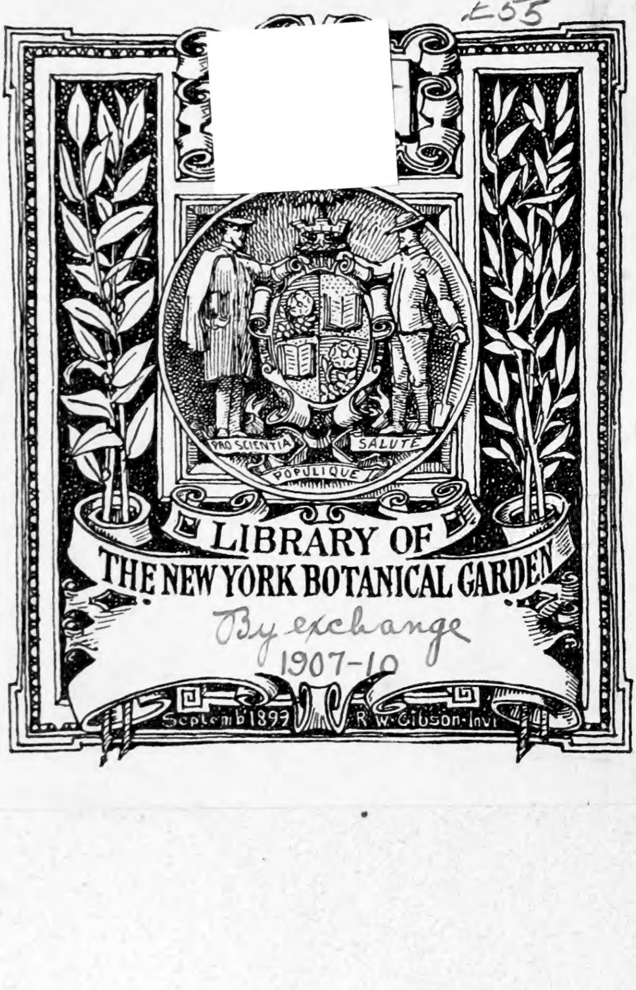
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MEMOIRS OF THE DEPARTMENT OF AGRICULTURE IN INDIA

BOTANICAL SERIES

VOL. II

AGRICULTURAL RESEARCH INSTITUTE, PUSA

PUBLISHED FOR
THE IMPERIAL DEPARTMENT OF AGRICULTURE IN INDIA

BY
THACKER, SPINK & CO., CALCUTTA
W. THACKER & CO., 2, CREED LANE, LONDON

CALCUTTA:
PRINTED BY THACKER, SPINK AND CO.

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VOL. II.

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VOL. [illegible]

March, 1907　　Botanical Series　　Vol. II, No. 1

Memoirs of the Department of Agriculture in India

SOME DISEASES OF CEREALS CAUSED BY SCLEROSPORA GRAMINICOLA

BY

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Price, Re. 1-8

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PLATE I.

Ears of Pennisetum typhoideum affected by Sclerospora graminicola.

SOME DISEASES OF CEREALS CAUSED BY SCLEROSPORA GRAMINICOLA.

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A CURIOUS disease of Pennisetum typhoideum (*bajra*) occurs sporadically in most provinces of India where this cereal is grown. It is not usually of sufficient intensity to attract much notice; but at times, particularly in low-lying ill-drained land, it develops into epidemics of varying severity. Its chief interest is, however, at present pathological, for it is one of a small number of diseases, caused by parasites, which produce deep alterations in the reproductive parts of plants, resulting in great modification in the floral organs and entire or partial sterility.

The general appearance of diseased ears is represented in plate I. The spicate inflorescence, from which this species obtains its name of the bulrush millet, is transformed wholly or in part into a loose green head, composed for the most part of small twisted leaves. Every stage can be found between ears in which the greater part ripens its grain normally, only a small proportion showing the characteristic deformity, and ears entirely affected and absolutely sterile.

To understand the changes in the inflorescence to which this appearance is due, it is necessary, in the first place, to have a clear idea of the structure of the normal inflorescence. The *bajra* ear is composed of crowded spikelets arranged around a woolly, unbranched axis, the whole ear being up to a foot long, by one, or one and a half inches broad. The spikelets (plate II, fig. 1) are pedicellate, the pedicel being jointed below a bristly involucre, which encloses usually one, but sometimes two to six (Prain) or eight (Gammie) spikelets. I have rarely found more than two on the diseased ears which are those that I have chiefly dissected. The rachilla of the spikelet is simple, and not prolonged beyond the upper floret. In the other Penniseti, when ripe, the pedicel breaks below the involucre which is carried on the fallen spikelet. In cultivated *bajra* the involucre is, however, usually persistent. The involucre consists of simple, or more usually, feathery bristles, unequal in length, but normally projecting slightly beyond the glumes. The lower two glumes on each spikelet are sterile; the lowest being always minute and sometimes altogether absent. Its veins are not visible. The second is often also minute, but may be nearly equal to the fertile glumes, and is three, five, or seven veined. Both these are obtuse, or the first is occasionally, and the second more often truncate or retuse and ciliated near the tip on the margins. The third and fourth glumes are usually fertile; the third enclosing a palea within which are three stamens. The paleæ and stamens are sometimes absent. The lower floret is, therefore, male or sterile. The fourth glume is paleate, and encloses three stamens and an ovary, or only the latter. There are two minute lodicules. The fertile glumes III and IV are boat-shaped, with a more or less shortly mucronate apex, ciliate at the margins, and with five or seven veins. The paleæ are enclosed by the fertile glumes, and resemble them except in being more delicate. On ripening, the fertile glumes and paleæ become hardened. Within them, in perfect florets, are two minute lodicules, three stamens with capillary filaments and versatile anthers, slightly bearded at the tip, and the ovary with a simple style crowned by two long stigmatic plumes.

The modifications undergone by diseased ears affect the secondary axes of the inflorescence only; and certain parts of these to a much greater extent than others. The following account is based on the dissection of some hundreds of spikelets from about forty diseased ears. Owing to the variation which I have found between individual ears, it is more than probable that changes other than those described will be found on further search.

1. The bristles of the involucre are very often hypertrophied, the hypertrophy affecting some only of the bristles (plate II, fig. 4). These are enlarged into tough, simple spines, usually non-plumose, ribbed, and showing various degrees of longitudinal torsion. They may be one inch long, by one-sixteenth of an inch thick, and may be flattened, round or angular. The upper part is sometimes spirally twisted, corkscrew-like. The bristles are also transformed in some cases into leathery, brown, flattened or contorted bodies, but they never show any approach to a leafy structure.

2. The pedicel sometimes bears two spikelets, the lower being laterally seated and sessile, a little way above the involucre (plate II, fig. 3). Only two spikelets have been seen thus, arising from the one rachilla.

3. The number of florets on a spikelet is sometimes increased to three or four (plate II, fig. 3, upper spikelet). One or two of these may remain as mere aborted buds, usually at the lower part of the rachilla.

4. In the individual spikelets the lower glumes I and II are never altered. As in normal ears they are often minute, and the lower usually difficult to see, and sometimes suppressed. The succeeding glumes III and IV, with their enclosed paleæ, are sometimes unaltered. More usually they are elongated, sometimes to over an inch in length (plate II, figs. 2, 3, 5). They never lose their character as glumes, and no division into sheath and blade was observed in any case, though they are occasionally virescent and usually softer and more membranous, than normally. Torsion, particularly of the upper part, often occurs; and sometimes the glume is split into segments as a result of a local action of the parasite, which will be more fully described under the leaf alterations to be mentioned below.

5. The lodicules are unaltered or suppressed.

6. The stamens are variously modified (plate II, fig. 6) or suppressed. The changes affect both the filament and anther.

The former may be prolonged to a length of over half an inch, or reduced, so that the anther is almost sessile. It may remain capillary, or become flattened and plumose, particularly at the base (e, g). The anther may remain unaltered on the modified filament, or may be reduced (e), elongated (c), plumose (d), or, rarely, contorted. The whole stamen may be changed into a leafy structure, colourless or brownish, narrow, with nearly straight sides, usually ciliate and sometimes with a transverse fringe, marking a division into a sheath-like and a blade-like portion (k, l, m, n). When thus flattened, the middle is often marked by a distinct vein (l). Sometimes the stamen appears as a brown, leathery, pointed body, with no differentiation into filament and anther, and almost circular in transverse section, thus becoming staminode-like. No increase in the number of stamens was observed.

7. The main alteration takes place above the stamens. The central portion of the floret is usually prolonged in diseased ears into a leafy shoot, consisting of reduced foliage leaves, much twisted or malformed (plate II, figs. 2, 3, plate III, fig. 2). This prolification occurs chiefly in the upper, perfect floret of the spikelet, but is accompanied usually by a similar, though less marked prolification of the lower, male or sterile floret. Sometimes the two are nearly equally affected. The maximum length observed in leaves thus axially produced within the stamens, was three inches, and the maximum breadth one quarter of an inch. Usually a well-marked division into sheath and blade occurs, the sheath being often more developed than the blade, which may be very imperfectly formed and much inrolled. The colour is either green or brown. A tendency to longitudinal shredding is often shown, a feature shared, as will be seen below, by the diseased normal leaves of affected plants. Longitudinal torsion occurs here also, and usually there is some degree of crinkling into longitudinal or transverse folds, particularly in the blade (plate II, fig. 2).

In place of a simple axial leafy shoot, the centre of the floret may be occupied by a branched reduced shoot with simple, soft, brown elements, crowded together in minute buds (plate III, fig. 1). This condition appears to be rare. An intermediate stage occurs sometimes in the prolificated male florets, where the centre may consist of four or five small, brown, simple or branched elements enclosed by the paleæ. Some of these may be staminodes, but the central ones are more probably reduced shoots, as it is difficult otherwise to explain the branching.

Central prolification of the floral axis in plants may be of different kinds. It may be what is often described as viviparity. This term appears to be very loosely applied in teratology. Strictly speaking, it implies the germination of the seed while still attached to the parent plant. It is also employed to denote sprouting of the inflorescence buds under similar conditions. But it is used, especially in the case of grasses, to cover cases of virescence of the outer floral whorls, or of prolification of the floral axis below the gynæcium, conditions in which it is difficult to justify the terminology. Thus Penzig (1894, Vol. II, p. 465) uses it to specify two cases described by Toumey (1891) of malformation in *Phleum pratense*, in one of which the floral glume was prolonged into a leaf, and in the other the axis above the glumes was elongated, and bore at its apex a perfect flower. It appears probable that many cases of so called viviparity in grasses, belong really to the class of changes next referred to.

This is the form of central prolongation of the axis of the flower called by Moquin-Tandon ‘‘ median prolification’’ (‘‘ diaphysis,’’ Englemann). Two varieties of this are described by Masters (1862, p. 360). In one, the new growth proceeds from between the carpels, which are formed, though they may be much modified. In the other the carpels are absent. The new growth is usually a flower bud (‘‘ median floral prolification,’’ ‘‘ floriparous diaphysis ’’), but it may be a leaf bud (“ median frondal prolification ”; ‘‘ frondiparous diaphysis’’). Masters points out that the change occurs very frequently in such plants as normally show a tendency to prolongation of the floral axis, indicated, for instance, by their having, free central placentation, or an enlarged thalamus (Rosaceæ, Ranunculaceæ), or elongation of the axis between two of the floral whorls, as in Dictamnus. The prolification is therefore in Masters' opinion one, not of the pistil, but of the upper segment of the floral axis, which may occur either above the carpels or may involve them. Two instructive cases are described by Masters in this paper. In one, a species of Campanula, the calyx was free, the corolla double, the stamens with petaloid filaments, and in the place of the pistil, there was a bud consisting of several series of green bracts, arranged in threes and enclosing quite in the centre three carpellary leaves detached from one another and the other parts of the flower and open along their margins where the ovules were placed. In the other, a Fuchsia, the calyx was similarly detached from the ovary simultaneously with the extension of the axis. Here the petals were increased in number and variously modified, the stamens also; while in the centre and at the top of the flower, conjoined at the base with some imperfect stamens, was a carpel open along its ovuliferous margin. These cases indicate a lengthening of the floral axis, immediately below the gynæcium, and in the second case the stamens were carried up on the prolongation.

The axial sprouting in the florets of Pennisetum in this disease, is a case of median frondal prolification, and belongs to the second variety of this, mentioned above, *i.e.*, that in which the whole segment of the floral axis, which bears the pistil, is prolonged, the pistil being at the same time entirely suppressed. In no case examined, was any trace of the pistil to be found. Further two cases were seen in which the stamens were carried up on the prolificated axis: in one, three stamens arose from the dorsum of the outer leaf of the new bud (plate II, fig. 7*a*); in the other, two of the stamens occupied their ordinary position at the base of the bud, while the third was carried up, and arose a couple of millimeters above the other, on the outer side of the sheath tube of the first leaf of the bud (fig. 7*b*).

In one head examined, the greater part of the florets were produced into an axial horn, a hollow organ entirely closed at the margin and produced from within the staminal whorl. This was, in many spikelets, produced equally from the lower (normally male) as from the upper (perfect) floret of the spikelet. Though, at first sight, it resembled a hypertrophied pistil, its structure was that of a leaf, and it must be considered as merely a modification of the commoner form of median prolification, in which the bud consisted, instead of a leafy shoot, of a leaf united at the margins to form a tube, within which, at the base, the rudiments of a second leaf were often formed. Hairs and stomata occurred on both surfaces, within and outside the tube wall. In some cases the union of the margins was imperfect, only occurring at the base, while the top was an inrolled blade.

It must not be supposed that all these changes occur in each diseased ear. As a matter of fact, there is the greatest possible variation between one diseased ear and another. In some, the bristles alone are affected, in others, the glumes show the most marked alterations, while in others median prolification is almost universal in the florets.

Besides the ears, the leaves of plants affected with this disease show more or less considerable changes. In young plants, or in early stages, many leaves may be seen with the usual fresh green colour changed wholly, or in part to whitish, and later to brown. The whitening of young leaves is visible usually as long streaks, often occupying half or more of the leaf surface, in transverse diameter, and extending almost the whole length of the leaf. In older plants the leaves affected are chiefly those from whose axils the ear stalks spring. These are more completely whitened than in younger plants, and the colour rapidly changes to yellowish brown. At the same time the leaf is deformed, being twisted and transversely folded, and shows a great tendency to shredding of the blade towards the tip (plate IV, fig. 1). This shredding is also shown in plate IV, figs. 2, 3, in other plants affected with the same disease, but is not usually so evident in Pennisetum, as in these. In old plants, when the green ears are fully developed, the upper leaves are mostly browned, and many of them similarly split. Many leaf buds in branching stalks are contorted, a mass of small white or brown twisted leaves being enclosed within the contorted outer leaf sheath (plate IV, fig. 1).

A considerable number of cases of virescence, prolification, and other modifications of the flowers of plants is known to be the result of insect or fungus attack. Many instances of the latter are mentioned by Tubeuf and Smith (1897, p. 26) and Rostrup (1886). Thus Peronospora violacea causes the stamens of Knautia arvensis to become petaloid. Ustilago violacea causes the rudimentary stamens of the pistillate flowers of Lychnis dioica to develop fully. The reverse occurs under the influence of several Ustilagineæ, ovaries developing in staminate flowers, as in Carex præcox infected with Ustilago Caricis. Physoderma deformans Rostr. causes virescence and malformation of the flowers of Anemone nemorosa. The extraordinary hypertrophies and distortions of the flowers of Cruciferæ attacked by Cystopus candidus are well known. Molliard (1901) has even shown that parasites acting at a distance can produce these modifications; as, for instance, in Primula officinalis, where double flowers result from the attacks of a Dematium on the roots; and petalody of the stamens of Scabiosa Columbaria was experimentally induced by him by inoculation of the roots with Heterodera radicicola.

In grasses, several instances of floral modifications of this nature are known, the most important of which are caused by fungus parasites of the genus Sclerospora, one of the Peronosporaceæ. It is to one of these that the disease just described is due.

The mycelium of the parasite is found in all parts of the attacked plants which show the alterations mentioned above. Thus it has been found in the stem, leaves, rachilla, bristles of the involucre, glumes and prolificated shoots.

The hyphæ are large, unseptate, very variable in size, up to nearly 10μ in diameter, and run chiefly intercellularly (plate IV, fig. 4). They are found in the ground tissues of the stem, and the mesophyll of the leaves chiefly, but branches penetrate the bundle sheaths in the leaves, where they lie between the sheath cells, and others collect under the stomata and in young leaves send out clusters of condiophores through these into the air. Only in rare cases, chiefly in late stages, have hyphæ been observed in the inner walls of the epidermal cells sending haustoria into them. The xylem and phloem elements proper never contain the fungus, though in some of the distorted bundles, where it is difficult to distinguish between the sheath and the outer layers of the xylem, cells may occasionally be found, apparently lying in the xylem, containing hyphæ. These are really sheath cells, infolded into the xylem by the distortion of the whole.

As in the case of several other fungi whose habitat is chiefly between the cell walls, some branches penetrate the latter and pass into or across the cell cavity. These intercellular hyphæ are of two kinds. The one are similar to the haustoria of other Peronosporaceæ, being simple or branched, thin-walled processes, arising from intercellular hyphæ, and sometimes forming small fungal clumps within the cells (plate V, fig. 1). The others correspond to the "Verbreitungshyphæ" described by Guttenberg (1905) in Ustilago Maydis, and like them are thick-walled filaments, often clothed with a distinctly two-layered cellulose sheath (plate V, fig. 3). This sheath, as in the maize parasite, consists of an outer portion deposited by the host cells around the penetrating hypha, in a defensive attempt to check its growth. The attempt often succeeds and the resulting thick-walled pegs projecting into the lumina are not uncommon (plate V, fig. 4). The inner part of the sheath is the wall of the fungus filament itself.

The intercellular mycelium is sparse in the stem and attains its greatest development in the leaves. The hyphæ frequently occupy the intercellular spaces at the angles of the mesophyll cells, but are also found in the lamellæ between two cells. They branch freely, have thick, rather gelatinous, cell walls, and clear protoplasm. In the stem, haustoria are not common, and are chiefly small, often button-shaped, processes, not unlike those of Cystopus. Their full development occurs in the leaves (plate V, fig. 1). Here, they are often extraordinarily numerous and usually simple or branched finger-shaped processes, sometimes much convoluted and occupying a fair proportion of the cell cavity. Their wall is thin while young, but older ones often have distinct cellulose caps (fig. 2) which are possibly provided by the host plant after the organ has ceased to be active, as in the case of Cystopus candidus (Guttenberg, 1905, pp. 8 and 9).

In fully infected leaves the mycelium is collected chiefly between the cells of the mesophyll adjoining the bundles and also in the inner layers between these (plate III, fig. 3). When sporangium formation is about to begin, tufts of mycelium reach the air chambers of the stomata, which are, as in many grasses, arranged in parallel, longitudinal rows, one on each side of each vein. Sporangium formation is accompanied by great assimilative activity of the fungus, which so increases its demands on the living cells of the host, as to cause the latter to collapse and finally die. Prior to this, the chlorophyll of the assimilating cells is wholly or in part destroyed, and starch is noticeably absent in the cells which harbour the haustoria of the parasite. Hence the pale streaks, which are the first indication that young leaves are affected, are visible before any conidiophores are extruded, and these streaks only turn brown, from death of the cells, after sporangium formation has reached its maximum.

The effects of the fungus on the tissues are evident both in the mesophyll and the bundles of the leaf. The former undergoes hypertrophy (" hyperplasie," Küster, 1903), the number of layers being increased without any modification in the structure of the cells. These remain always large, thin-walled cells, with small air spaces in the angles between adjacent cells. In the sheath, where a hypoderm of a single layer is often demarcated from the mesophyll on the upper surface, this may be increased to two or three layers. In the blade there is no hypoderm, and the increase takes place in the ordinary mesophyll layers, but is never considerable and is sometimes absent. On the whole, it may be said that the fungus occurs in greatest quantity in the blade of the ordinary leaves, and in the sheath of those produced by median prolification, and the hypertrophy produced is most evident in these parts.

In the bundles, the number and size of both the xylem and phloem elements are increased. In normal bundles of moderate size, the xylem consists of a central spiral vessel, with a second (annular) vessel, or an air space, inside it, and two large lateral vessels, one on each side. The phloem consists of a group of sieve tubes with their companion cells. In diseased leaves, the vessels are increased in size and number, groups of two or three large vessels occurring on either side (plate IV, fig. 4). The sieve tubes are increased in number and are slightly larger than normal. These modifications occur both in the sheath and blade of attacked leaves. From the collapse of the central layers of parenchyma which follows on sporangium-formation, and the consequent flattening of the leaf, the bundles are, in old cases, often distorted. being broadened transversely or sometimes infolded, so that the xylem projects laterally outside the phloem. In these cases the large vessels are flattened to a remarkable degree (plate IV, fig. 5).

