying the rôle of latex in plants, and hitherto it has in the main been disregarded. If latex does serve as a water reserve, then perhaps it is chiefly valuable for the growing organs.

Our knowledge of the function of latex can hardly be regarded as having advanced as yet much beyond the domain of hypothesis. There is a considerable amount of work to be done before we can arrive at the true meaning of such a richly developed system of milk-tubes as that in an *Euphorbia*. We know very little about the metabolic processes which result in the production of the secretions—tannin, resin, caoutchouc. We are still very ignorant of the way in which the sievetubes with their companion cells deal with proteids, though it has been suggested that the laticiferous tubes might relieve them of part of their work.

The problem is one of much interest in physiological botany, and not without its direct practical bearing on the production of the commercial articles, indiarubber and guttapercha. The solution of it may show that latex does not play such important parts in the plant's economy as has been claimed for it in the past.

EXPLANATION OF FIGURES IN PLATE XII.

Illustrating Mr. Parkin's paper on Latex and its Functions.

The figures all refer to Hevea brasiliensis.

Fig. 1. Diagram of the attachment of the petiole to the stem (nat. size). p., petiole; s., stem; b., axillary bud; sc., scar of stipule. The rest is explained in the text.

Figs. 2-6 refer to the laticiferous system of the young seed.

Figs. 2 and 3. Diagrams of median longitudinal and transverse sections respectively of young seed, which is nearly full size, but considerably off maturity (\times 3). *lat.*, laticiferous tissue exaggerated in size; *f.*, funicle; *r.*, raphe with main fibrovascular bundle; *c.*, chalaza; *oi.*, outer integument; *ii.*, inner integument with fibrovascular bundles; *ol.*, outer limiting layer of cells of inner integument which lengthen greatly in the radial direction and sclerose to form the hard coat of the seed; *il.*, inner limiting layer of cells of the inner integument, external to which is situated the laticiferous tissue; *n.*, remains of nucellus; *e.*, developing endosperm; *em.*, embryo; *m.*, micropyle; *cc.*, central cavity.

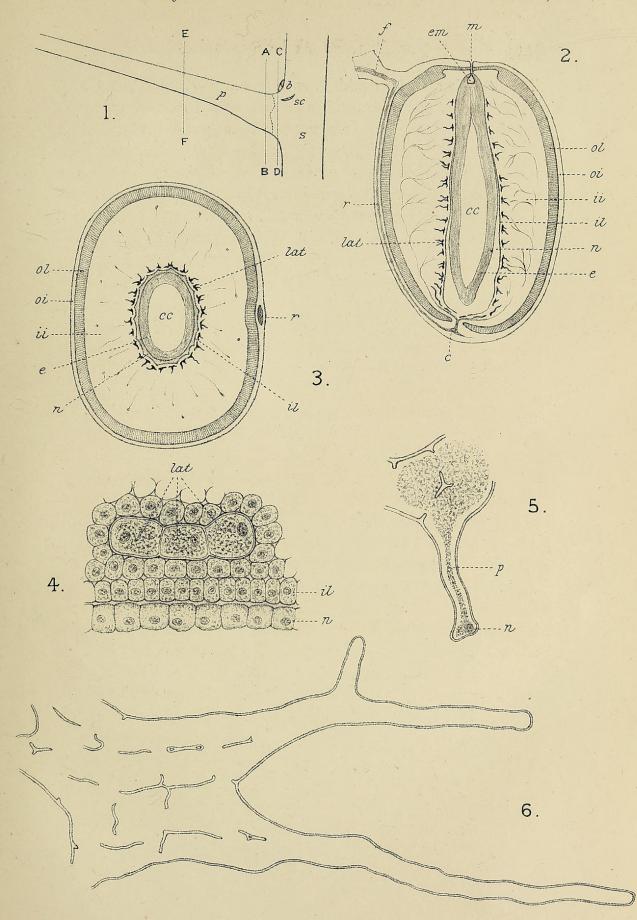
Fig. 4. Early stage in the formation of the laticiferous tissue (\times 550). *lat.*, three laticiferous cells differentiated from the surrounding parenchymatous cells; *il.*, inner limiting layer of cells of inner integument; *n.*, outer layer of cells of nucellus.

Fig. 5. A piece of the laticiferous tissue at a later stage (\times 550); cells in communication, due to the partial dissolution of the intervening walls. *p*., process; *n*., nucleus.

Fig. 6. Portion of laticiferous tissue fully developed; cell-walls only represented, contents having been dissolved out by chloroform. Note the partial dissolution of the intervening walls of the laticiferous cells and the long processes given out. $(\times 55^{\circ})$

Annals of Botany

Vol.XIV, Pl.XII.



J. Parkin del.

University Press, Oxford.

PARKIN. - OBSERVATIONS ON LATEX.



Parkin, John. 1900. "Observations on latex and its functions." *Annals of botany* 14, 193–214. <u>https://doi.org/10.1093/oxfordjournals.aob.a088774</u>.

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