Sporangia are produced only on the normal leaves of the host, never in the inflorescence. Following on the appearance of the whitish streaks which are the first outward sign of the presence of the parasite in the leaves, a cloud of thick, pale conidiophores bursts from the stomata, covering the surface of the streaks with a greyish white haze easily visible to the naked eye. A single or several conidiophores may project from each stoma (plate V, figs. 5, 6). They are broad, rather short, stalks, measuring about 100μ in length, by 12-15μ, unbranched in the lower part, but usually with a few short, thick branches, dichotomously or trichotomously formed at the top, and crowned with numerous papillæ of characteristic shape, on which the sporangia are borne. The latter are hyaline, broadly elliptical, slightly pointed at the free end, with a thin smooth wall, and 22-30μ by 12-16μ in diameter. They fall early without any stalk, and germinate rapidly in water, liberating zoospores (plate V, fig. 8). The number of zoospores varies with the size of the sporangium, from three or four up to a dozen or more. They are irregularly kidney-shaped, unequal sided, flattened bodies, with two cilia from the concave side, the posterior of which is the longer (plate V, fig. 8). The zoospores after coming to rest round off, measuring 9 to 12μ in diameter in the quiescent state, and germinate rapidly by a hypha.

After the formation of sporangia the conidiophores early collapse, the whole asexual stage of reproduction being evanescent, and only to be found in young plants. Once the characteristic deformity of the ears is visible, sporangia are not likely to be found.

Oogonia are formed in immense quantity, at a late stage in the life history of the parasite.* After fertilization they are large brown bodies, visible from their size and colour to the naked eye. They occupy the parenchyma of the leaf blades, both of the foliage leaves and of those formed in the inflorescence. Very rarely they occur in the sheaths of the foliage leaves and in the glumes, while in contrast to the foliage leaves, the sheaths of inflorescence leaves often contain them. They are often arranged in longitudinal rows on each side of the veins, as a result of oogonium formation taking place chiefly in the layers of parenchyma bounding the bundles, where, as already mentioned, the mycelium shows a tendency to collect. The ripe oogonium after fertilization, thickens its wall, which is closely applied to the wall of the oospore without, however, fusing. Hence, the whole fruit is characterised by the possession of a very thick wall in two layers, the outer of which is the oogonial wall, and the inner only belongs to the oospore.

The oospore is usually perfectly spherical, with a smooth wall, yellow in colour (Saccardo's "Chromotaxia" No. 23), and of even thickness all the way round. The oogonial wall, on the other hand, is deeper in colour, approaching tawny (between Nos. 31 and 32 of Saccardo), and is often irregular, being provided with thickenings, which gave the whole fruit an elliptical, angular or irregular shape, according to their position, but prevent it being ever quite spherical. The ripe fruit (plate V, fig. 9) measures 34 to 52μ in diameter (average of 25 measurements, 42μ), the oospore proper being 22·5 to 35μ in diameter (average of 50 measurements 32μ). After trials extending over two years, I have not succeeded in germinating the spores, though from the evanescent nature of the asexual stage, and the regular manner in which the disease appears in certain places every year, it is highly probable that this occurs

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* A rough calculation, made by counting the number of oospores in a measured part of the field of the microscope, gave 480 oospores to the square millimeter, in a portion of leaf where they were arranged in an almost solid mass.

freely in nature under suitable conditions. My trials have been made in the north of the Gangetic plain where I have never observed the disease to occur.

Three other examples of Sclerospora disease of cultivated Gramineæ occur in India.

The first of these is common in some places on Andropogon Sorghum (*jowar*), and I have collected it from several parts of the Bombay and Madras Presidencies. It is also the disease referred to in Madras by Mr. C. A. Barber (1904, p. 278), under the heading of "shredding of the leaves." Any disease of this most important crop which holds the possibility of epidemic extension, as this certainly does, is worthy of note.

It occurs frequently on low-lying land and does not appear to be easily detected on young plants. The affected plants become whitened at the top, irregular streaks forming in the upper leaves. Axillary branches are frequently deformed, a crowded bud being held imprisoned in the sheath of the subtending leaf, or the internodes are shortened so that the leaves stand out in a fan-like manner. Later on the usual shredding occurs, from destruction of the parenchyma between the veins (plate IV, fig. 2). At this stage, or earlier, the oospores are distinctly visible to the naked eye as small reddish points, arranged in parallel rows. These have been found in the leaf blades only, not in the sheaths. The ears may or may not be affected. In many cases they are not formed at all. In others they are deformed and much reduced but without the profound alterations of the flowers seen in the ears of Pennisetum. Mr. Barber says that in attacked plants no grain is produced. Hence, complete sterility is possibly a feature of this disease, though I have not had sufficient opportunity to examine this question personally. No sporangium formation has been discovered.

Anatomically the fungus occupies the leaf blade chiefly, having the same general distribution in the tissues as in Pennisetum. A dense fungus layer surrounds the bundles in advanced cases, lying outside the bundle sheath. In this the oospores are chiefly developed. The hyphæ are not usually as large as in Pennisetum and are hence more difficult to see. Similarly the haustoria are less developed, those seen being chiefly simple finger-like processes entering the parenchymatous cells.

Excepting for the absence of a sporangial stage, the fungus agrees with that on Pennisetum. The oogonia are similar in shape and colour and measure 38 to 50μ (average 41μ), thus being slightly smaller than on the first host. The oospores are 27 to 33μ (average 32μ), thus agreeing with the other. I can find no constant difference sufficient to refer the fungus on the two hosts to different species.

The third cereal disease caused by a Sclerospora in India is very briefly referred to by Mr. Barber in the same paper as the above. It occurs on Setaria italica in Madras, being very abundant in some parts. I have only examined specimens kindly provided by Mr. Barber, and have not seen it in the field. These showed the same distortion and shredding of the leaves as in the previous cases (plate IV, fig. 3). The latter were crowded with oospores, agreeing with those on the other hosts in shape and colour, and 36 to 46μ (average of twenty measurements 41·5μ) and 26 to 34μ (average of twenty measurements 30μ) respectively, in diameter. Hence, though the asexual stage was not observed, the fungus cannot be separated from those on the other hosts.

The last of the Indian Sclerospora diseases which I have seen was found on Euchlæna (Rheana) luxurians on the Poona Government Farm, in 1905. The sporangial stage alone was observed, and agreed perfectly with that on Pennisetum which was common in the vicinity. Only early stages of the disease were seen, and hence oospores could not be discovered. The host plant was being experimentally grown on the farm and is not, so far as I am aware, cultivated anywhere in India, though an important fodder in some parts of the world. The disease is therefore of minor importance in this country.

The whole of the characters of these fungi correspond to the type of the genus Sclerospora. Of this three species have been recognized in the most recent work on the genus, and a fourth should probably be added, to include Peronospora Maydis Raciborski (1897). Thus extended, it embraces all the Peronosporaceæ which occur on grasses, and all of its members are found on these hosts, excepting the least studied, S. Magnusiana Sorokin, which was found by Sorokin on Equisetum in Russia.

Peronospora Maydis Racib. agrees entirely with Sclerospora in its asexual stage, differing from all other Peronosporaceæ in the broad, short conidiophores, with short, thick, dichotomously formed branches at the top, provided with broadly conical papillæ on which the conidia are formed. The mycelium and haustoria also agree, the latter being of the button-shaped type found in the stem of Pennisetum. The oogonia differ somewhat, having a not very thick, though persistent, membrane. This is not smooth, but provided with irregularly arranged, small, conical, warty thickenings. In the older descriptions the oogonial wall of Sclerospora was described as fusing with that of the oospore on ripening, but Berlese (1902, p. 69) is clearly not of this opinion, and it is easy to ascertain from sections or by long maceration that the two coats are perfectly distinct. In Raciborski's species therefore, the separation of the two walls mentioned by the author does not tell against the fungus being a Sclerospora. No doubt the figure accompanying the description is about as unlike the oospore of a Sclerospora as could be, but it is evidently highly diagramatic, and omitting the figure, the description would apply sufficiently to Sclerospora. In Berlese's Monograph it is also suggested that the species is a Sclerospora, but a definite opinion is not given there, and cannot be given here, in the absence of an examination of original specimens. The fungus causes the most intense cereal disease produced by the Peronosporaceæ, epidemic outbreaks in Java (where it is known as "lijer"), destroying whole fields of maize. It has not so far been reported elsewhere.

The remaining grass parasites of the genus have been critically examined recently by Traverso (1902 (1)). As a result of a careful study he gives the following classification, reducing to two the three species which had been usually accepted:

Oospore 28-35μ. d.; hybernating spore with undulated contour, with wall of the oogonium very thick, rubiginous. *Scl. graminicola.*

Oospore 40-60μ. d.: hybernating spore with smooth contour, with oogonial wall not or little thicker than that of the oospore, pale yellow. *Scl. macrospora.*

As an asexual stage has only been found in Scl. graminicola, Traverso bases his classification on the sexual stage alone. It is in this stage only, that the majority of students of the genus have seen their species.

Sclerospora graminicola (Sacc.) Schroet. has been recorded up to the present only on species of Setaria, chiefly S. viridis, but also S. italica, S. glauca and S. verticillata, in Italy, France, Germany, Austria, Russia, the United States and Japan. The influence of the parasite is very similar to that above described, virescence of the ears and distortion and shredding of the leaves being common. An excellent illustration of the disease of S. italica ("Awa") in Japan is given in Arata Ideta's Lehrbuch der Pflanzenkrankheiten in Japan (1903) with a description in Japanese. In this, the prolification of the spikelets and shredding and torsion of the leaves is well shown, and the fungus is clearly figured. It will be remembered that this is one of the cereals mentioned above, as being subject to Sclerospora disease in India. Similar effects on the other host plants have been referred to by several authors.

Sclerospora macrospora Sacc., under which Traverso, apparently with good reason, includes Scl. Kriegeriana Magn. (1895) occurs on a number of grasses, having been found in Australia on Alopecurus sp.; in Germany on Phalaris arundinacea; in France on oats; and in Italy in recent years, on wheat, maize, oats, Avena fatua, Agropyrum repens, Glyceria maritima (?), Phalaris coerulescens (?), Ph. arundinacea (?), Ph. canariensis, Lolium perenne, Agrostis alba (?), Holcus mollis (?) and Phragmitis communis. Its conidial stage has not been discovered. The Italian species, which was, after critical study, referred to this species by Traverso, was first considered by Peglion (1900 and 1901), who had chiefly investigated it in the field, to be Scl. graminicola. In the neighbourhood of Rome in 1899 a rather severe outbreak occurred in wheat, due chiefly, according to Peglion, to flooding of the fields by the Tiber in that year. The ears were deformed and virescent, and no grain was matured in affected plants. The disease on this host has been several times observed since in different parts of Italy. A similar disease of maize was described by Cugini and Traverso (1902) near Modena, and its effects on this host as described by D'Ippolito and Traverso (1903) are similar to those of Scl. graminicola on Setaria. On the other cereal hosts mentioned above, the damage caused appears to be less considerable, and outside of Italy these new cereal diseases, which nevertheless are threatening enough, appear to have attracted little notice.

In the tropics I have been able to find only two references to disease produced by the genus, leaving out the "lijer" disease of maize. In neither is the parasite correctly determined. One is that by Mr. Barber (1904) mentioned above; the other a brief description of a Pennisetum disease, similar to that in India, from specimens collected by Dr. W. Busse in German East Africa, by F. C. von Faber (1905). In the first of these the parasite is taken to be probably one of the Chytridiaceæ, since the mycelium was not clearly seen, and the sporangial stage not observed. The resemblance of the oogonia to the resting sporangia of some Chyridiaceæ is considerable. In von Faber's paper the mycelium and oospores are described but not the sporangial stage, and the author was unable to determine if the Chytridiacean-like bodies (the oospores) were in organic connection with the mycelium, and attributes the disease to the mycelial infection. His description of the pathological changes in diseased plants differs somewhat from that given above. The glumes and bristles of the ear are said to be prolonged into leafy structures, a condition never seen in my specimens, and in the latter case difficult to accept on morphological grounds. The leaves are thickened by the development of a many layered hypoderm. Since, however, I have found a wide range of variation in the character of the deformity produced in different ears, it is quite possible that the action of the parasite in Africa differs from that in India. There appears to be no reason for supposing that the diseases are different.

It remains only to determine the species to which these Indian Sclerospora parasites belong. After a careful examination of all my material and comparison with the specimens of Scl. graminicola issued in Sydow's Phycomycetes and Protomycetes (Nos. 36, 37 and 165) and Scl. macrospora issued in Briosi and Cavara's Funghi parassiti No. 352, no doubt remains that the Pennisetum parasite is Scl. graminicola. This is somewhat surprising when we consider the much wider range of hosts in Scl. macrospora, while this is the first time that Scl. graminicola has been found on other hosts than Setaria. The sporangial stage agrees fully with that already described in Germany by Schröter (1879) and Fischer (1902), and in Japan as figured by Arata Ideta (1903), though the sporangia are larger, being 22-30μ by 12-16μ as against 20 by 15-18μ (Fischer). The sporangia are, however, variable bodies, since Berlese (1902) quotes measurements by Malbranche and Letendre, giving 12-15 by 10-11μ as the diameter. Scl. graminicola is so far the only species known to have this stage, if we omit Peronospora Maydis.

The hybernating spore also agrees. Traverso (1902 (1)) gives a very full description of the fruit and finds from a number of measurements that the oogonium averages 45·9μ in diameter and the oospore 32μ. The measurements given above for the Pennisetum parasite (42μ and 32μ respectively) agree in the most important item, the oospore, and are much smaller in both than the corresponding measurements for Scl. macrospora. The specimens in Sydow's exsiccata collected by Sydow on Setaria glauca near Berlin (No. 36) and by Kabat on S. viridis in Bohemia (No. 165) agree in measurements, and in the colour and shape of the fruit, very closely with the Indian fungus. Excepting, therefore, the difference of hosts the Setaria and Pennisetum Sclerosporas agree in all respects.

The fungus on Andropogon Sorghum corresponds with the above in the oogonial stage, which alone has been found. It is, of course, possible that sporangia will be found on this host also, when it is more fully examined, as I have not had sufficient opportunity for watching it on the living plant. In all the systematic works which treat of Sclerospora the characters of the ripe fruit are taken as the basis for classification, and on this basis it is impossible to separate the species from Scl. graminicola.

On Setaria italica similarly, only oogonia and oospores have been observed in India. These are identical with the above in shape and colour, and are almost exactly the same size. As Scl. graminicola is already widely known on this host, this merely adds a new locality for its ravages. Traverso (1902 (2)) has found a special form. Scl. graminicola var. Setariæ italicæ—in Italy, differing from the type, in having larger oogonia and oospores ; but the fungus in India agrees in all respects with those on other Setariæ in Sydow's exsiccata and from the measurements given must be referred to the type species, not the variety.

Finally the fungus on Euchlæna luxurians agrees in its asexual stage with Scl. graminicola and, as no other species is known to possess this stage, may be referred provisionally to it.

Agricultural Research Institute,
Pusa,
12*th February*, 1907.

E. J. BUTLER.

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DESCRIPTION OF THE PLATES.

Plate I.

General appearance of ears of Pennisetum typhoideum affected by Sclerospora graminicola (Sacc.) Schroet.

Plate II.

Effects of the fungus on the inflorescence of Pennisetum typhoideum.

Fig. 1. Normal spikelet of Pennisetum: 1. lower sterile glume; 2 upper sterile glume; 3 and 4 fertile glumes. P. paleæ. The upper floret is perfect, the lower male. X 7.

Fig. 2. Spikelets showing prolification. Figures and letters as before. X 1½.

Fig. 3. Pedicel with two spikelets arising above the involucre. That on the right and lateral bears two florets, f. 1. the lower, f. 2 the upper. That on the left and terminal bears three florets, f. 3., f. 4. and f. 5., 1. 1. lower sterile glumes; 2. 2. upper sterile glumes; 3. 3. 3. 3. 3. fertile glumes; P. P. P. P., paleæ; the floret, f. 3. being without a palea. s. s. s. s. s. the axial leafy shoots in the centre of each floret. These consist of a small number of narrow leaves, inrolled and contorted. X 1½.

Fig. 4. Hypertrophied bristles of the involucre. Natural size.

Fig. 5. Modified glumes from affected spikelets. Natural size.

Fig. 6. Modified stamens from affected spikelets. See text pp. 3 and 4 for further description. X 2.

Fig. 7. Stamens carried up on the prolificated shoot. Natural size.

Plate III.

Fig. 1 Apex of the floral axis of an affected spikelet, consisting of a cluster of bud-like structures on a branched stalk. X 16.

Fig. 2. Dissection of two spikelets borne on one pedicel, as in Plate II, Fig. 3. i involucre of unaltered bristles: 1. and 2. lower and upper sterile glumes; 3. fertile glumes; P. paleæ, there being

none on two of the florets; st. stamens variously altered, and with two suppressed in the floret on the right; s. prolificated shoots arising within and above the staminal whorl. In the left hand floret this was a simple horn. In the others it consisted of some contorted reduced leaves, which have been in part dissected out in the two right hand florets.

Fig. 3. Diagram showing the position occupied by the fungus mycelium in the mesophyll of the leaf of Pennisetum.

Plate IV.

Fig. 1. Contorted leaf bud of Pennisetum typhoideum affected with Sclerospora.

Fig. 2. Leaf shredding in Andropogon Sorghum affected with Sclerospora.

Fig. 3. Leaf shredding in Setaria italica affected with Sclerospora.

Fig. 4. Section of an infected leaf of Pennisetum showing the distribution of the fungus hyphæ in the mesophyll and adjoining the bundle sheath.

Fig. 5. A leaf bundle distorted as a result of the action of the parasite in causing collapse and flattening of the mesophyll cells.

Plate V.

Fig. 1. Haustoria of Sclerospora graminicola in the mesophyll cells of an infected leaf of Pennisetum. On the left simple and branched finger-shaped haustoria, the type which predominates in the leaf. On the right two club or button-shaped haustoria, a type more commonly seen in the stem. X 500.

Fig. 2. Old haustoria with a distinct cellulose cap. X 500.

Fig. 3. Intracellular hypha, showing the wall of two layers, the outer of which connects with the cell wall and belongs to the host plant. X 500.

Fig. 4. a. Intracellular hypha running obliquely across two cells. Note the very thick wall and almost occluded lumen; b. b. peg like processes projecting into the cells, but arrested in further growth by the deposition of a thick cellulose cap. X 500.

Fig. 5. Conidiophores of Sclerospora graminicola from Pennisetum after the sporangia have fallen, showing the mode of branching. X 400.

Fig. 6. Conidiophores bearing immature sporangia. X 400.

Fig. 7. Conidiophore with mature sporangia. X 400.

Fig. 8. Sporangia germinating after having fallen into water; and zoospores. From Pennisetum. X 500.

Fig. 9. Oogonia and oospores of Sclerospora graminicola, after ripening: a. from Pennisetum typhoideum, b. from Andropogon Sorghum; c. from Setaria italica. Optical section, diagrammatic. X 550.

PLATE II.

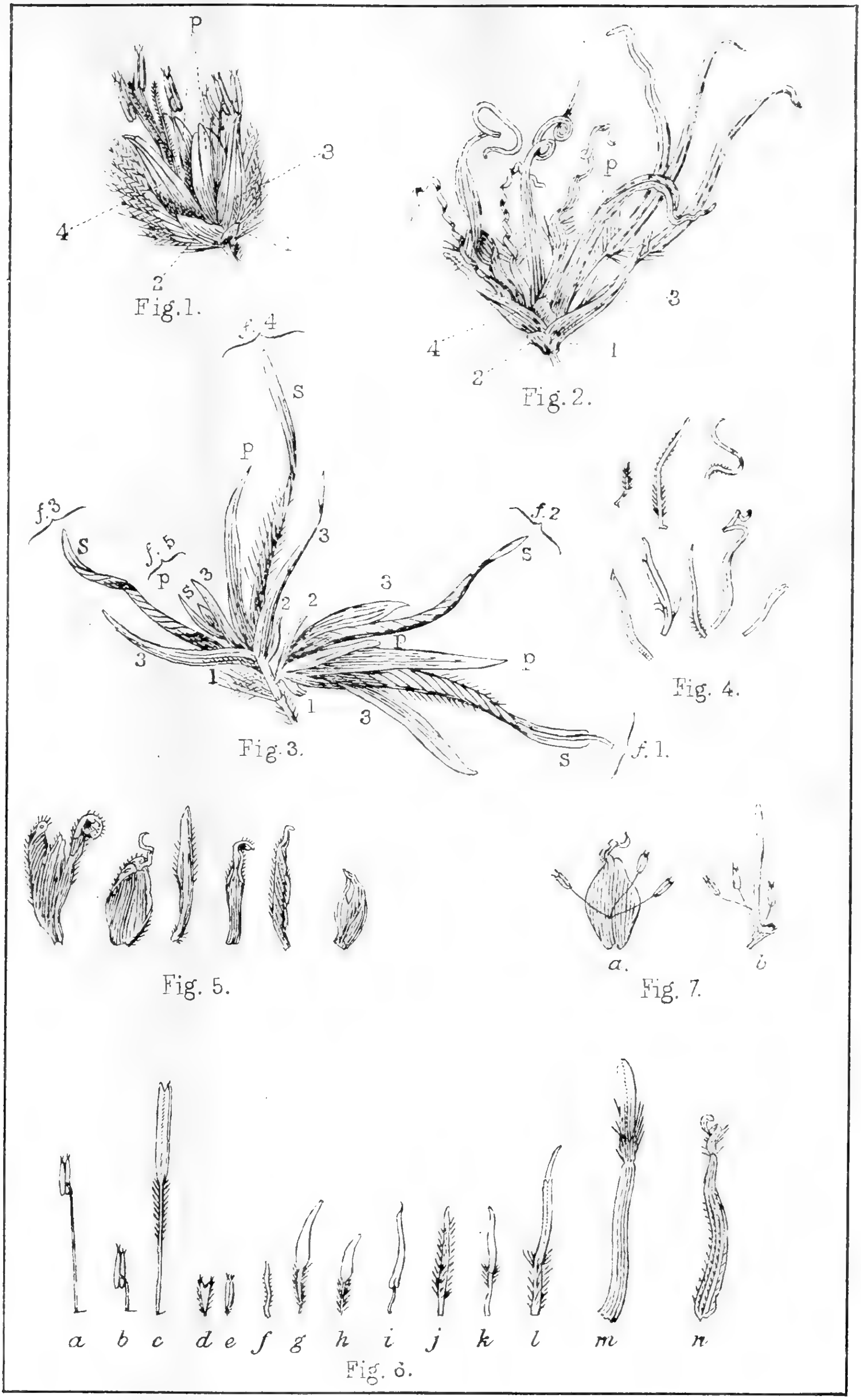
p
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Fig. 1.
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Fig. 3.
Fig. 4.
Fig. 5.
a.
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Fig. 7.
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Fig. 6.

PLATE III.

Fig. 1.

Fig. 2.

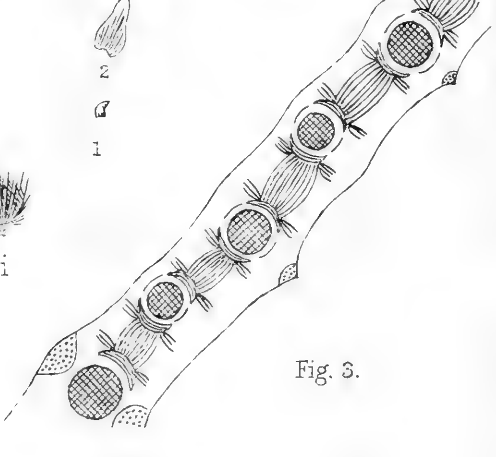


Fig. 3.

PLATE IV.

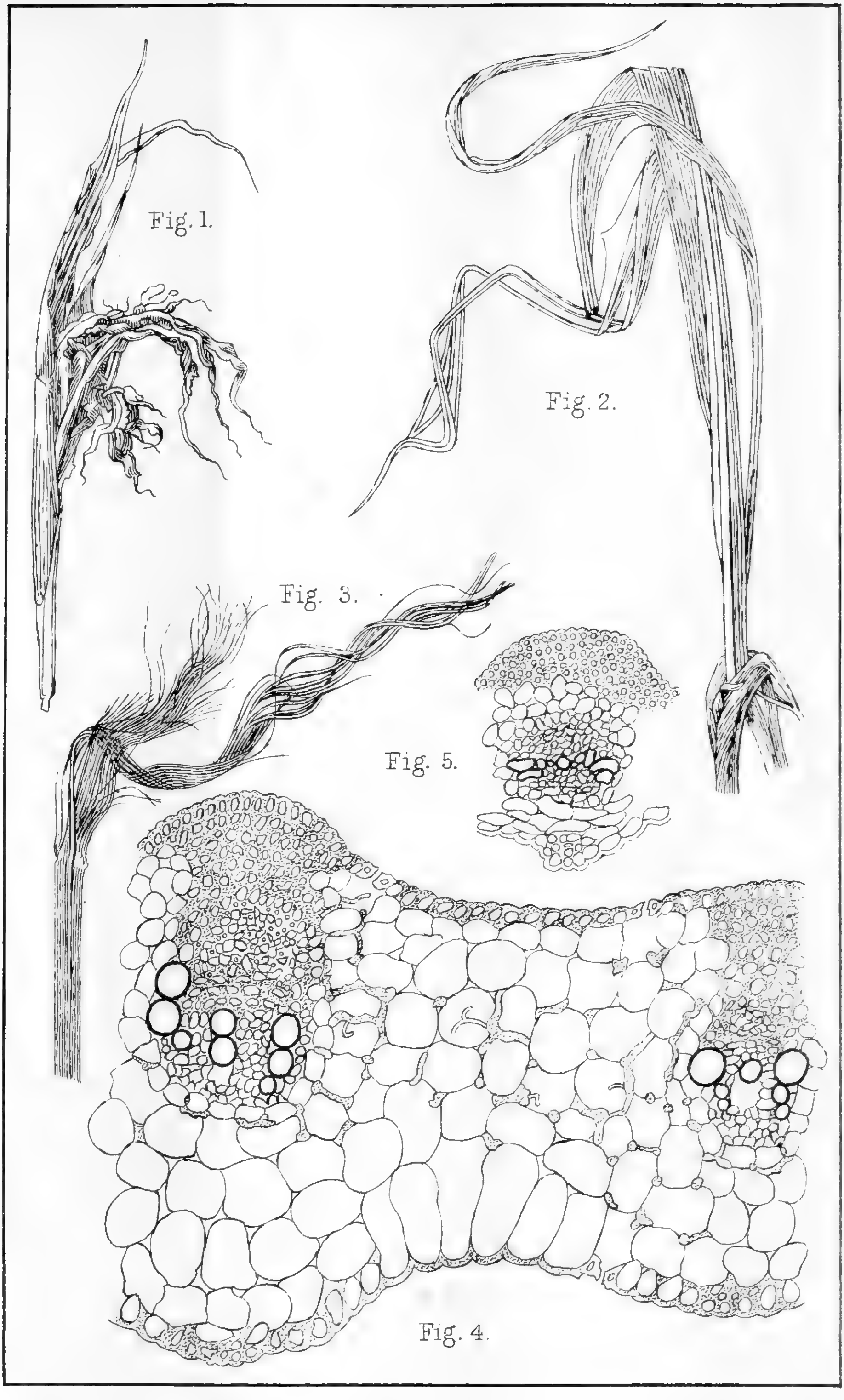
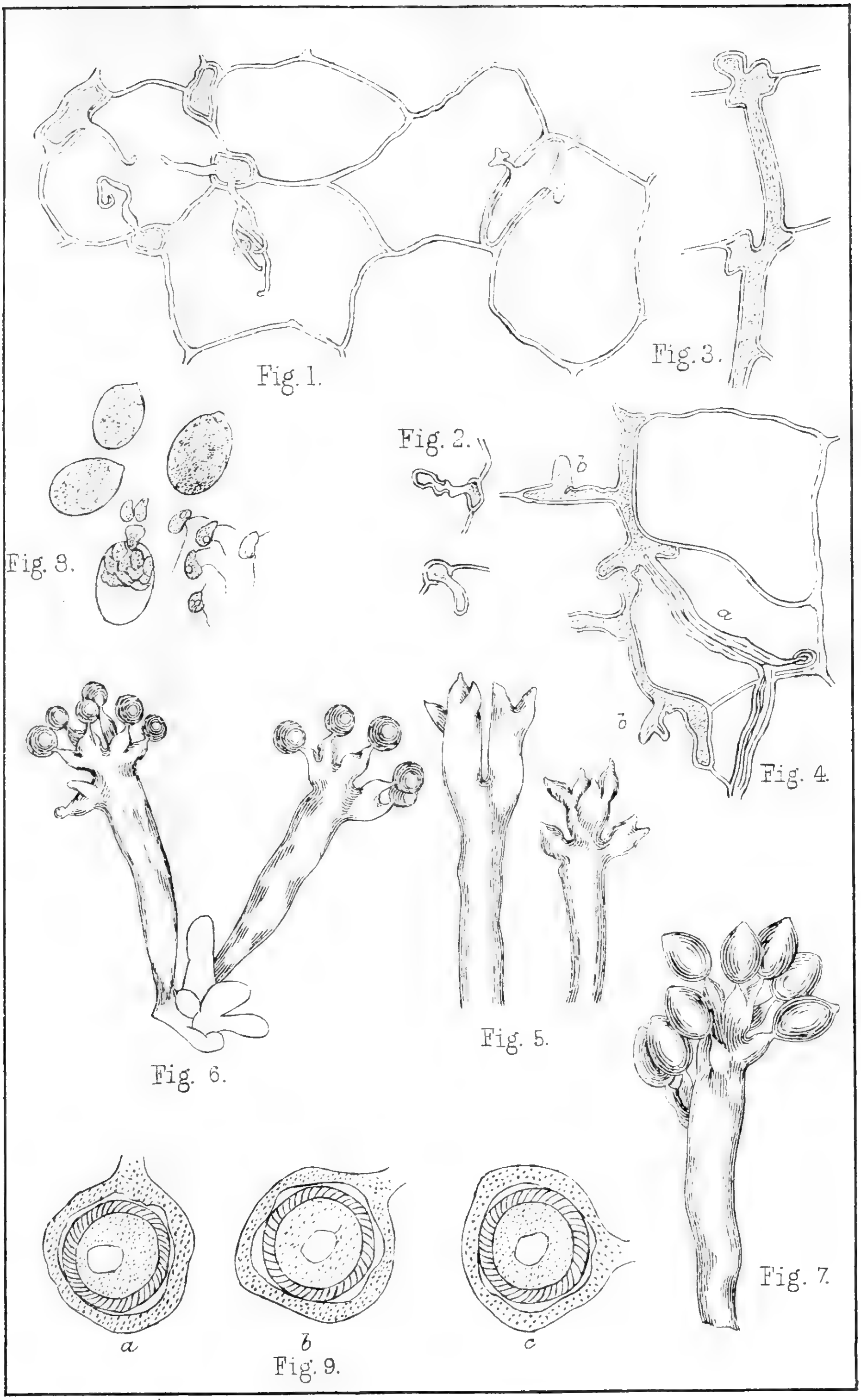


PLATE V.



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September 1907 **Botanical Series** **Vol. II, No. 2**

Memoirs of the Department of Agriculture in India

THE INDIAN COTTONS

BY

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CONTENTS.

THE INDIAN COTTONS.

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CHAPTER I.

GENERAL REMARKS.

The cultivated cottons of India possess the following characters in common. Erect, large or small shrubs, with long tap roots and few lateral roots. *Stems* woody and brittle below, herbaceous toward extremities, usually wandlike ; growth cymose from the first so that the whole plant forms a *Sympodium ;* inner bark of long tough fibres. *Branches* ascending or spreading, becoming successively shorter upwards, their disposition affording valuable diagnostic characters ; all young parts except the flowers, covered with partially deciduous, hirsute, simple and stellate hairs. *Leaves* membranous or subcoriaceous, varying from entire to 1- 3- 5- 7-lobed, palminerved, margins of lobes entire or sinuate ; accessory lobes often rising from or above the sinuses ; the central rib and usually the rib on either side of it with a *gland* on the under surface. *Stipules* falcate, entire or toothed. (The leaves of seedlings and those appearing during the rainy season are larger, more flaccid, with more distinct basal lobes, folds and sinuosities than those which are developed after a partial shedding in the cold weather. *Inflorescence* cymose, of single flowers on terminal or secondary and tertiary axes, erect or spreading, always pendulous in fruit ; *peduncle* and *pedicel* short, trigonous ; *involucre* or *epicalyx* of three bracteoles connate at their broadly cordate bases, margins rounded, with deep or shallow teeth, which either extend over the whole margin or are confined to the apex, which is obtuse or acute, venation longitudinally sub-parallel. *Calyx* gamosepalous, campanulate or cupular, *limb* entire or irregularly toothed, accrescent and usually splitting in fruit, with three *glands* often secreting a nectar-like exudation at the base externally. *Corolla* polypetalous, *petals* 5, contorted dark purple, pink, yellow or white with a dark eye, straight or reflexed, adnate to the base of the *andrœcium*. *Stamens* indefinite, monadelphous, lower part of the tube usually naked, upper part (exclusive of the very apex) with one-celled *anthers* on short erect or spreading *filaments*. *Ovary* superior, syncarpous, 3-4-celled, *ovules* numerous on axile *placentas*, lower part of *style* entire, the upper exserted part of 3 to 4 more or less connate and twisted arms bearing the stigmatic surfaces. *Capsule* or *boll* usually 3- but sometimes 4-celled, almost spherical or ovoid, subtrigonous acuminate, the point consisting of the short, persistent basal part of the style ; *dehiscence* loculicidal, *valves* strongly reflexed so that the cotton becomes pendulous. *Seed* with a hard testa and spiny hilum, naked or covered with short down called fuzz or velvet and longer unicellular twisted, white or tawny hairs which constitute the cotton of commerce.

It is customary amongst botanists to assume that the numerous forms of cotton plants have become inextricably complicated and difficult to understand and distinguish through hybridization. After seven years of almost constant observation of a large series of Indian cottons grown in parallel plots in one block on the farm at Poona, I consider that this position is untenable and select the following facts to support my contention that Indian cottons are normally self-fertilized. A large number of varieties procured from almost every part of the country has been grown in contiguous lines without hybridization occurring. Although a number of hybrids has been artificially produced, not one of these can be matched with any known variety. The stigmas are usually pollinated immediately on the opening of the flower which, moreover, remains open for a very short time. Bees and small flies are fond of visiting the glands *outside* the calyx for the sake of the nectar ; some beetles eat the petals ; but few insects enter the flower itself before it is fertilized. The results of a long series of experiments conducted by Mr. S. V. Shevade show that emasculated flowers allowed to remain uncovered usually drop off unfertilized. In the few cases where he observed that pollen was carried to the stigmas by insects, bolls were not subsequently developed. These observations are confirmed by the experience of Mr. F. Fletcher, M.A., B.SC. (Deputy Director of Agriculture, Bombay), in Egypt and India. Many of the varieties grown in India are separated by long distances, in which cases hybridization is, of course, a physical impossibility. In districts where a mixture of varieties is habitually grown by the cultivators, no hybrid plants are to be found. The progeny of plants which are artificially cross-fertilized are usually more fertile than their parents. This proves that cross-fertilization is really of great service to the plant. The form of its flower with a dark base is an ideal insect lure, and it is difficult to understand why cross-fertilization should not prevail. The only solution to the problem appears, therefore, to lie in the fact that, in the Indian cottons, these so-called species and hybrids are merely cultivated races, evolved by time and environment from one prototype. All the evidence available to me appears to prove, almost without the probability of a doubt, that *Gossypium obtusifolium*, Roxb., the *Rozi* of Gujarāt, the most widely distributed wild and cultivated cotton in the old world, is the parent from which all our present forms have sprung. The progeny from the plants of this species grown in Poona for seven years now show characters which bring it into close relation with *G. herbaceum* and *G. indicum*. In the field it is easily distinguishable as a species by habit alone, but I find it very difficult to separate it with certainty from *G. herbaceum* or *G. indicum* in the Herbarium. The bracteoles, which are relied upon as diagnostic characters, are also misleading as they are indifferently toothed or entire in flowers from the same plant. *Gossypium Stocksii*, a wild plant of Sind, is by some considered the parent stock of Indian cottons. I cannot concur in this opinion. It resembles no Indian cotton and possesses certain characters which induce me to surmise that it is a degeneration of some American cotton.

No species cultivated in Sind at the present time resembles it in any particular.

All Indian cottons can be hybridized freely by artificial means. Hybridization of American and Indian varieties has been invariably unsuccessful both in India and in America.

A few more years of experiment and observation are necessary to prove absolutely that climate, soil and general environment are the factors which influence the tendency to variations in the cottons. If botanists and agriculturists will devote careful attention to the cottons growing in the fields throughout their provinces, a confirmation or refutation of my theory will soon be arrived at.

CHAPTER II.

A PROPOSED CLASSIFICATION OF THE INDIAN COTTONS.

THE following classification is suggested after a close study (extending over seven years) of numerous varieties grown systematically at the Poona Farm, supplemented by field observations in the cotton districts of Bombay and by information generously supplied by observers in other parts of India. This season the United States Department of Agriculture has supplied me with seeds of a long series of American forms, and I defer attempting to compile a history of the nomenclature of the cottons until I have studied these in a living state.

No method adopted in any of the numerous works extant on the Systematic Botany of the whole or parts of India has been found to meet the requirements of our present knowledge. Three years ago I worked at the subject in England and found but little enlightenment, as the material in the Herbaria is not only scanty but has never been critically examined. Parlatore's work, entitled "Le Specie dei Cotoni descritte" and that of Todaro called "Relazione Sulla Cultura dei Cotoni in Italia seguita da una Monagraphia de Genere Gossypium" are the two principal works dealing with the botany of cotton. In default of anything better I have attempted to correlate Todaro's descriptions and figures with our plants.

As these notes are drawn up primarily for the use of Indian agriculturists, I have multiplied the number of species and varieties, knowing from my own experience that such a procedure assists to simplify what even then must still remain a subject difficult to understand. From a botanical point of view it is clearly evident that we have at the most only one true species of cotton in India, *Gossypium obtusifolium*, with its two sub-species, *G. arboreum* and *G. herbaceum*. All other forms should be treated as derivatives of these. The following species and varieties which I describe are really agricultural races, which remain fairly constant to their characters in the environment within which they have been evolved or cultivated for some considerable time. Sharing in the same descent, they are capable of being crossed with facility and their descendants are fertile.

A. Rozi and Dev Kapas Group, all the branches ascending and thickly crowded, not drooping at their extremities. *Leaves* with basal lobes and lateral folds in the sinuses. *Bracteoles* entire or only slightly toothed on the margins and apex. *Flowers* small, dark purple, pink purple or yellow. *Bolls* small or large.

1. Gossypium obtusifolium, *Roxb.*—Whole plant green. *Corolla* yellow. *Cotton* white.

,, ,, ,, *Var. nov.* Coconada. *Cotton* drab.

,, ,, ,, *Var. nov.* hirsutior. *Plant* more hairy, with a strong tendency towards *G. herbaceum.*

,, ,, ,, *Var.* Nanking. *Plants* with a tendency towards *G. neglectum. Bolls* and *bracteoles* large.

1. Gossypium obtusifolium, *Roxb.*—*Var. nov.* sindica. *Branching* more sparse than in type, upper branches with a strong tendency to become successively shorter. *Plants* with a tendency towards *G. indicum.*

2. Gossypium arboreum, *Linn.*—Perennial. Whole plant and corolla dark purple or red. Velvet of seeds green. Lobes of leaves narrow.

„ „ „ *var. nov.* platyloba. Lobes of leaves broad.

„ „ „ *var. nov.* vagans. *Lint* khaki.

3. Gossypium sanguineum, *Hassk.*—Annual. Plants dark purple. *Corolla* dark purple.
   (*a*) broad lobed forms.
   (*b*) narrow lobed forms.

„ „ „ *var. nov.* minor. *Corolla* pink purple.
   (*a*) broad lobed forms.
   (*b*) narrow lobed forms.

B. Herbaceum Group.—Bushes round-headed or with the apex of the stem slightly prolonged and sparsely branched. All the branches usually long and spreading *Leaves* softly hairy, light green, folds lateral only in the sinuses. *Bracteoles* round, uniformly gashed, usually spreading in fruit. *Flowers* yellow with a dark eye. (The eye in the corolla of *herbaceum* varieties shows a yellowish white circle in the centre, from which arises the staminal tube and style. This circle throws out obliquely radiating yellow narrow bands or patches unoccupied by the dark crimson of the eye. In other types this circle is represented by a perfectly regular pentagon, having no radiating yellow lines).

4. Gossypium herbaceum, *Linn.* *Valves of boll* thoroughly reflexed so that the cotton is pendulous.

,, ,, ,, *var. nov.* madraspatana. With smaller bolls but otherwise as in type, of which it is probably a degenerated form.

,, ,, ,, *var. nov.* melanosperma. As in the last, but testa of seed naked.

,, ,, ,, *var. nov.* sakalia. *Bolls* large, not opening widely.

C. The Jethia Group.—Round-headed bushes, apex of stem seldom produced, branches ascending more sharply than in *G. herbaceum*. *Leaves* dark green, with lateral folds and rarely basal lobes in the sinuses. *Bracteoles* sub-triangular, gashed on the whole margin or more or less entire, not spreading in fruit.

5. Gossypium intermedium, *Todaro.* *Flowers* yellow. *Bracteoles* deeply gashed.

,, ,, *var. nov.* alba. *Flowers* white. *Bracteoles* often entire. A link with *G. neglectum.*

D. The Bani Group.—Tall sparsely branched plants. *Lower branches* long slightly ascending, median and upper sparse, short, more or less drooping, becoming successively shorter, apex of simple stem much produced. *Leaves* yellowish green, entire to 3-lobed usually, lobes broadly ovate. *Bracteoles* triangular, entire or slightly toothed upwards. *Petals* reflexed, yellow or white. Cotton scanty and fine in the most typical examples.

6. Gossypium indicum, *Lamk.* *Flowers* yellow.

,, ,, ,, *var. nov.* Mollisoni. *Flowers* white.

E. Jari and Varhādi Group.—Tall sparsely branched plants. *Lower branches* long, slightly ascending, median and upper sparse, more or less drooping, becoming successively shorter, apex of simple stem much produced. *Leaves* dark green, strongly heliotropic. *Bracteoles* triangular, entire or slightly toothed upwards. *Petals* reflexed, yellow or white.

7. Gossypium neglectum, *Todaro var. nov.* vera. Lobes of leaves narrowly oblong, base not deeply cordate. *Flowers* yellow. *Cotton* copious and coarse.

,, ,, ,, *Sub. var. nov.* kathiavarensis. Lobes of leaves broad, ovate-oblong. *Cotton* moderately fine.

,, ,, ,, *Sub. var. nov.* malvensis. Habit of type; but *Cotton* of superior quality.

,, ,, ,, *Sub. var. nov.* bengalensis. Lobes of leaves narrow, radiating. *Bolls* and *bracteoles* larger than in type. *Cotton* coarse.

,, ,, ,, *Sub. var. nov.* Kokatia. As in the last, but lint drab coloured.

,, ,, ,, *Sub. var. nov.* burmanica. As in *bengalensis*, but lobes of leaves broad. *Lint* white.

,, ,, ,, *var. nov.* rosea. Lobes of leaves narrow. *Flowers* white. *Cotton* coarse.

7. Gossypium neglectum, *Todaro*. *Sub. var. nov.* cutchica. Lobes of leaves broad, ovate-oblong. *Cotton* moderately fine.

" " " *Sub. var. nov.* avensis. Lobes of leaves broad. *Bracteoles* and *bolls* larger than in type.

F. Kil Group.—Low plants. Lower branches drooping, upper becoming successively shorter. *Leaves* dark green, with narrow, radiating lobes. *Bracteoles* large, triangular, acuminate, entire or only toothed at apex, longer than the flowers, reflexed in fruit. *Flowers* normally white. *Bolls* usually large.

8. Gossypium cernuum, *Todaro*. *Cotton* white.

" " " *var. nov.* silhetensis. *Cotton* drab.

G. Dharwar American Group.—Low rounded bushes. *Leaves* rather membranous, yellowish green, simple to 5-lobed, usually 3-lobed, lobes short, triangular, with straight margins. *Bracteoles* rounded with caudate acuminate teeth. *Flowers* light yellow, without a dark eye. *Bolls* large spherical.

9. Gossypium hirsutum, *Mill.* *Cotton* white.

" " " *var.* rufa, *Todaro*. *Cotton* drab.

1. GOSSYPIUM OBTUSIFOLIUM, *Roxb. Fl. Ind., III.*, 183; G. herbaceum, *Linn* var. obtusifolium (*Roxb*). *Masters in Fl. Br. India*, I, page 347; G. Wightianum, *Todaro, Osser sui Cotoni*, page 47. Attaining the height of 7 feet and upwards. *Stems* robust, internodes short, all the branches acutely ascending and crowded. *Branches* dark red, with close, very short, stellate hairs mixed with longer, simple pilose hairs as are also the petioles and leaves. *Leaves* small, standing on the same plane as the petiole or at right angles to it, yellowish green with a distinct red blotch at base, 5-lobed, lobes ovate, rather obtuse mucronate, sinus broad or narrow, with a small extra lobe or fold, margins of some of the larger leaves sinuate. *Stipules* rather short, lanceolate, falcate.

Peduncles 1 or 2, on secondary and tertiary divisions, reflexed, trigonous. *Bracteoles* $\frac{3}{4}$ to 1 inch by $\frac{5}{8}$ to $\frac{7}{8}$ inch, ovately triangular acute, teeth rather shallow and acute, usually confined to the upper third but occasionally present on the whole of the margins. *Calyx* loose, campanulate, truncate or minutely 3-toothed, with three distinct glands on the base externally. *Corolla* up to $1\frac{3}{4}$ inch long, yellow with a dark eye, fading red. *Stigmas* united, slightly twisted. *Bolls* $1\frac{1}{8}$ to $1\frac{1}{4}$ inch by $\frac{3}{4}$ to $\frac{7}{8}$ inch, long pointed when 3-celled, short pointed when 4-celled. *Cotton* scanty, moderately fine and curly, *seeds* with a greenish gray velvet.

Indian Forms.—Rōzi or *Jaria*, a perennial growing for 6 or 7 years, cultivated on the light soils of Gujarāt. Professor Middleton says that it readily runs wild and in hedges assumes a climbing habit and then the cotton turns yellow and very short in the staple, the velvet at the same time becoming long; that it strongly resembles *G. arboreum*, the chief difference being a yellow flower and the absence of the marked reddish tinge possessed by that species.

Nadam. Madras. Mr. Benson, M. R. A. C. (late Deputy Director of Agriculture, Madras), says that Nadam and Bourbon are the crops of the lighter and more gravelly soils.

G. obtusifolium, *Roxb. var. nov.* Coconada. This differs from the type in having drab instead of white cotton. Mr. Benson says that the centre of trade in this cotton is at Gūntur.

G. obtusifolium, *Roxb. var. nov.* hirsutior. Plants more hairy, leaves larger and altogether with a strong tendency towards *G. herbaceum.*

Two forms have been received from Baluchistan under the names of *Keehi Kapās* and *Karpās.* I place these plants here mainly on account of their manner of growth. Many of their characters bring them very closely indeed to *G. herbaceum.* The majority of the forms, ranging from Baluchistan westward to the Mediterranean, arranged under *G. herbaceum*, may really belong here, but I have seen only herbarium examples of these.

G. obtusifolium, *Roxb. var. nov.* Nanking. With most of the characters of the type, but leaves of a darker green resembling those of *G. neglectum. Bolls* and *bracteoles* comparatively large.

The types are *Wa-gale* and *Wa-gyi* of Burma with good cotton and two cottons from seed imported from China. This may be *G. Nanking,* Meyen. The Chinese plants have not grown well, but they seem closely allied to the two Burmese forms included with them.

G. obtusifolium, *Roxb. var. nov.* sindica. Branches more sparse and spreading than in type, upper with a strong tendency to become successively shorter. *Leaves* larger, of a bright yellowish green colour resembling those of *G. indicum.* This variety may be a connecting link between *G. obtusifolium* and *G. indicum.* The type is recorded from Sind only.

The extra-Indian distribution of *G. obtusifolium,* Roxb. includes the Philippines (*Vidal*), where it is wild, Timor, Letti and Lakor in the Malayan Archipelago, Nyassa Land, Central Africa, Transvaal, Madagascar, Hadramant (*T. Bent*), Zambesi, Somali Land and Rhodesia. Dr. Masters says in Fl. Brit. India, I, page 347, that this was the form found in Ava by Griffith, Journals, page 147. Many of the extra-Indian specimens quoted under *G. herbaceum* may more properly come here, but it is impossible to decide the matter from herbarium materials alone.

2. Gossypium arboreum, *Linn. Sp. Pl., p.* 693 (1753); *Todaro l.c. G. album,* Ham, *teste Herb. Wight,* 176; *Roxb. Fl. Ind., III,* 183. Perennial, reaching 7 feet in height. *Stems* robust, internodes short, all the branches acutely ascending. *Branches* dark red with close, very short stellate hairs mixed with longer, simple, pilose hairs, as are also the petioles and leaves. *Leaves* 5-lobed, lobes narrowly oblong or ovate-oblong sub-obtuse mucronate, sinus broad, often with small accessory basal or lateral lobes. *Inflorescence* in short secondary and tertiary divisions of lateral branchlets, drooping. *Bracteoles* ovately triangular acute, 1 inch by $\frac{7}{8}$ inch average length and breadth, quite entire or 1—3

toothed at apex or with teeth extending throughout two-thirds of the margins. *Corolla* about one-third longer than the bracteoles, dark red, fading almost to a black colour. *Calyx* loose, campanulate, limb truncate or with a few minute teeth, tube with three distinct glands at the base externally. *Bolls* brown, opening fully when ripe so that the cotton hangs down, as long as or a little longer than the bracteoles, ovate pointed, obtusely trigonous, $1\frac{1}{8}$ inch long by $\frac{7}{8}$ inch broad, cells usually 3. *Cotton* scanty, moderately fine and curly ; *seeds* 3 to 8 in each cell, *velvet* greenish grey.

The type has the lobes of the leaves narrow. Many examples have been received from Gujarāt, United Provinces, Madras, Central Provinces, Burma and Central India. Wherever found, it seems to be cultivated only on a very small scale. According to Hove, this red-flowered perennial cotton was cultivated largely in Gujarat.

G. arboreum, *Linn. var. nov.* platyloba. This only differs from the type in having the lobes of the leaves broad. Examples were obtained from Madras Presidency only. Mysore, *Heyne*, in Herb. Kew. Serampore, Bengal, *Griffith*, Herb. Kew.

G. arboreum, *Linn. var. nov.* vagans. This differs from the type in having drab-coloured cotton. The only examples are from Central India and Madras. A form of this variety may be partly *G. Nanking*, Meyen.

The extra-Indian distribution of *G. arboreum*, Linn., includes the type in Java (Horsfield) and Siam (Zimmermann). The *variety* platyloba is found in Japan (Oldham, Maximowicz), Pekin (Bushell, Index Floræ Sinensis under *G herbaceum*, L.), Yunnan (Delavay), China (cultivated, A. *Henry*, No. 11.024), Formosa (cultivated, A. *Henry*, 1899), Shanghai (cultivated, Carles, 388), China (Fortune), Celebes (Riedel), Abeokuta (Irving), and Central Africa.

3. GOSSYPIUM SANGUINEUM, *Hassk. Cat. Hort. Bog.* 200, (1844), *Todaro, l. c.*, G. rubicundum, *Roxb. Ic. Ined. et in Herb.* This differs from *G. arboreum* in being of more spreading growth, not so decidedly red in colour and in the foliage

being of a more glaucous hue. The typical form has dark red flowers.

(*a*) *Leaves* with broad lobes. Types—*Bagar siah*, *Bagar safed* and *Lyallpur Farm selected*, all from the Punjab.

(*b*) *Leaves* with narrow lobes. Types—Forms of *Bagar siah* and *Bagar safed* of the Punjab.

G. sanguineum, *Hassk. var. nov.* minor. As in type, but plants with pink flowers.

(*a*) *Leaves* with broad lobes. Forms of *Bagar siah*, *Bagar safed and Deshi Multan* of the Punjab.

(*b*) *Leaves* with narrow lobes. Forms of *Bagar siah* and *Bagar safed* of the Punjab.

The extra-Indian distribution of *G. sanguineum* is uncertain and probably coincides with that of *G. arboreum.*

4. GOSSYPIUM HERBACEUM, *Linn. Sp. Pl. I., p. 693* (1753) *Masters in Fl. Brit. Ind., I., p. 346* (excluding all the four varieties), *Todaro l. c.* Varying in height from 2 to 7 feet, basal branches long and spreading, median and upper also long and spreading, drooping in fruit; older parts greyish brown, slightly hairy, young parts green covered with black dots and soft, white spreading hairs; the sides of the branches facing southwards gradually turning to a dark red colour. *Stipules* ovate to linear lanceolate, falcate, about ½ inch long, the broader ones sometimes lobed towards apex. *Leaves* rather membranous, yellowish green, shallowly cordate rotundate, palmately 3—5 more lobed, lobes deep ovate obtuse or acute, margins quite entire or sinuate, sinus folded; basal lobes, when present, are above the sinus and do not rise from it. *Inflorescence* on short secondary or tertiary axes. *Bracteoles* spreading in fruit, rounded, with about 8—10 lanceolate acuminate teeth, reaching one-fourth of the way down. *Calyx* cup shaped, entire, accrescent and irregularly splitting, with three external basal glands. *Corolla* yellow with a black eye, fading to yellow suffused with red, ½ to ¾ inch longer than the bracteoles, *anthers* dark yellow with rather short filaments, *stigmas* short, channels straight or slightly twisted. *Capsule* 3-

or 4-celled, almost spherical or ovate, pointed, shorter than the spreading bracteoles. *Seeds* 5 to 8 in each cell.

Typical examples are *Lālio* of Kathiawar. *Kumpta* and *Jowāri Hatti* of the Southern Mahratta Country, *Broach*, *Gogāhri*, *Lālio* (Chhārodi) and *Kānvi*, all of Gujarat.

G. herbaceum, *Linn var. nov* madraspatana. With smaller bolls but otherwise as in type, of which it is probably a degeneration. Typical examples include the *White-seeded Jowāri Hatti*, *Mungari* or *Billai*, *Uppam*, *Northerns* (Cuddapah), *Proddatur*, all of the Madras Presidency. *Manva* (Pratabgarh) is the solitary representative in the United Provinces. Mr. Benson says that 'Westerns' include *Jowāri Hatti* (white and black seeded). *Mungari* and *Bilé Hatti* and that these are found on the loams and clays. The trade term 'Northerns' includes the Northerns of this list and *Yerraputti* (*G. indicum*), the distribution being mainly according to soil as above. *Salems* include three different varieties, *viz.*, *Uppam*, *Nadam* or *Ladam*, and *Bourbon*. The *Uppam* resembles in every way, except that the lint is harsher, the *Uppam* of the districts further south and is the crop of clays and loams. The trade term 'Tinnies' includes the *Uppams* and "*Mundai kai* and *Karunganni*" or "*Manji kai*" varieties. These two sorts are habitually sown mixed, but the proportion of *Uppam* is larger in the north and of *Karunganni* in the south. It seems probable that the latter is the true Tinny Cotton, for *Uppam* is known in some places as *Udamalpet* cotton, Udamalpet being a town in the 'Salems' area. *Mungari* is a special sort which appears to differ from the ordinary *Jowāri* (not *Jowāri Hatti*) in respect of the time of sowing. *Karunganni* belongs to *G. obtusifolium*, Roxb.

G. herbaceum, *Linn. var. nov.* melanosperma. As in the last, but testa of seed naked. There is only one typical example from the Madras Presidency, said by Mr. Benson to be included in 'Westerns.'

G. herbaceum, *Linn. var. nov.* sakalia. *Bolls* spherical, with broad valves splitting so slightly when ripe that the cotton does not emerge, mostly 3-celled, averaging one inch in length and breadth. The typical examples are two only; *Wāgad* and *Sakālio* of Gujarat.

I am altogether in doubt as to the extra-Indian distribution of G. herbaceum, *Linn.*, having never seen living examples of the cottons ranging from the western frontiers of India to Eastern Europe and included under this name. Specimens from the following countries seem to belong to this species, but they may just as well be considered forms of *G. obtusifolium*, Roxb.: Turkey, Greece, Armenia, Persia, Cephalonia, Crete, Khorasan (*Aitchison*), Afghanistan, Gilgit (*Giles* and also *Winterbottom*).

5. GOSSYPIUM INTERMEDIUM, *Todaro, Osser sui Cotoni, p. 41 (1863)*; G. intermedium, *Tod. var.* Royleanum, *Tod. l.c.* = ? broad-lobed type; G. neglectum, *Tod. var.* Roxburghianum, *Tod. l.c.* = ? G. herbaceum *var.* Dacca Cotton, *Roxb. Fl. Ind. III, 184,* teste *Tod. l.c.* = ? *Jethia* of Bengal. Attaining 5 to 6 and more feet in height, *branches* ascending more sharply than in *G. herbaceum*, reddish. *Leaves* dark green, sub-coriaceous, glabrescent, palmately 5—7-lobed, lobes ovate acute, sinus broad with a fold or rarely with an extra-basal lobe. *Bracteoles* not spreading, subtriangular, ovate, gashed more or less on the whole margin. *Bolls* small $\frac{7}{8}$ by $\frac{5}{8}$ inch, round and pointed. *Cotton* scanty, short, moderately fine; *seeds* 3 to 8 in each cell, velvet greenish white. The following forms are transitional between the Burmese and Chinese types of *G. neglectum* and *G. herbaceum.*

(*a*) Lobes of leaves broad. *Dēshila* or *Dēshi* and *Jēthi* of Bengal, *Bāgil* of Gorakhpur, U. P.

(*b*) Lobes of leaves narrow, *Sūltānpur: Rādhiya kapās; Mānva* of the United Provinces.

G. intermedium, *Tod. var. nov.* alba. *Flowers* white. *Bracteoles* often entire. A form nearer *G. neglectum* than *G. herbaceum.* Type from United Provinces only. Mr. Moreland (Director of Agriculture, United Provinces) says that these cottons are cultivated on a small scale only on the eastern side of the Upper Provinces.

The extra-Indian distribution of *G. intermedium*, Tod., is unknown. The plant is probably endemic. There are no specimens at Kew.

6. GOSSYPIUM INDICUM, *Lamk. Dict. Encycl. 2, p. 134* (1786): G. Wightianum. *Tod. Osser sui Cotoni, p. 41* (in part). *Stems* up to 8 feet in height, simple, tapering gradually from base to apex; basal branches long, ascending, medial moderately long, uppermost small. *Leaves* varying from entire to usually 3- or occasionally 5-lobed, base cordate, lobes broadly ovate, sinuses broad. *Bracteoles* ovate-pointed, entire or few toothed at apex. *Bolls* ovate acuminate, 3- 4-celled; *cotton* scanty, staple silky, long; *seeds* in each cell 4—10, covered with grey brown velvet. Typical plants have yellow flowers. Bengal and Madras have each one form; the United Provinces have two; the remainder come from Central India, the Punjab and the Central Provinces.

Of *Yerraputti* Mr. Benson says that it seems, like *Karunganni*, to partake more of the *G. indicum* than of the *G. neglectum* type, but possibly it includes more than one variety. Plants so named are found widely as scattered plants in greater or less proportion over the areas where both Northerns and Westerns are produced. Properly speaking, this variety is not one to be grown on "Cotton soils."

As regards the Central Provinces, Mr. Standen (Director of Agriculture) says that *Bani* is a more delicate and later ripening variety with longer and silky staple. It used to be grown largely in the Wardha district as well as in the neighbouring parts of Berar, but is being thrust out by the *Jari* (G. neglectum), because the latter even in the most favourable years pays better than *Bani* in all but the most suitable localities. The Assistant Director of Agriculture believes that *Nimari* is *Bani*, of which the character has been somewhat altered by transfer to a drier climate. The *Chandā Jari* is a cold weather variety yielding a smaller outturn than *Jari* or *Bani*, but producing cotton of better quality than either. From Mr. Shevade's report on the cotton of Barsi in the Sholapur District, it would appear that *Bani* once formed the bulk of the so-called Barsi cotton.

Gossypium indicum, *Lamk. var. nov.* Mollisoni differs from the type only in having white flowers. The examples are all from Central India and the Punjab, with the exception of one from the Central Provinces and two from the United Provinces.

The species seem to be endemic to India.

7. GOSSYPIUM NEGLECTUM, *Todaro, Osser sui cotoni, p. 35 (1863)*. G. herbaceum, *Linn var.* hirsutum, *Masters* in Herb. Kew. G. arboreum, *Linn.* (in part) *Fl. Br. Ind., I, 347.* Plants varying in height from 3 to 7 and more feet. *Stems* simple, wandlike, tapering gradually from base to apex, bark brown, tessellated, quite glabrous below, with simple, white short deciduous hairs above, herbaceous parts brownish red, specially so on the southern side. Lower branches sparse, long, spreading, medial short, uppermost very short; whole plant usually nodding if well covered with fruit *Leaves* palmate or palmatipartite, lobes 3 to 5 or more, oblong lanceolate, ovate acute or sub-obtuse, sinuses broad or rising up into small extra lobes, base shallowly cordate; *glands* either altogether absent or present on the central rib or faintly present on the three central ribs; *stipules* lanceolate falcate acuminate or broad ovate few toothed at the apex. *Flowers* one from each node of the lateral branches, *peduncles* erect but drooping in fruit. *Bracteoles* deeply cordate, ovate acute, quite entire towards apex or sometimes toothed there. *Calyx* cup-shaped, entire or very shortly lobed. *Corolla* a little longer than the bracteoles, upper part of petals reflexed; *filaments* comparatively long; *stigmas* 3-grooved, scarcely rising above the upper anthers, channels with or without black dots. *Bolls* ovate, obtusely pointed, invested at base by the ruptured enlarged calyx, 3—4-celled, very distinctly black dotted, valves separating and recurved when ripe. *Cotton* harsh, clinging more or less firmly to the seed, which is covered by grey velvet.

G. neglectum, *Tod. l.c. var. nov.* vera. Lobes of leaves narrowly oblong, base not deeply cordate. *Flowers* yellow. *Cotton* copious and coarse. This variety is represented by forms from the Punjab, United Provinces and Central India. The latter area seems to have been the place of origin of both this species and *G. indicum.*

G. neglectum, *Tod. var. nov.* vera., *sub. var. nov.* malvensis. Similar to the last but lobes of leaves usually broader and the *cotton* of superior quality. This form is a connecting link with *G. indicum.* Examples are from Sind, Punjab, Central India and the United Provinces.

G. neglectum, *Tod. var. nov.* vera, *sub. var. nov.* kathiavarensis. Lobes of leaves broad ovate oblong. *Cotton* moderately fine. It is represented by two varieties from Kathiawar, *Hirvāni* and *Mathio* and doubtfully by a variety called *Barkley*, Ralli Brothers, in the Central Provinces.

G. neglectum, *Tod. var. nov.* vera, *sub. var. nov.* bengalensis. Lobes of leaves narrow, radiating. *Bolls* and *bracteoles* larger than in type. *Cotton* coarse. It is represented by several examples in Bengal, three in Assam and one in the United Provinces. It is closely allied to *G. cernuum.*

G. neglectum, *Tod. var. nov.* vera, *sub. var. nov.* burmanica. As in bengalensis, but lobes of leaves broad, *cotton* white. It is represented by a series of similar forms from Burma and by three varieties from Assam. The Director of Agriculture states that *Lassing Anguangba* or *Tissing Anguangba* is grown in Manipur.

G. neglectum, *Tod. var. nov.* vera, *sub. var. nov.* Kokatia. Characters as in the last, but *cotton* drab coloured. One example from Bengal, two from Assam and a short series from Burma. This may be one of the forms included by authors under *G. Nanking*, Meyen.

G. neglectum, *Tod. var. nov.* rosea. G. roseum, *Tod. Osser sui Cotoni*, p. 22. This is separated from G. neglectum, *var.* vera, only by the white flowers. There are examples from the Central Provinces, Punjab, United Provinces, Bengal and Sind.

G. neglectum, *Tod. var. nov.* rosea, *sub. var. nov.* cutchica. Lobes of leaves broad, ovate oblong; *cotton* moderately fine. Represented by three white-flowered cottons of Kathiawar, *Hirvāni*, *Mathio* and *Mōtō mathio.*

G. neglectum, *Tod. var. nov.* rosea, *sub. var. nov.* avensis. Lobes of leaves broad. *Bracteoles* and *bolls* larger than in type. Represented by two Burmese cottons and one doubtful plant from the United Provinces.

The extra-Indian distribution of *G. neglectum, Tod.*, is unknown.

8. GOSSYPIUM CERNUUM, *Tod. Osser sui Cotoni*, p. 31. General characters as in *G. neglectum. Leaves* usually with very narrow radiating lobes. *Bracteoles* ovate acute, quite entire towards apex or with 3 to 6 acuminate teeth; dimensions in flower 1 to 2 inches long, ¾ to 1¼ inch broad. *Corolla* about ¾ inch longer than the bracteoles, white or pale yellow, with a dark eye, dying pink. *Bracteoles* in fruit up to 2½ inches long, slightly shorter or longer than the bolls which are ovate pointed, 3—4 celled, very distinctly black dotted. It is represented by a series of forms in Assam, by an introduced variety in Sind and by another variety, perhaps also introduced, in the United Provinces. The Director of Agriculture, Assam, states that the *kil* is grown in the Garo Hills and probably also on the northern slopes of the Khasia Hills. Its pods are very large, being sometimes as much as eight inches in length. The quality of the lint is harsh and only fit for mixing with wool. *Bor Kapah* and *Soru Kapah* are grown in the Mikir Hills and in the adjacent plains country in Nowgong and Golaghat by the hill tribes (mostly Mikirs). They are also grown to a very small extent in some plain's mauzas of Kamrup.

G. cernuum, *Tod. var. nov.* silhetensis. Differs from the type only in having drab-coloured cotton. It is represented by four examples from Assam, one introduced into Sind and one Chinese. The last may be one of the forms known as *G. Nanking*, Meyen.

The extra-Indian distribution of *G. cernuum, Tod.*, is doubtful, but it is probably endemic in North-Eastern India and China.

9. GOSSYPIUM HIRSUTUM, *Mill.* n. 4 (1759) = G. jamaicense, *Macf. Fl. of Jamaica*, p. 72 = ? G. punctatum, *Thon. and Sch.* Guin Pl. p. 2, p. 84. Upland Georgian cotton, *Royle, Cotton Cultivation, tab.* 3, *fig.* 4. Upland Georgian cotton; Short Staple cotton; Bourbon cotton; Louisiana cotton (*Parlatore*). From 2 to 4 feet high. Lower branches erect, upper spreading

so that a well-grown plant forms a round-headed bush; older parts of the stems and branches smooth, grey; younger parts green, gradually turning brown, covered with moderately stiff spreading white hairs and minute black dots; *stipules* lanceolate, falcate, about ½ inch long. *Leaves* sub-coriaceous, dark green, drying red, varying much in shape, ovate or ovate cordate entire, cordate with 1 to 3 shallow lobes or palmately cordate with 3 shallow or very deep triangular or ovately triangular acute lobes which point forwards, base of blade with a red blotch. *Bracteoles* rounded, upper half of the margins with about ten falcately lanceolate acuminate teeth, the central ones exceeding the corolla in length, in bud and fruit clasping over like the fingers of two hands. *Calyx* campanulate, accrescent but not usually splitting in fruit, with 5 distinct triangular lobes. *Corolla* pale yellow without an eye, fading red. *Anthers* with rather long filaments so that they droop. *Stigmas* long, consolidated, twisted. *Bolls* usually 3-, sometimes 4-celled, spherical ovate obtuse shortly mucronate with the persistent base of the style a little longer than the bracteoles. *Cotton* silky, long in the staple. *Seeds* densely covered with grey velvet, 6—9 in each cell.

This species is only included amongst the Indian cottons, as it has become quite naturalized in some parts of India, especially in the Karnatak. There are examples from Dharwar, Nagpur, Central Provinces, Assam, Bengal, United Provinces and Punjab.

G. hirsutum, *Mill. var.* rufa, *Todaro.* Only differs from the type in the cotton being drab coloured. Synonymy according to Parlatore is, G. siamense lana rufa, *Ten. l. c.* G. religiosum, *Moris. Fl. sard. 1*, p. 309. Coton de Siam, Cotone Isabelle of the French, Cotone siamese, Cotone maltese, Cotone Rosso, Cotone color di legno. We have examples from the Punjab, United Provinces and Central India.

As regards the extra-Indian distribution of G. hirsutum, *Mill.*, Parlatore gives Mexico and Galapagos as the habitat. It is cultivated in Central and North America, Canary Islands, Cape Verde, Western Coast of Tropical Africa, Algeria, Egypt, Abyssinia, Isle of France, Bourbon, Southern Italy, Sicily, Sardinia, Malta, Crete, Indo-China, Amboyna, Queensland, New South Wales and New Holland. I have personally examined specimens from the following localities: Angola, St. Jago, San Domingo, Lagos, (wild cotton of Radajry District), Zambesi, Egypt, Alabama, Florida (under G. uliginosum, *Linn.*), Costa Rica, Mexico, Florida (under G. racemosum, *Poir.*).

DESCRIPTIONS OF THE PLATES.

PLATE I.—G obtusifolium, *Roxb.*; A. *Nadam of Madras*, B. *var.* Coconada, open boll. C. seed without cotton.

PLATE II.—G obtusifolium, *var.* hirsutior; A. part of plant; B. open flower; C. half ripe boll; D. ripe boll; E. seed with cotton; F. seed without cotton; G. bracteole.

PLATE III.—G. obtusifolium, *var.* Nanking; A. part of plant; B. open flower; C. half ripe boll; D. ripe boll; E. seed with cotton; F. seed without cotton; G. bracteole.

PLATE IV.—G. obtusifolium, *var.* sindica; A. part of plant; B. open flower; C. two types of bolls; D. bracteole.

PLATE V.—G. arboreum. *Linn*; A. part of typical plant; B. leaf of *var.* platyloba; C. ripe boll and cotton of *var.* vagans; D. ripe boll and cotton of type; E. seed with cotton of type; F. seed without cotton of type; G. bracteole.

PLATE VI.—G. sanguineum, *Hassk*; A. part of plant of *var.* minor; B. petal of same; C. a broad-lobed leaf; D. flower of type; E. bracteole of type; F. seed with cotton; G. seed without cotton; H. unripe boll of *var.* minor; I. ripe boll of *var.* minor; J. ripe boll of type.

PLATE VII.—G. herbaceum, *Linn.* A. part of plant of type; B. boll of *var.* madraspatana; C. seed with and without cotton of *var.* melanosperma; D. ripe boll of *var.* sakalia; E. half ripe boll of type; F. open flower of type; G. ripe boll of type; H. seed with and without cotton of type.

PLATE VIII.—G. intermedium, *Tod.*; A. part of plant of type; B. part of plant of *var.* alba; C. D. bracteoles of *var.* alba; E. half ripe boll of *var.* alba; F. ripe boll of same; G. seed with and without cotton of type.

PLATE IX.—G. indicum, *Lamk.*, and G. neglectum, *Tod. var.*; A. part of plant of type; B. flower of *var.* Mollisoni; C. half ripe boll of type; D. ripe boll of type (marked G. in left hand lower corner); E. seed with and without cotton of type; F. ripe boll of *Lassing Anguangba*; G. seed with and without cotton (transferred to G. neglectum, *var.* vera. *sub-var.* Kokatia).

Plate X.—G. neglectum, *Tod. vars.* vera. and rosea; A. part of plant of G. neglectum, *var.* rosea; B. flower of *var.* vera.; C. leaf of *var.* vera. *sub. var.* malvensis; D. bracteole of *var.* rosea; E. ripe boll of the same; F. seed with and without cotton of the same.

Plate XI.—G. neglectum, *Tod. sub. vars.* cutchica and kathiavarensis; A. part of plant of *var.* rosea, *sub. var.* cutchica; B. flower of *var.* vera. *sub. var.* kathiavarensis; C. bracteole of *sub. var.* cutchica; D. ripe boll of same; E. seed with and without cotton of same.

Plate XII.—G. neglectum, *Tod. sub. vars.* burmanica and Kokatia; A. part of plant of *var.* vera, *sub. var.* burmanica; B. flower of same; C. bracteole of same; D. half ripe boll of same; E. ripe boll of same; F. seed with and without cotton of same; G. ripe boll of *sub. var.* Kokatia.

Plate XIII.—G. cernuum, *Tod.*, G. neglectum, *var.* vera, *sub. var.* bengalensis; A. part of plant of type; B. bracteole of type; C. half ripe boll of type; D. ripe boll of same; E. ripe boll of *var.* silhetensis; F. flower of G. neglectum, *var.* vera., *sub. var.* bengalensis; G. half ripe boll of same.

Plate XIV.—G. hirsutum, *Mill.* A. part of plant of type; B. flower of same: C. bracteole of same; D. half ripe boll of same; E. ripe boll of same; F. seed with and without cotton; G. ripe boll of *var.* rufa.

R.K.Bhide, del.

Huth, Lith^{r} London.

G. OBTUSIFOLIUM Roxb

Plate II.

R.K. Bhide del

G. OBTUSIFOLIUM var HIRSUTIOR.

Huth, Lith^r London

R. K Bhide, del. Huth, Lith^r London.

G. OBTUSIFOLIUM Roxb. Var. NANKING.

Plate IV

R. K. BL[illegible]

[illegible]

G. OBTUSIFOLIUM Roxb. var. SINDICA.

R. K. Bhide, del

Huth, Lith^{r} London

G. ARBOREUM. Linn.

R.K Bhide, del.

Huth, Lith^r London

G. SANGUINEUM. Hassk.

R. K. Bhide del.

Huth, Lith' London

G. HERBACEUM Linn.

R. K. Bhide, del. Huth, Lith^r London.

G. INTERMEDIUM Tod.

R. K. Bhide. del. Huth, Lith^{r} London

G. INDICUM. Lamk. and G. NEGLECTUM. Tod. var.

Plate X

R. K. Bhide del. G. NEGLECTUM Tod. vars. VERA and ROSEA. Huth Lith. London

R.K Bhide. del. [illegible]

G. NEGLECTUM. Tod.
sub. vars CUTCHICA and KATHIAWARENSIS.

R. L. Price del   Bale lith London

G. NEGLECTUM. Tod
sub. vars BURMANICA and KOKATIA

R.K. Bhide del.

Huth Lith^r London

G. CERNUUM. Tod.
G. NEGLECTUM. var VERA sub.var. BENGALENSIS.

R. K. Bhide, del

Huth, Lith^r London

G. HIRSUTUM. Mill.

NOTICE.

THESE Memoirs, dealing with scientific subjects relating to Agriculture, will appear from time to time as material is available. They will be published in separate series, such as Chemistry, Botany, Entomology and the like. All contributions should be sent to the Editor, the Inspector-General of Agriculture, Nagpur, Central Provinces, India. Contributors will be given, free of charge, fifty copies of their contributions.

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NOTE ON A TOXIC SUBSTANCE EXCRETED BY THE ROOTS OF PLANTS

BY

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Deputy Director of Agriculture, Bombay Presidency

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CALCUTTA:
PRINTED BY THACKER, SPINK AND CO.

NOTE ON A TOXIC SUBSTANCE EXCRETED BY THE ROOTS OF PLANTS.

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It has more than once been suggested that plants, like animals, excrete (from their roots) material that is no longer of use to them or that are bye-products of the process of metabolism, and that such substances are injurious to the kinds of vegetation by which they are excreted. Brugmans was apparently the first to suggest this, and it has, at various times, been affirmed by Plenk, Humboldt, Cotta, De Candolle and others, denied by Hedwig, Braconnot, Walser, Boussingault, Unger, Meyen and others and has for long been considered as non-existent except with regard to carbon dioxide and possibly an acid phosphate and formates.

Again, Dr. Gyde (Trans-Highland and Agricultural Society, 1845-47, pp. 273-92) in water cultures obtained on evaporating the residual liquid, a very small amount of yellowish or brown substance, a portion of which was organic in character. He concluded that the amount excreted was very small, and that the substance was not injurious to the plants that gave rise to it.

From observations on crops growing in the field, the writer some years ago (while in Egypt) came to the conclusion that certain phenomena could only be explained on the theory of excretion. This was especially the case with cotton crops in which a grass was allowed to grow as a weed. The cotton, grown under irrigation, did not revive on application of more water ; its poor state was therefore not due to lack of moisture in the soil. Manures likewise seemed to have comparatively little effect towards improvement ; appropriation by the weed of food materials was therefore not the cause of the poor growth. Aeration had as little effect as manure.

Observations in the field were resumed in India, and these tended to very materially strengthen the view that materials injurious to other crops were excreted by the roots of certain common crops in India; this was especially the case with sorghum. The system of mixed crops very prevalent in the unirrigated tracts in India gave full opportunity for a number of observations to be taken, and on the strength of these, experiment was resumed both in the field and in water culture.

FIELD EXPERIMENTS.

The results of field experiments which commenced (in India) in the season 1903-04 were unreliable in the two following years owing to the failure of the monsoon. In the season of 1906-07, the rains were more nearly normal, and the following observations were made on the Surat Experiment Station; they agree in kind and differ only in degree from those obtained in the previous year under a short rainfall.

This Station is on typical deep black cotton soil and receives an annual rainfall of about 42 inches, all falling between the middle of June and the end of September.

The soil is very retentive of moisture as will be obvious from the fact that cotton sown in June survives until the end of March, though no rain is received during the last six months previous to the final picking of the crop. The composition of this soil, as kindly analysed by Dr. Leather, is as follows :—

MECHANICAL COMPOSITION.

Fine Gravel, 1 mm.		2·2
Sand,	1 mm. –0·2	3·4
,,	0·2—0·05 mm.	42·2
,,	0·05—·01 mm.	22·8
,,	·01 mm.	20·8
		91·4
Stones		3·6
Fine earth, 2 mm.		96·4
		100·0

CHEMICAL COMPOSITION.

Insoluble silicates and sand	68·06
Ferric oxide	8·83
Alumina	11·07
Lime	2·79
Magnesia	·54
Potash	·42
Soda	·31
Phosphoric acid	·09
Sulphuric acid	·06
Carbonic acid	·94
Chlorine	·07
Organic matter and combined water	6·82
	100·00
Total nitrogen	·036
Nitric nitrogen	·00014
Available phosphoric acid	·016
Available potash	·012

The observations were taken as follows :—

Plots of various crops were grown side by side, each plot being sown by means of a drill in such a way that the rows of crops (2 ft. apart) were parallel in all the plots. Further, several plots were left fallow as it was found that some crops growing on the border of a fallow yielded at a rate as much as 10 times as great as the rate in the centre of the plot (Annual Report of the Bombay Farms for 1904-05). Again, cotton and sorghum were sown in alternate rows in the same plot.

The following observations were then made :—

(1) The yield of the row of each crop bordering on fallow.

(2) The yield of the row of each crop bordering on a plot bearing another crop.

(3) The yield of a row of each crop in the centre of a plot bearing only that crop.

(4) The yield of a row of cotton when grown with a row of sorghum of each side (at a distance of 2 ft.).

(5) The yield of the row of sorghum when grown with a row of cotton on each side (at a distance of 2 ft.).

In all cases the results given are the mean of a large number of observations.

Observation (1) is the nearest approach possible under the conditions of the experiment, to the yield of a crop when grown isolated, *i.e.*, influenced neither by plants of the same nor of other species. In the present season it is hoped to obtain a nearer approximation.

The results obtained (1906-07) are given in the table following, the total yield per acre (dry weight) of the crops being given in lbs. :—

TABLE I.

CROPS (of which yield is given.)	YIELD (fruit and vegetative portion) in lbs. per acre of the crops in first column when grown bordering on a plot of :				
	Fallow.	Sorghum.	Cajanus.	Cotton.	Sesamum.
Sorghum	10,735	4,830	8,051	8,802	8,158
Cajanus	4,633	694	1,621	1,621	2,409
Cotton	3,817	229	763	1,145	1,259
Sesamum	1,650	*Nil*	198	247	643

Taking the yield next to the fallow as a rough approximation to the yield of the isolated crop, we get the following percentage reduction in these yields produced by a neighbouring plot* of another crop :

TABLE II.

CROPS (of which percentage decrease is given).	Percentage DECREASE in yields of crops in first column when grown near			
	Sorghum.	Cajanus.	Cotton.	Sesamum.
Sorghum	55	25	18	24†
Cajanus	85	65	65	48
Cotton	94	80	70	67
Sesamum	100	88	85	61‡

---

* In the present season observations will be made on the yield of crops when a row is bordered on *both* sides by another crop.

† Since sesamum is extremely sensitive to the presence in its vicinity of other plants whether of the same or other species, the yield next to fallow (Table II) is probably lower than the *isolated* yield by a much greater extent than in the case of all other crops, since the latter are less sensitive. The figures in the bottom line of Table II should therefore all be increased.

‡ This is the result of one observation only and is probably too high since sesamum will not grow at all within 2ft. (the width of the rows) of sorghum.

It is to be noted that pending further and more precise experiment the figures in Table II are to be considered as indicating only the order of the influence of various plants on one another and that too only under the particular conditions of soil and climate under which the experiment was conducted. On lighter soils and under a more evenly distributed rainfall the percentage reductions are apparently less. With this reservation and since the decreased yields are not restored by either irrigation, manure, aeration or light,* it appears legitimate to draw the following conclusions :—

(1) All plants excrete substances which are toxic both to themselves and to other species.

(2) The quantity of material excreted by the different crops varies when reckoned per unit area of a field sown in the ordinary way.

(3) The sensitiveness of crops to the same quantity of the excreted substance varies with the variety of the crop.

(4) The substance excreted by all crops is apparently identical.

The last statement is made under a further reservation pending the isolation in a pure state and analysis of the excreted substance or substances. There is, however, nothing in the facts so far observed either in the field or in water culture inconsistent with the identity of the substance excreted by all plants. On the other hand, if the substance excreted varied with the species, we should not expect the regularity found in Table II. Thus, reading that table vertically, the order of sensitiveness to a given amount of the substance excreted by sorghum appears to be (beginning with the least sensitive) :—sorghum, cajanus, cotton, sesamum. The same order holds good for the same plants towards the substance excreted by cajanus, by cotton and by sesamum. If now the excrement from sorghum differed not only in quantity but also in kind from that of cajanus, we should

---

* All these factors have been proved by experiment to be incapable of correcting except very partially the poorer growth except in the case of certain manurial substances (*see* later).

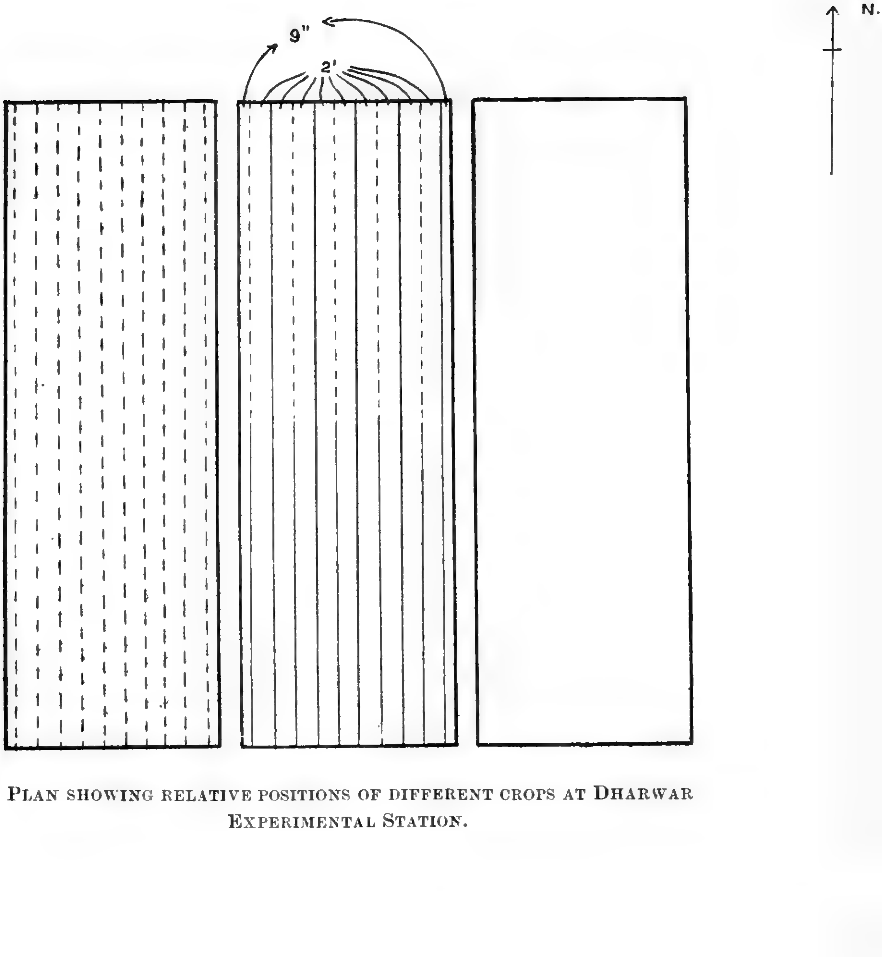
expect that if in two species of plants one was the more resistant to a given quantity of sorghum excrement, yet the other might be the more resistant to the excrement from, say, cajanus. This has, however, been observed to be the case neither in the field nor in water cultures.

Further, the amount of substance excreted (per unit area of a field sown under the conditions of the experiment) by the various crops *appears* to be in the same order. For, reading the columns of Table II horizontally, we find that sorghum excretes an amount of substance which reduces its own yield by 55 per cent., while cajanus excretes an amount that reduces the yield of sorghum by 25 per cent., cotton an amount that reduces the yield of sorghum by 18 per cent. The regularity of the table as read thus horizontally may, however, be deceptive.

On the Dharwar Experimental Station a few observations (on other crops) were made, which indicate that gram (cicer) is about equally sensitive and equally toxic with wheat, that both are equally sensitive with sesamum but less toxic than the latter, while linseed is similar to cotton in both respects except perhaps that it is more sensitive.

In the experiment where cotton and sorghum were grown in alternate rows (2 feet apart) the following results given below in Table III were obtained. The figures are so remarkable that they are given in full. The experiment was made on ¼-acre plots, each 191 yards long and 6½ yards wide, of which the record is known since 1897-98, when my predecessor, Mr. Mollison, laid them out for an excellent series of rotation and manure experiments. In numbering the rows, the numbers of the rows go in the same direction as the numbers of the plots themselves, so that the first row of a plot borders on the plot whose number is next lower and at a distance of 3½ feet from it. The relative positions of the different crops will be obvious from the accompanying plan of one of the plots in which dotted lines represent rows of cotton; continuous thin lines, rows of sorghum; and continuous thick lines, the border of the plot.

PLATE I.



Plan showing relative positions of different crops at Dharwar Experimental Station.

cases. The whole difference is, however, due to last year's cropping, series I being then under sorghum and series II under cotton except plots 11 and 14 which were fallow in both series. This accounts for the great difference in the yields of the northern halves of plots 1 and 2, 24 and 25, sorghum yielding much better after cotton (series II) than after sorghum (series I). The converse might appear to be the case with cotton which in series II (after cotton) has yielded less than in series I (after sorghum), and the whole might appear to be an example of the benefit of rotation. The small yield of cotton in series II is, however, due in part at least to the more vigorous growth of the sorghum with which it was sown as a mixed crop and only to a small extent to the fact that the preceding crop was cotton.

WATER CULTURES.

A large number of experiments in water culture were started some years ago. It is unnecessary to give the preliminary investigations on this point. The greater part of the results obtained by me have been brought together for a final test during the last few months, and these only will be here recorded.

Preparation of Solution of Excreta.

In December last, final water cultures were started on the Dharwar Experimental Station in a number (in all 20) of earthenware dishes (12 inches in diameter and 4 inches inside depth). In each of these dishes 4 litres of well water was placed, and over this a circular teak board perforated by 90 holes, $\frac{1}{4}$ inch in diameter, was supported by strings, to which were attached counterpoise weights hanging over the outside of the dish. Seeds were germinated in crushed quartz, and when the radicle was about an inch long, were transferred to the water culture dishes; a radicle was passed through each hole in the board and held in place by a small wad of cotton. In each 4 litres of water therefore 90 seedlings were planted; those that failed were replaced by others.

The crops were harvested, roots and all, every 21 days, and in all, three crops were taken from each dish between the 10th of January 1907 and May 15th. The water in the dishes was kept up to 4 litres by adding well water every few days.

The crops grown were cotton, sorghum, cajanus indicus, sesamum, wheat, gram (Cicer arietinum).

The air dry weights (including the roots) of the three harvests of the several crops is given in Table V.

TABLE V.

Air dry weights of crops and the amount of water into which the excreta had passed.

No.	Name of crop.	No. of plants grown.	Air dry weight in grammes.	Volume of well water in which their excreta was finally contained.	Total volume of water evaporated and replaced.
				Litres.	*Litres.*
1	Cotton	246	9·170	2·3	19·00
2	Sorghum ...	224	6·026	2·3	18·25
3	Cajanus	157	6·407	2·3	19·25
4	Sesamum ...	133	0·746	1·2	18·75
5	Wheat	261	7·766	1·2	19·75
6	Gram	261	19·308	1·2	27·75

The volume of water remaining in the dishes on harvesting the third crop was allowed to stand in a room until its volume was reduced to the quantity stated, this quantity having been indicated in previous tests to be the best for the final test.

Water culture in the excretory solution.

For brevity the various solutions obtained will be called 'cotton water,' 'sorghum water,' etc.

The water cultures were made in wide-mouthed bottles holding 100 c. c. when filled up to the neck. The mouth was plugged with a teakwood stopper in which four holes ($\frac{1}{4}$ inch diameter) were bored. Through these holes the radicle or the plumule of seedlings germinated in crushed quartz was passed, the seedlings being supported in place by a small wad of cotton.

In the case of cotton, cajanus and sesamum, the root was passed downwards through the stopper; in the other cases the plumule was passed upwards. In the latter cases the plant was adjusted so that the seed was in position just above the surface of the water in the bottle.

The seedlings were very carefully chosen from several hundreds grown in crushed quartz, so as to be as nearly equal among themselves as possible. The state at which the seedlings are best suited to the purpose in hand was found by repeated experiment to be as follows :—

(1) *Cotton* when the spread of the cotyledons is 1½ inches.

(2) *Sorghum* when the first and second leaves are equal (both about 1 inch long).

(3) *Cajanus* when the 'spread' of the first leaves is 4 inches.

(4) *Sesamum* as soon as the cotyledons have assumed a horizontal position.

(5) *Wheat* as for sorghum.

(6) *Gram* when the first three leaves have expanded.

The strength of the solutions had been so arranged (by allowing to evaporate) that no plant (of the size indicated) would grow in any of them for more than about ten days. The time between transplanting into the bottles and the times of commencement of wilting and of complete drying up were carefully recorded. The bottles were also weighed every morning and in some cases several times a day to find the amount of transpiration, this amount having been proved (Bulletin No. 28, Bureau of Soils, U. S. A.) to be a measure of the increase of the plant in dry weight.

In all cases two, and in some cases as many as six bottles were treated in the same way, both as regards the solution they contained and the crops grown in them. It was found that with careful selection of seedlings of each size the difference between duplicates either in time of withering or in loss by transpiration was extremely small. The observations here recorded are in all cases the mean of the total number of bottles sown in the particular manner indicated. They are set forth in the following tabular statement :—

TABLE I.

Progress of crops named in Column 1 when grown in water containing matter excreted by crops in Columns 2 to 7 and in distilled water.

CROPS (*of which progress is indicated*).		Crops that had previously grown in the water.						Distilled water.	
		Sorghum.	Cajanus.	Cotton.	Sesamum.	Wheat.	Gram.	Period of growth.	Weight in grams of transpiration.
1		2	3	4	5	6	7	8	9
Sorghum ...	Period (in days) after which withering commenced ...	1	1	1	1	1	1	6	4·7
	Transpiration (in grams) in that time	0	0	0	0	0	0		
	Total period of growth (in days)	5	3	3	2	2	2		
	Number of plants that collapsed in this period ...	3	*all*	*all*	*all*	*all*	*all*		
Cajanus ...	Period (in days) after which withering commenced ...	*	*	7	3	3	3	10	18
	Transpiration (in grams) in that time	15·5	12·2	10·5	2·2	3·0	2·0		
	Total period of growth (in days)	10	10	10	8	10	5		
	Number of plants that collapsed in this period ...	0	0	1	*all*	*all*	*all*		
Cotton ...	Period (in days) after which withering commenced ...	*	8	5	3	4†	2	10	12·5
	Transpiration (in grams) in that time	8·7	6·7	4·7	2·0	3·7	0		
	Total period of growth (in days)	10	10	8	8	10	8		
	Number of plants that collapsed in this period ...	0	*all*	*all*	*all*	1	*all*		
Sesamum ...	Period (in days) after which withering commenced ...	1	1	1	1	1	1	10	6·0
	Transpiration (in grams) in that time	0	0	0	0	0	0		
	Total period of growth (in days)	4	4	3	3	4	3		
	Number of plants that collapsed in this period ...	*all*	*all*	*all*	*all*	*all*	*all*		
Wheat ...	Period (in days) after which withering commenced ...	7	6	4½	4	4	3	10	7·0
	Transpiration (in grams) in that time	3·5	1·9	1·4	1·0	1·2	1·6		
	Total period of growth (in days)	10	10	10	10	10	10		
	Number of plants that collapsed in this period ...	2	1	2	1	2	*all*		
Gram ...	Period (in days) after which withering commenced ...	*	*	*	*	*	1	5	17·7
	Transpiration (in grams) in that time	6·5	6·2	4·7	2·7	4·5	2·7		
	Total period of growth (in days)	5	5	5	5	5	5		
	Number of plants that collapsed in this period ...	0		0	0	0	*all*		

* Plants did not wither at all.

† Though the cotton did not wither, it ceased to transpire after the 3rd day.

The data given in the table prove that all the plants tried, wither in the same order in the different solutions; thus all do worst in the "gram water," "sesamum water" being the next most toxic, followed in order by wheat, cotton, cajanus, sorghum.

This order could of course be easily changed by diluting any one or more of the solutions, the strengths of which in the experiment are quite arbitrary.

The fact of this regularity appears to favour the view put forward above that the substances excreted by various plants are identical, and that the solutions used differ only in concentration and not in kind.

Nature of the Toxic Substance.

It was at first thought that the toxic matter might be an albumose or similar substance. The solutions, however, all gave negative results, on the application of the biuret and other tests for these compounds.

The fact that tannic acid precipitated and corrected the toxic material suggested the presence of an alkaloid.

It is interesting to note that leaves containing tannic acid are systematically used as manure in the spice gardens and rice fields of Canara* and that the cultivators' opinion as to the manurial value of the leaves of any particular variety of tree corresponds apparently to the amount of tannic acid contained in the leaf. Thus in the order of preference the leaves of the following trees (among others) are utilized in this way:—

Hirda (Terminalia chebula).
Matti (Do. tomentosa).
Honal (Do. paniculata).
Kanagal (Dillenia pentagyna).

That it is not the ash constituents of these leaves that produce the manurial effect is obvious from the fact that if the leaves be burnt and the ashes applied to pepper—one of the spices to

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* Mollison—"Cultivation of Betel, Palm, Cardamom and Pepper in the Kanara District of the Bombay Presidency" (Bulletin No. 20 of the Department of Land Records and Agriculture, Bombay, 1900).

which the leaf manure is applied—the pepper vine is killed. Similarly neither irrigation nor farm-yard manure serves the purpose of the leaves; the latter therefore serves neither for storage and regulation of water nor as a supply of nitrogen.

It was indeed these facts that first suggested to me the possibility of the toxic substance being either an albuminous substance or an alkaloid for both of which tannic acid acts as a precipitant.

A preliminary examination of the solutions only has been as yet made, but this appears to prove that it is an alkaloid that is excreted by all the plants experimented with, and further that the substance is identical in all cases.

The solutions examined consisted of both well and distilled water in which plants had grown.

The principal reactions obtained are as follows:—

Phosphomolybdic acid	A white precipitate.
Phosphotungstic acid	Do. do.
Mayer's Reagent	Do. do.
Tannic acid	Do. do.
Platinum chloride	Precipitates on standing.
Iodised potassium iodide	
Mercuric chloride	A coagulated white precipitate.

The subtance is thrown down in concentrated solutions only as a white flocculent precipitate on adding caustic potash. A similar precipitate is thrown down immediately on adding potassium nitrate, potassium chloride, potassium sulphate or sodium chloride and after some time on adding sodium nitrate or sulphate. Potassium chloride and sulphate and sodium chloride produce coagulated precipitates and apparently precipitate the substance most completely of the reagents tried. The precipitate is insoluble in water, alcohol and all the usual organic solvents, but soluble in acids and alkalies. This precipitate can be titrated with an acid using methyl orange as indicator. It is therefore apparently the base itself and not a salt. The salt formed on titration is acid to litmus as is also distilled water in which plants have grown. This fact apparently accounts for statements that free acids or acid salts are exuded by plant roots. Further, on precipitation the solution becomes distinctly acid to methyl orange.

Ammonium sulphate and dilute sulphuric acid also cause precipitation (of the sulphate ?) of the substance after some time ; so also do sodium acetate, ammonium (but not sodium) phosphate, ammonium molybdate (with nitric acid), ferric chloride (soluble in acetic acid).

With greater concentration doubtless other substances than those here indicated would cause precipitation.

The substance cannot be separated out by shaking its ammoniated solution with amyl alcohol, chloroform, or either, hot or cold. It is also insoluble in alcohol.

The solution produces after a few minutes a blue precipitate (in a green solution) with a mixture of ferric chloride and potassium ferricyanide. It also decomposes potassium permanganate in the cold with production of a stable red precipitate (of the permanganate ?) destroyed by boiling or excess of the reagent. Reduction also takes place with Fehling's solution and with silver oxide in ammonia.

It is easily decomposed by heating at 100°C when in the solid state.

The solid dissolves in strong acids and Frohde's reagent without colour, except in the case of nitric acid which gives a yellow solution. Potassium bichromate after strong sulphuric acid gives a green colour, changing to blue.

The above reactions were given by all the solutions named in Table V and appear to indicate the identity of the toxic substance in the case of all plants.

The substance is present in the solution in combination with citric acid. I could find no trace of phosphate or formate as stated to exist by Czapek, though the original solution before elimination of the base, similates many of the reactions of these salts.

Without having reference to the current literature on the subject it is impossible to compare the reactions above given with those obtained with any of the known alkaloids. Its marked insolubility appears to differentiate it from all the commoner alkaloids except pseudomorphine and rhæodine with which it is improbable that it is identical.

The amount of substance given out by the roots is not inconsiderable. For instance, the precipitate obtained by adding potassium sulphate to a solution containing the excrement of 10 cotton plants growing until their combined air-dry weight was ·4 gramme, weighed, when dry, ·21 gramme.

Sesamum in its early stages of growth, appears actually to excrete a greater amount of material than it builds up in its own substance.

Conclusion.

The bearing of the phenomena described in this article on the question of rotation of crops is obvious.

The question may, however, be put why cotton, for instance, which grows so feebly *near* sorghum (Table IV) grows at least as well if not better, *after* sorghum than after cotton. From experiments now in progress it appears that this is explicable as follows :—

When cotton is growing near sorghum the roots of the latter exude the toxic substance into the soil in large quantities. This spreads rapidly through the soil into the subsoil especially during the rainy season, and neighbouring cotton plants are not protected by the fact that their tap roots go down far below the zone in which the sorghum roots are situated. When cotton follows sorghum, however, the condition of affairs is different ; the toxic substance remaining, at the time of harvesting, in the roots of the previous sorghum crop is now being given out slowly in the course of the decay of those roots,* and is held entangled in the organic matter of the roots, largely in the zone of soil in which the roots of sorghum spread. Each crop thus fouls the soil for a crop of the same variety, whose roots will take the same course as the previous crop, more than for a crop whose roots spread in another layer of the soil.

The precipitation of the toxic substance by most of the mineral manures in common use indicates the manner in which many manures act in increasing crop yields.

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* That the roots of sorghum and other crops exert an extraordinarily toxic effect when mixed with soil in which plants are then grown has been proved by the writer in a set of pot experiments.

While this note has been going through the press I have received Bulletin No 40 of the Bureau of Soils, (United States of America) by Messrs. Schreiner and Reed on "Some factors influencing soil fertility." In this Bulletin the authors come to the conclusion that "the excreta of the cow pea roots are very slightly toxic to roots of wheat seedlings" (page 35), and that "the excreta of oats are more toxic to the roots of wheat seedlings than those of corn or cow peas—a conclusion that is substantiated by the results obtained in crop rotations" (page 36).

The experimental data given in the Bulletin do not justify these conclusions but only indicate that the excreta from cow peas *when in the arbitrary concentration obtaining in their experiments* are very slightly toxic to roots of wheat seedlings *when these latter are at the stage of growth of those used in the experiment.*

I find that very young plants are not affected, by a toxic solution of given strength so rapidly as older plants, doubtless because the latter, owing to more rapid transpiration, take in the toxic substance in larger quantities.

Again, the impossibility of the statement made with regard to the excreta of oats being more toxic than that of cow peas or corn is self-evident, implying as it does that any quantity *however great* from oats is more toxic than any quantity *however small* from cow peas or corn.

The media that were compared contained quite arbitrary amounts of excreta from an arbitrary number of plants growing for an arbitrary period, it being stated that "the agar containing their excretions was obtained in each case by planting a large number of seedlings in a dish of soft agar and allowing them to grow for eight to fifteen days according to the kind of plant employed."

There are no data in the Bulletin under reference which indicate that the excreta from all the plants tried are not identical in character.

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Memoirs of the Department of Agriculture in India

STUDIES IN ROOT PARASITISM

THE HAUSTORIUM OF OLAX SCANDENS

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THE HAUSTORIUM OF OLAX SCANDENS.

In previous papers of this series the Haustorium of *Santalum album* was described in considerable detail.[1] It was at the same time noted that certain *Olacaceæ* had been found to be green root-parasites in much the same manner as the sandal. Collections have been made in South India of haustoria of *Cansjera Rheedii, Olax scandens, Ximenia americana* and *Opilia amentacea.* The present paper deals with the parasitism of *Olax scandens,* this plant having been selected because of important differences between its haustorium and that of *Santalum album.* These differences are less marked in the mature haustorium, and lie chiefly in the manner of development of the various tissues, the limits of nucleus and cortex, the formation and structure of the gland, the number of cortical folds, the composition and place of origin of the collapsed layers and the arrangement of the vascular system. In most of these characters the haustorium of *Olax scandens* appears to differ from those of the other haustoria named above as well as from those of *Osyris* and *Thesium* and, in describing it, these characters will be dealt with much more fully than those in which there is agreement with the haustorium of *Santalum album.*

A careful perusal of the literature on root-parasites reveals the fact that suggestions have been offered in the past as to the

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[1] Studies in Root-parasitism.—The Haustorium of *Santalum album.* Part I.—Early stages, up to Penetration. Part II.—The mature Haustorium. Memoirs Dept. Agri. India, Botanical Series, Vol. I, No. 1, Parts I and II—1906-07.

parasitic nature of the *Olacaceæ*, but, just as similar suggestions regarding *Santalaceæ* were long before they bore fruit, those on the *Olacaceæ* have been disregarded. So important a character as parasitism could not have been without interest to systematists, and the absence of all knowledge on the subject must be put down to the fact that the bulk of the systematic study of the higher plants is carried on in herbaria, where large collections of dried branches are stored, and therefore far away from the natural haunts of the plants themselves.

The parasitism of *Thesium humifusum* was proved by Mitten[1] in 1847 : Planchon[2] discovered that of *Osyris alba* in 1858 : Scott[3] noted the parasitism of *Santalum album* in 1871 : comparatively recently Shirai[4] discovered that *Buckleya Quadriala* possesses the like character. And in most of these cases, if not in all, the discovery was made quite independently of the known occurrence of this character in the Order. Planchon, when he found haustoria on *Osyris*, remarked that probably all *Santalaceæ* and, from their affinity, *Olacaceæ* would prove to be root-parasites, but neither this nor Heckel's note[5] on the parasitism of *Ximenia americana* seedlings produced any further results. The discovery of root-parasites among *Olacaceæ* in South India was, as already described (*Santalum*, Part I), made quite accidentally while searching for haustoria of *Santalum album*.

2. *Olax scandens* is a sprawling shrub growing in the midst of thickets. Its trunk is not usually very conspicuous, but sometimes reaches 6—8 inches in thickness, with numerous dorsiventral,

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[1] W. Mitten, Sur le Parasitisme des Racines du *Thesium humifusum*. Ann. d. Sc. Nat. III Ser. Bot. 1847. Vol. 7, pp. 127-8.

[2] J. E. Planchon, Sur le Parasitisme de l' *Osyris alba* (C. R. d. l' Acad. d. Sc. 26 July 1853). Bull. d. l. Soc. Bot. d. France, V., 1858.

[3] J. Scott, Loranthaceæ . . . germination and mode of attachment. Journ. Agri-Hort. Soc. Ind. II, 2, 1871.

[4] S. Kusano, Studies on the Parasitism of *Buckleya Quadriala*, B. et. H., a Santalaceous Parasite, and on the structure of its Haustorium. Journ. Coll. Sc. Imp. Univ., Tokyo. Japan, xvii, 10, 1902.

[5] A. Heckel, Sur le Processus germinatif dans le graine de *Ximenia americana L.*, et sur la Nature des Ecailles Radiciformes, Rev. gen. d. Bot. XI. 401-9. 1899.

half-climbing branches. It is thorny, but only on the older parts of the stem. The leaves are two-ranked, oval or oblong, shortly petioled, dark green, with a blunted apex, 2—3 inches long and 1 inch broad. In the axils of the leaves there are small bunches of whitish, sweet-scented flowers and, later on, globular or ovate fruits. The latter are whitish in colour and have yellow flesh.

The plant occurs all along the eastern coast of the Madras Presidency and for a considerable distance inland, chiefly at low elevations. It is also found in the low, dry part of Ceylon and various parts of Northern India. It is common in Burma and is found in Java. It belongs to a small genus of 25—30 species confined to the tropical parts of the Old World.

Its associates in South India are pretty generally indicated by the appended list of the hosts examined, all ordinary inhabitants of the mixed (evergreen and deciduous) plains' flora of the east coast. This flora is adapted to withstand great heat and drought but in places receives from 30 to 40 inches of rain during the wet half of the year. Leguminous trees such as *Acacia arabica, A. leucoxylon, Dichrostachys cinerea, Pithecolobium dulce, Pongamia glabra, Albizzia Lebbek, Cassia siamea ; Azima tetracantha, Capparis* sp., *Streblus asper, Morinda tinctoria, Melia Azidarachta, Feronia Elephantum :* climbers like *Jasminum sessiliflorum, Tragia involucrata, Rivea hypocrateriformis, Asparagus racemosus, Solanum trilobatum :* succulents such as *Opuntia Dillenii, Jatropha gossypifolia, Vitis quadrangularis ;* and various small shrubs and herbs found in waste places or under the shade of trees, *Ruellia, Phyllanthus, Phaseolus, Ocimum, Carissa* and the smaller *Cassias.* All of which are dwellers on the Coromandel coast.

3. The fruit is a drupe of somewhat curious form, apparently arillate from the fusion of the accrescent calyx with the pericarp to near the top (Plate I, fig. 1). The single seed is heavy and filled with oily endosperm in which lies the minute cylindrical embryo. The radicle is superior. The abundant food in the seed enables the young plant to lead an independent life for a

considerable period. The fruit is said to be relished by birds, and would thus be carried from one tree to another and there dropped among the roots. We find a similar arrangement in the fruits and seeds of *Santalum*, *Cansjera*, *Buckleya*, and *Osyris*, while the smaller fruit of *Thesium*, surrounded by its fleshy calyx, falls at the base of the plant among the grass roots. Such thick-sowing ensures the presence near at hand of the roots of other plants and also explains the half-gregarious mode of occurrence so often seen in root-parasites. So in the *Rhinanthaceæ* we hear of comparatively heavy seeds and germination of the young plants at the foot of their parents' stems, forming the "milky ways" of the Eyebright and causing the Yellow Rattle to be found in such masses as to suggest their having been "sown by the bushel."[1]

Upon germination the root emerges, carrying with it a warty mass of endosperm reminding of a carbuncle, becomes positively geotropic and passes downwards. The cotyledons increase in size and form two plates folded on one another in the endosperm (Plate I, fig. 4), their free surfaces developing a well-marked epithelial absorbent layer. A great extension of the hypocotyl now takes place and, as in *Santalum*, forms a green loop above ground connecting the root and seed. The cotyledons are soon broken off at the base and are left behind in the empty seed, while the young stem is borne aloft and the first pair of leaves unfolded. These stages are illustrated in figures 2—5 on Plate I.

4. As it was not found possible to observe the seedlings of *Olax* in nature, a number of seeds were sown in pure sand in pots in a garden in Madras. In 40 days the young plants had attained a length over all of about six inches, a pair of small green leaves being unfolded two or three inches above the surface. Below ground a sinuous tap-root gave off secondary horizontal branches at intervals. The whole root-system at this stage as

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[1] Kerner and Oliver, Natural History of Plants, I, 184. 1894.

well as part of the hypocotyl below ground was covered with a thick coating of root-hairs. In place of the radish-like swelling of the sandal seedling, the lower part of the stem and the upper part of the tap-root were more or less thickened, doubtless acting, as in sandal, as a store-house for reserve materials to the young plant.

The series of seedlings in these pots were examined at intervals for some 16½ months, when the experiment had to be discontinued. The root-system developed rapidly under these conditions, as in the similar experiments with *Santalum*, forming a dense mass of copiously branching rootlets. This root-system attained its maximum in about the sixth month and, by this time, some half dozen leaves of small size had appeared (Plate I, fig. 6). But these leaves lacked the bright green colour of the first pair : as time went on they became chlorotic and many of them dropped—evident signs of lack of nutrition. Comparatively few haustoria were at any time found in the pots but, at any rate while the roots were healthy, there was a fairly copious supply of root-hairs. These disappeared entirely in the later stages, a number of swellings appearing at the same time which were traced to an attack of eelworms (*Heterodera radicicola*).

At one year, the plants were all of them in a struggling condition, the leaves yellow and dropping and the root-system devoid of the finer branches and, as in sandal, covered with dark scars (Plate I, fig. 7). Some of the young plants were then transferred to ordinary garden earth, and these during the next few months showed much improvement, new roots being formed and the leaves assuming again the dark green colour of the earlier stages.

From these incomplete observations it would appear that *Olax scandens*, like *Santalum album* and many other parasites, develops at first like an ordinary non-parasitic plant, that it is capable of living for a long period upon the nutriment stored in its endosperm and, later, in its swollen stem and tap-root. Its rich development of root-hairs speaks of nutriment derived from the soil, and the brightening of the year-old plants when transferred from pure sand to vegetable mould suggests a considerable independence of growth. It is unfortunate that experiments were not tried in growing seedlings in garden earth from the commencement, but those grown in sand were chiefly intended to supply material for the study of the young stages of the haustorium, in which respect the results were disappointing.

The difference from *Santalum album* in the development of root-hairs is not confined to the young plants, for in old roots in nature the parts immediately behind the broad white ends were found to be covered with a felt-work of delicate hairs, in striking contrast to the smooth white rootlets in sandal (Plate II, fig. 3). On the other hand, the copious development of haustoria on the young roots grown in sand, so striking a character in *Santalum*, was much less evident in *Olax*. A few haustoria were found, but they were widely scattered, few self-attachments were met with and not nearly so many cases of adhesion to pebbles or grains of sand (Plate II, fig. 4).

The free development of unattached haustoria in *Santalum* was regarded by Scott as indicating waning parasitism. This character must be extended to *Thesium* where many haustoria are unattached in the young roots, as has been pointed out by Leclerc du Sablon and others and observed by myself in Indian species. In both of these genera the root-system, as such, is poorly developed and root-hairs are more or less absent. These facts appear to indicate not so much a waning parasitism as a very well-developed one. In *Olax* on the other hand, the comparative rarity of haustoria in the earlier stages of growth, the well-developed root-system and the abundant root-hairs even in old plants, suggest rather *incipient* parasitism. According to Heinricher,[1] in plants becoming parasitic, haustoria are probably first developed, and then reduction of the root-system takes place. The parasitism of *Olax scandens* thus appears to be in a comparatively elementary stage, judging by the absence of the multitudes of unattached haustoria in the seedlings, the well-developed root-system and the abundance of root-hairs in both

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[1] E Heinricher, Die grünen Halb-Schmarotzer, II *Euphrasia*, *Alectorolophus* and *Odontites*. Jahrb f. wiss. Bot. XXXII, 1898.

young and old stages of the plants. For the illustration of these points the reader is referred to the figures on Plates I and II.

5. The haustoria of *Olax scandens* differ but little in appearance from those of *Santalum album.* More or less conical, whitish as a rule, but frequently discoloured grey or brown by the surrounding earth or, in older specimens, by the corky layers formed and, in the latter case, lacking the bright red-brown colour of the sandal root-system. The older haustoria are perhaps more irregular than those of sandal and appear, on the whole, more frequently to be compressed and distorted or flattened, scale-like and circular. In size there is little to separate the two, the ordinary haustoria in *Olax* being 1—5 mm. high, 5—10 mm. long and 4—8 mm. broad (Plate II, figs. 5—8 of which 6 and 7 are of natural size).

Occurring as it does in thickets, *Olax scandens* has abundant roots at hand to which to attach itself, and examination shows that it avails itself very readily of the opportunity. It was also noticed at the very commencement with what frequency self-attachment occurred in nature. Indeed, the very first specimen which drew attention to its parasitism was the case drawn in figure 8 of Plate I, where a seedling has attached itself by a series of haustoria to another, older *Olax* plant.

Nothing definite can be said regarding the preferences of *Olax* roots for particular hosts. The only means available of judging was to determine in how far it was easy to collect haustoria from the plants growing near or with it, a matter depending largely on opportunity and locality. In the area from which the specimens were obtained, the following have earned the character of being favourites :—*Albizzia Lebbek, Casuarina equisetifolia, Jatropha gossypifolia, Pithecolobium dulce, Pentatropis microphylla, Dichrostachys cinerea, Azima tetracantha, Cephalandra indica* and *Feronia Elephantum.* On the other hand certain plants, occurring in fair abundance among the *Olax* thickets, were searched repeatedly with little success for connections. Such were *Euphorbia reticulata, Cassia siamea, Melia Azidarachta,* *Zizyphus Jujuba and Opuntia Dillenii.* It is not, however, possible to form any definite conclusions on this point without a very great deal of study in other localities. All that can be said is that, from the very limited series of plants in which the roots have been laid bare, there are some grounds for assuming a certain amount of preference for certain hosts.

6. In the many haustoria examined in the preparation of this paper, a number of young ones, attached but not yet penetrated, were encountered, and a study of these has proved to be of exceptional interest (Plates III—VI). No attempt will be made here to trace the embryonic stages of the haustorial development or to determine the tissues of the mother root from which they were derived. It will suffice to say that there are evidences that the development of the haustorium from the mother root is similar to that described by Leclerc du Sablon[1] for *Thesium* and assumed by me for *Santalum*, but it will serve a better purpose to deal with this subject in several species together and the necessary material has not as yet been collected.

In its first appearance the haustorium of *Olax scandens* resembles that of *Santalum album* closely. The root-system of the pot-plants which were expected to furnish many young stages proved disappointing, but a certain amount of material was collected in nature (Plate II, fig. 2). It may be noted that even in the youngest stages the haustoria were smooth, although the roots on which they occurred were well clothed with root-hairs. This appears to be rather unusual among root-parasites. Root-hairs have frequently been noticed on the haustoria of *Santalum*, while they appear to be a constant feature in the *Rhinanthaceæ*.

The haustoria in *Olax* appear to be able, as in sandal, to develop without the aid of foreign root-stimulus, but proofs of this are not so clear as in that plant. Be that as it may, many of the haustoria become fairly large before they

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[1] Leclerc du Sablon, Recherches sur les Organes d'Absorption des Plantes Parasites (*Rhinanthaceæ et Santalaceæ*). Ann. d Sc. Nat., Bot., Ser. VII, vol. vi, pp. 90-117, 1887.

make any impression on the root attacked. We shall proceed to consider the internal structure of such.

In the earliest stages of development met with in the sections examined a differentiation has already occurred in the tissues. These are divided into an outer and an inner zone (Plate III, fig. 1). A peripheral zone of irregularly arranged, more or less permanent cells surrounds the whole of the rest as a sort of mantle. The contents of these cells have largely disappeared, there is little or no starch, and rows of calcium oxalate crystals have made their appearance. Not infrequently the cells are crushed in places and intercellular spaces occur here and there. This crushing of the tissues is most pronounced at the inner border of the zone where it joins the central mass, and here too the intercellular spaces are not infrequently united to form a series of lacunæ.

The inner zone is at once seen to be the living, active part of the haustorium. The cells are small and full of contents, arranged in radial rows and rapidly dividing in a plane parallel to the surface of the host. Curves of growth are thus produced. In the case figured they are already commencing to bend inwards towards the middle line.

At the proximal end the vascular elements of the mother root enter the haustorium, bringing the materials for its development (Plate III, fig. 2). Where, as in fig. 1, the section is not quite median, masses of smaller, darker cells indicate the place where the vascular loop will make its appearance and unite the haustorial axis with that of the mother root. These procambial masses are formed in the zone of radiating cells.

There is yet another differentiation which has already made its appearance. The contents of the radiating cell are not equally distributed through the zone. The parts nearer the host's root are distinctly clearer than those outside them and, in thick sections, a band of cells with darker, starchy contents may be traced right round near the line of separation of inner and outer zones. This dark area forms a sort of cap over the inner, clearer portion and it is presumed that it is due mainly to the greater meristematic activity in the distal end of the haustorium. There is less opportunity for the deposition of starch where the cells are in such active division, and the deposition of such starch indicates a tendency in the cells to cease dividing and become permanent.

7. Shortly after the haustorium comes into contact with the root of a host, important changes take place in its tissues. An oval area of clear cells altogether free from starch appears among the radiating cells in the median line. This oval area is the first indication of the "nucleus" of the haustorium, the parts on either side forming the "cortex" (Plate III, fig. 2). It should be borne in mind that these terms are purely empirical and a matter of convenience. The regions so called do not correspond with definite portions of the mother root, nor are they homologous altogether with the similar regions in the haustorium of *Santalum*. The term "nucleus" in any haustorium refers to that median portion which in early stages is differentiated by the character of its cell contents from the parts outside, undergoes rapid cell division and takes the chief part in the formation of the axis. It is probably only the lower part of the oval area now described which forms the nucleus in *Olax*.

The cortex of the haustorium is seen to consist partly of the outer permanent mantle of irregularly arranged cells already mentioned and partly of that portion of the radiating rows of cells of the last stage which are not included in the nucleus, but clothe it on either side. While thus the nucleus is employed in cell division and its cells are prevented from growing in length by the opposition of the host's root, the cortical cells expand and grow along the outer side of the root attacked, forming the cortical or clasping folds which thus early help to fix the haustorium to the host. This takes place with a certain amount of force, as is evidenced by the burrowing action of the folds in the bark of the host (Plate III, fig. 2).

The outer, irregularly arranged cells have become a permanent mantle round the tissues inside them, perforated at the proximal end by the strand of vessels from the mother root.

The denser portion of the cortex, laden with masses of starch, now occupies a position half way between the surface of the haustorium and the host's root. It has become more sharply defined and, in most cases, the outer radiating cells, formerly filled with starch, have commenced in their turn to lose their contents. The denser portion is moving inwards. A separation layer will shortly be found between the outer, denser part of the cortex and the inner, clearer rows of cells. Although this line of demarcation is not yet clearly seen, it is frequently possible at this stage to form an idea as to where it will be formed.

The haustorium, as a whole, is becoming crescent-shaped, and the lines of growth curve more distinctly towards the median line. This is brought about by the expansion of the outer cells of the radial rows tangentially, and they are seen to be distinctly broader than those within (b and c). The inner, clearer cells are in fact smaller in all directions, being confined in a narrower space.

The oval, central area also shows a certain amount of differentiation. Its upper limit is not at present clearly defined and the development of this part may be left out of consideration for a time. The junction of the axis of the haustorium with the mother root forms, in fact, a transitional region at present undifferentiated. In the lower part, however, a dense vertical shadow is seen in the middle line, extending almost to the surface of contact with the host's bark. The cells of this shadowed area appear to be dividing more rapidly in the vertical than in the horizontal direction and thus already appear to be elongated transversely to the axis of the haustorium. This elongation is shown well in figure 2d′ of Plate III, taken from a young haustorium of this age. The vertical shadow may be regarded as showing the first stage in the development of the gland.

The zone of the radiating cells described in the previous section (Plate III, fig: 1) has thus undergone considerable changes. But the cells of the haustorium, although somewhat disturbed, are still arranged in the same rows more or less at right angles to the host's surface and curving inwards to the axial line. It is still possible to trace continuous rows of cells from the cortex right to the centre of the nuclear area, and it is difficult to draw any sharp distinction between cortical and nuclear regions where they pass into one another. The radial arrangement of the cells becomes gradually obscured in the nucleus by the rapid divisions taking place, while the cortex, as a whole, retains a radial arrangement for almost its entire existence (see paragraph 16).

8. It has been found difficult in the sections available to trace the stage just considered further, so much so that one is tempted to suggest two independent lines of development in *Olax* haustoria. The stage next met with shows sharp constriction at the top of the oval area and its consequent division into an upper and lower part. Two cases have, it is true, been met with where such a constriction may be thought to be actually taking place by the filling of a small triangular mass of cells on each side with starch grains, and thus simulating an ingrowth of the cortex, but the sections are not always very convincing. We shall assume that fig. 1 on Plate IV is the next stage in development, and that the small triangular areas *t t* divide the meristematic area into two parts.

The separation of nucleus proper from the vascular loop is well seen on Plates IV—VI. Leaving the vascular loop, which is usually quite immature, alone for the present, we find a series of remarkable changes taking place in the nucleus and cortex. The nucleus as a whole remains meristematic and unaltered save for the massing of plastic materials in its cells, but the gland develops rapidly, and largely at its expense. This organ has become sharply marked out as an oval region inside the nucleus, at first surrounded on all sides by protoplasmic cells (figs. 1—3), but, later on, growing to such a size and taking up so much for the nuclear space that it is not possible to say whether any of the latter tissue remains outside it excepting at the proximal end (fig. 4).

A great change has also taken place in the arrangement of the starchy and clear cells of the cortex. While the gland is young and "unopened" there may still be some difficulty in locating the exact line of separation between the outer, starch-laden and the inner, clear tissues; the transition is as yet gradual. When, however, the gland is fully formed and throwing out its secretions, this line of separation is so striking that it arrests the attention at once (Plate IV, fig. 4, and Plates V and VI). This will be dealt with later.

The haustorium, as yet without penetration into the host's tissues, but possessed of the complicated structure shown in fig. 1 on Plate V, may be assumed to have reached its complete youthful form. As we shall see, the mere act of entering causes a complete change and presents us with an entirely different structure whose parts are difficult to recognize. The development having reached a certain stage, it will be well to consider the appearances in detail, as well as to compare the arrangement of the tissues with that of the haustorium of *Santalum* at a similar stage. For this latter purpose, we may refer to figure 22 on Plate V of Part I of the description of *Santalum* haustoria. A single glance at that figure is enough to show what great differences there are in the development of the haustoria in these two plants.

The nucleus in *Olax* cannot be made to agree with that in *Santalum.* In *Olax* there is a sharp separation between nucleus and vascular loop: in *Santalum* they are merged in one another and the nucleus passes some way up, projecting as a mass of parenchymatous cells in the median line between the two arms of the loop (Plate IX, figs. 2 and 4). The starch-filled cells in *Santalum* surround the nucleus closely and, further out, a distinct line separates them from the clearer outer cells. The reverse is the case in *Olax*, the denser cells being outermost. Moreover, this line of separation between the clearer and denser cell elements abuts, in *Santalum*, on the axial region at the middle of the vascular loop, in *Olax* opposite the middle of the gland, which is much lower down. The sucker in *Santalum* is formed of nucleus and cortex, but in *Olax* only the former takes part in its construction. And these differences are but the prelude to others in the structure of the gland itself, of the collapsed layers and the vascular system. These parts of the haustorium will be dealt with in succession.

9. The gland is a very constant feature in the haustorium of *Olax scandens*, so constant that I have not been able to convince myself that it is ever absent excepting in the very smallest. This is at variance with what was observed in *Santalum*, where the gland was frequently absent and was regarded rather as an additional means of penetration in difficult cases.

It first makes its appearance as a dark shadow in the lower half of the nuclear axis (Plate III, fig. 2), and an examination of this shadow has shown us that it is caused by an accumulation of plastic materials in the cells, together with a very rapid sub-division into small cells transversely elongated (Plate III, 2d and 2d′).

At an early stage of the development of the gland a dark "cap" is seen to be formed over its upper, broader end, while the lower half is narrower and only imperfectly developed (Plate IV, figs. 1 and 2). The upper half rapidly expands, a wide clear "lumen" being formed traversed by faint dark horizontal lines, the cap at the same time becoming more pronounced and clothing the whole of the upper half of the gland. The lower half is narrower, is not bounded by such a dark layer but develops a lumen like that above it. Below the gland a dark vertical shadow is traceable connecting it with the host's root (Plate IV, fig. 2).

It will be well to examine such a stage carefully, because the glandular cells quickly undergo disorganization and, in the next stage (fig. 3), have already lost much of their character. The cap is seen to consist of a great number of very small cells closely packed together and densely filled with dark contents, being sharply marked off from the cells of the nucleus outside. These form the "bed" of the gland, giving rise to the secreting cells (Plate IV, 2b *x*). The walls of the lower half of the gland consist of similar cells, but they are neither so small nor so closely packed, and pass by easy transitions into the rest of the nucleus (fig. 2a). The clear space, both above and below, is seen to be traversed by irregularly jointed, dark parallel lines, and as these can without difficulty be traced into the rows of cells at the sides composing the wall of the gland, it is fair to assume that they consist of the contents of broken down glandular cells. These are shown in Plate IV, figs. 2a and 2b, which illustrate the lowe and upper halves of the gland lumen respectively.

The next change which takes place in the gland is the great development of its lower half. This rapidly increases in breadth and becomes lobed. At the same time its walls become less distinct and the separation of the upper and lower halves becomes more pronounced (Plate IV, fig. 3). This stage does not, however, last long. While the upper half retains its cap, the lower increases in width until little if any of the nucleus is left at the sides. At the same time the gland tissues in this region become completely disorganised, and a large lumen is formed filled with a glairy substance and occasional indications of what were once rows of secreting cells (see Plate V, fig. e, where such cell remains are drawn). Meantime the shadow spoken of in describing figure 2 has become much more definite and, when carefully examined, proves to be a well-defined channel through the dense, compressed cells of the lowest part of the nucleus to the tissues beyond, whether of haustorium or host. This is the duct of the gland and is constantly present (see also Plate V, fig. d).

We see then that, while in *Santalum* the gland is formed by the separation of two sets of cells by a subcuticular secretion formed layer by layer until the lumen is filled (*Santalum*, Part I, Plate V), in *Olax* long lines of cells are decomposed, the contents becoming more and more attenuated until they disappear entirely in a glairy matrix. The gland in *Santalum* is more or less schizogenous, while that of *Olax* is essentially lysigenous.

10. In the stages thus far examined we have again and again had occasion to draw attention to the peculiar way in which the starchy and clear areas of the cortex are arranged. In the

earliest case examined (Plate III, fig. 1) a peripheral layer of irregularly arranged cells surrounds the actively growing part of the haustorium, and in this layer the cells are clear of starch. In the radiating cells of the growing part, on the other hand, starch is abundant, but it is denser in the outer cells, those nearer the host's root being clearer. This general arrangement has been met with in all subsequent stages of development, the densest layer being, however, formed further in in successive stages. It is fair to assume that the outermost clear cells have yielded up such starch as they had because they have ceased to take part in the life of the haustorium and (from the accumulation of calcium oxalate crystals) become moribund, merely functioning as a protective layer to the tissues within. Growth in the haustorium being centrifugal, it is natural to suppose that the comparative clearness of the inner layers is partly due to the cells being in a more meristematic condition. They are actively dividing and have protoplasmic contents. The deposition of masses of starch will presumably indicate that the meristematic condition has been passed or is in abeyance. The absence of dense masses of starch in the inner zone is thus readily explained, as also is the constant inward movement of the region where the masses of starch are densest, the outer cells becoming in turn permanent or moribund and yielding their starch to those within them as the latter lose their early meristematic condition. This region of greatest density is seen in thick sections as a dark shadow and may be followed by comparing the figures on Plates III—VI.

But while the comparative clearness of the inner layers presents no great difficulty in our study, when the gland appears we are confronted by a very puzzling phenomenon. The line of demarcation between dense and clear regions, at first very indefinite and difficult to locate, becomes sharp and the transition sudden, when the gland becomes mature. A perfectly clear inner zone with watery contents is differentiated, and this zone is bounded outwards by cells containing the densest masses of starch, the line of demarcation being thus intensified to the last degree. We have, if possible, to account for this curious fact, completely at variance with all that we have seen in the *Santalum* haustorium

The line of separation appears to be closely connected with the gland, and always abuts on the nucleus nearly opposite to the middle of the gland, about where the "cap" reaches its lower limit. From the nucleus outwards it passes downwards on each side in a well-marked curve, more or less across the lines of growth, and terminates either indistinctly in the end of the cortical fold or curves round and ends sharply on its inner surface (Plate V, figs. 1 and b).

Obviously some other factor than the more or less meristematic condition of the tissues enters the case. In fact, the cells of the clear region soon *lose* their meristematic character and, when they reach the clearest stage, are permanent and more or less moribund. We may consider the food requirements of the developing tissues of the axis. Such would undoubtedly help to keep the inner cells of the cortex clear of starch and, with the great and sudden development of the gland, these requirements are intensified. The upper parts of the nucleus may be presumed to be supplied with nutriment by the strands of vessels from the mother root. But the needs of this rapidly developing upper part and the density of the tissues in this region cuts off, so to speak, the lower parts from this source of supplv. The inner cells of the cortex are therefore laid under contribution. We have seen that at a certain stage the lower part of the gland swells enormously and rapidly becomes disorganized with the secretion of a mass of glairy substance. It is just at this stage that the inner cells of the cortex become cleared of their visible contents, and the cells thus cleared are exactly opposite to the swelling region of the gland. It appears probable therefore that the clearing of the inner cells of the cortex is due to the passage of their contents to the developing lower part of the gland.

And if this be the case, and explains the upward termination of the line of separation, it is not impossible that its downward continuation may be due to the same cause, less material being required as the scene of activity is receded from. This is not offered as a full explanation of the phenomenon, and it is almost certain that other factors enter into the case. Such sharp lines of separation do not usually occur in homogeneous tissues rising from the same meristem, however much their contents may be wanted by the adjoining tissues (see for instance the action of the scutellum in emptying the endosperm of seeds), and there is evidently a profound alteration in the character of the cells in the clear zone at this time. Their after history shows that they are of no further use to the haustorium and take no further part in its activity. The remarkable clearness of the cells, taken together with their evident turgidity, lastly, suggests the possibility that the clear zone may act as a sort of transfusion tissue. It has already been noted that the lower part of the gland is widely removed from the vascular strands coming from the mother root (Plate VI, fig. 1). The formation of such masses of secretion as are seen in the final stage of the gland will require a considerable amount of water. Such a supply cannot presumably be rapidly passed from above—because of the absence of vascular continuity, the great development at the same time taking place in the upper part of the nucleus and the density of the glandular "cap." It is possible then that the clear zone represents a water reservoir on which the lower swelling part of the gland may draw when it reaches its period of maximum activity.

It should, however, be remarked that sharp lines of separation between starch-laden and clear cells are occasionally found in other parts of the haustorium of *Olax scandens*, although with less precision. In an older stage, for instance, as shown on Plate VIII, where the entry of the sucker into the host's root may be presumed to draw rapidly upon the surrounding tissues, the inner cells of the cortex become emptied of their contents and the line of separation between the clear and starch-laden cells is very distinct (Plate VIII, figs. 1 and 2 at *x*).

11. For entrance into the host's root the haustorium of *Olax scandens* appears, excepting in very small haustoria, to be

largely dependent on the dissolving action of the glandular secretion. In *Santalum* we saw that penetration could be effected without this organ and that, if the first attempt proved unsuccessful, the axial tissues next to the host were able to, so to speak, reconstruct the nucleus again and again, each time also producing a new pair of clasping folds. A compound haustorium was thus produced (*Santalum*, Part I, Plate V). There is only one nucleus and one pair of folds in *Olax.* Its haustorium is never compound. The reason for this is not far to seek. In the first place, the gland is exceedingly large and takes up the whole of the lower part of the nuclear meristematic tissues; and the tissues of the cortex immediately adjoining are, as we have seen, cleared of all their contents and, when the gland is mature, rapidly become moribund. In the second place, it is probable that the gland is a much more permanent structure than that in *Santalum*, and the "cap" in the upper part continues to supply cells which pour out their secretion long after the lower part is completely disorganized. One reason for assuming this long continued activity of the gland is the frequency with which the mature gland is met with in the sections. While such stages as are shown on Plate IV, figs. 1—3, are rarely met with, mature glands such as that on Plate V are quite common—indicating, I think, that the gland continues in this active stage for a considerable period, while it passes through the preliminary stages quickly. The need for secondary nuclei and cortical folds is not, therefore, felt by the haustorium in *Olax* and, if it were, there is no meristematic tissue left near the host's root which could produce them.

The figure on Plate VI appears to represent a very late stage of the gland: the whole of the lower part has been crushed, and the cap is still composed of many layers of secreting cells. There is some probability that the haustorium would have succeeded in entering this root, for a minute crack has appeared in the host's bark in the middle line and certain of the cells of the haustorium are projecting into it.

There are, however, other points of interest to be noted in the haustorium shown on this and the preceding plates. In

Plate V a fully mature gland is figured. Its lower part and the whole of the nucleus around it are completely disorganized, but some considerable growth has commenced in the nucleus above the gland, pushing the cap down into the lumen of the gland. The cells of this meristem are seen to be dividing so as to form rows of cells radiating from the lumen and they are also separated into two distinct regions, a median and a lateral (fig. c). The median strand consists of much smaller cells, divisions here taking place both in the radial and the tangential direction. This strand appears to be the first differentiation of what will be the axial plate of vessels. In Plate VI this nuclear meristem has grown considerably and the stage there illustrated may be taken to represent the last in a haustorium as yet wholly outside the host's root.

The downward thrust of the glandular mass exerts considerable pressure in the interior of the haustorium. This is seen in the flattened shape of the peripheral cells of the nucleus and those of the adjoining cortex. It is also seen in the crushing out of recognition of the lower part of the gland. But of more interest is its effect upon the zone of clear cells and the adjoining starch-filled parenchyma of the cortex. We have here in fact the first step in the formation of the *collapsed layers* clearly depicted. These are at first formed entirely from the outer cells of the clear layers (Plate VI, fig. 3) but, later, the outer starch-filled cells also take part, those about to be added to the collapsed layers losing their contents with fragmentation of the starch grains and becoming clear (Plate VI, fig. 2, and Plate VIII, figs. 1—3). A reference to what happens in *Santalum* will show that this formation of the collapsed layers is entirely at variance with what happens there. But this is not all. The collapsed layers of the mature haustorium in *Olax* are made up of three distinct parts, each formed at a different time and in a different manner, whereas in *Santalum* the collapsed layer on each side is uniform in its origin. The part of the collapsed layers formed at this stage of development in *Olax* is the lowest one. The middle portion is not formed until after penetration, and the small, upper portion only after secondary thickening has greatly added to the diameter of the haustorium. The collapsed layers in *Santalum*, on the other hand, appear as lines of pressure in the cortex when the nucleus begins to expand, little or no difference being observable in the cell contents on either side of them during their formation (*Santalum*, Part I, Plate V, figs. 22 and 31, and Part II, Plate I).

As regards the vascular loop, there is thus far comparatively little change. In both this and the last stage, however, a horizontal plate of tracheides, divided in the middle line, has appeared immediately above the nuclear meristem (Plate V, fig. 1, and Plate VI, fig. 1).

12. No single instance has been observed among the 130 haustoria examined in the preparation of this paper of one in the act of entering the root of the host. We are justified in supposing from this that, as in *Santalum*, the haustorium enters very quickly. The tissue behind the gland, consisting of an immense number of small active cells charged with protoplasm, has become greatly elongated as soon as a breach has been made in the host's root. Profound changes in these tissues, chiefly due to the extension of the cells, have taken place in the act of entering, and it is, in most cases, difficult to trace their relative positions before and after penetration. The only method that has suggested itself of determining the extent of these changes is to select a haustorium which has entered some soft root or part of root and has thus been less distorted under the entering pressure, also which, by certain signs, as for instance the traces of a former gland, is seen to be in a youthful condition, and to compare it with that figured on Plate VI. This method has served to throw a good deal of light on the subject, as will be seen from figure 1 on Plate VII, where a young haustorium has penetrated a root of *Asparagus racemosus* but has as yet been unable to rupture the vascular cylinder, has not been cut off from the host's cortex by bands of cork and has a distinct trace of a former gland, all signs of comparatively recent entry.

This specimen is unusual in certain respects (due partly to the fact that the root entered is that of a monocotyledon) and therefore not altogether useful in the series, but it has the great advantage over the other sections obtained of forming a stepping stone between the younger gland-bearing stage and those which have penetrated and lost all signs of that organ, and, after a comparison with the stage shown on Plate VI, we are able to locate most of the tissues. The nuclear meristem has, indeed, changed almost out of all recognition, having thrust itself into the breach in the form of the sucker and swollen out there, besides developing a thick central strand of vessels. But, with the exception of the latter, the change in the tissues is chiefly such as would inevitably result from a great and sudden elongation of all the cells. There are probably not many more cells in the nuclear region of Plate VII than in that of Plate VI. The cortical cells have taken small part in the great expansion which has led to the formation of the sucker, excepting perhaps on the two sides where a small portion may have been dragged in. This might be expected from the much more meristematic nature of the nuclear cells than those of the surrounding cortex, and the small cortical masses dragged in have no part in the activity of the sucker. We see in this a further difference between *Olax* and *Santalum.* In *Olax* the sucker is formed of the cells of the nucleus, while in *Santalum* the cortex takes a distinct share in its formation, accompanying the nuclear tissues on each side. This difference has its explanation in the destructive action of the gland in *Olax* on all the tissues below it and at its sides.

The great advantage of the section on Plate VII, however, over all others met with of a similar age is that, by a careful comparison with that on Plate VI, we can at once lay our finger on the *zone of clear cells* with the collapsed layers outside them. We see also that the collapsed layers are being extended upwards, but this region is irregular in the section and will be referred to in a later specimen.

The median vascular strand passes upwards into a horizontal band of vessels (already indicated in the two previous Plates), the base of the vascular loop, and the latter extends upwards, widely open, through the transitional region towards the mother root.

The region of the cortex with denser starch contents has in the section become narrower, the outer and inner cells of the radiating rows having become clear and devoid of contents.

13. The points referred to in the latter part of the preceding paragraph are more clearly brought out in the young haustorium figured on Plate VIII, entering a root of *Albizzia Lebbek.* Although the haustorium is still very young, the gland has completely disappeared, nor is the zone of clear cells certainly traceable without the aid of the section last described. In other respects this section is more regular than the last and shows the ordinary course of the haustorial development better. The root invaded is that of a dicotyledon and shows the sucker lobes passing on each side along the cambial line and throwing back the two cortical wings of the host's root. The vascular strand is simple, no secondary thickening having taken place. The tissues derived from the nucleus are sharply marked off from those of the cortex, being separated by collapsed layers or being readily distinguishable from the nature of their own contents (figs. 1 and 2).

The lower part of the collapsed layer curves abruptly inwards round the ends of the cortical wings of the host. This inward projection is of constant occurrence and is difficult to explain. As we shall see later on in this paragraph, it is probably derived from nuclear tissue and corresponds with the small bay of clear cells marked *d* in figure 2 of Plate VI. Whatever its origin, it undergoes no further development, but the part of the collapsed layer below it still increases in thickness, receiving accessions of crushed cells both from the zone of clear cells within and from the cortical cells outside it (fig. 3). Such cortical cells as are about to be added to the collapsed layer can be readily traced by their almost total lack of contents. The first change that appears in them is the breaking up of the starch grains into very fine particles and these, later on, disappear entirely. The cell walls remain white while those of the unaltered starch-filled parenchyma outside become slightly discoloured and browned (figs. 1—3).

The formation of the middle part of the collapsed layer is well seen in the section. It is formed entirely from cortical cells and follows the line of junction of cortex and nucleus. Its mode of origin from the innermost cortical cells is seen to agree with that described above for the increase in thickness of the lower part (fig. 3), so much so that the middle and lower portions of the collapsed layer appear as an undivided whole and form an unbroken curve, the inward projection half way up alone indicating the place of junction (figs. 1 and 2). The upper limit of the middle part of the collapsed layer is indicated by the ending of the clear cells outside it (fig. 2 *x*). The starchy cells beyond retain their character during the life of the haustorium, losing their contents very gradually. The third or uppermost part of the collapsed layer is unimportant, appears only in old haustoria with secondary thickening and follows a different course (see paragraph 16).

The axial tissues at this stage require a word of explanation. When the nuclear meristem undergoes its great extension and thrusts itself downwards into the host's root, its cells are stretched to their utmost limit. In one place this extension is too much for the cohesion of the tissue and it is ruptured, forming a characteristic and well-marked lacuna (fig. 2, *lac*, but better in Plate VII, fig. 1). The cells above and below this lacuna, being subjected to very different degrees of tension, are not affected in the same way. While those above become greatly elongated (Plate VIII, fig. 2, *a*), they remain connected with one another and retain their radial arrangement (they correspond with the cells marked *a* in Plate VI, fig. 2). They have delicate protoplasmic sacs and are readily distinguishable from the starchy cells which were early pushed in between the nucleus and the vascular loop (Plate IV, fig. 1, *t*).

The cells below the lacuna are more difficult to explain, and it is not altogether certain to what part of the nucleus they belong. They form a sort of "nest" of cells, oval in shape, rounded towards the collapsed layer and drawn out downwards in the direction of the sucker, and show a well developed and constant collapsed layer in the middle (Plate VIII, fig. 2, *b*). This nest of cells is apparently little affected by the changes which have taken place. They appear to lie in a sort of eddy in the conflicting currents of growth around them. As far as can be seen, they correspond with the area marked *b* in fig. 2 of Plate VI, and have been dragged inwards and downwards so as to occupy a horizontal instead of vertical position. If this is the case, the cleared cells at *d* in the same figure would naturally, as suggested above, be crushed and persist only as a minor collapsed layer, as at *b* in fig. 2 of Plate VIII.

The starchy cells of the cortex are well seen. The radially arranged cells are, as in Plate VII, cleared of contents both outwards and inwards and have a band of densely packed cells in the middle. And, in passing, it is remarkable how sharp is the line of demarcation between the starch-filled and the clearer cells about to be added to the collapsed layers (see end of para. 10). The denser layer does not undergo much further change, its cells have apparently entered the permanent stage and their walls are brown and firm. Such masses of cells, frequently with remnants of starch in them, are met with right on till the end of the life of the haustorium.

14. We have now studied the structure of young haustoria which have succeeded in penetrating monocotyledon and dicotyledon roots, and it is hoped have succeeded in bridging over the gap in the series before and after penetration. We have seen that the zone of clear cells, ending upwards opposite the middle of the gland, is traceable into the tissue that is thrust back against the collapsed layers by the opening cortical wings of the host's root. The lower part of the collapsed layers, at first arising from crushed cells of the clear zone, is afterwards added to by cells of the starchy cells outside, which have lost their contents. The middle part arises where nucleus joins cortex, above the former glandular region, and is formed entirely from the outside, that is from cortical cells. These lower and middle

portions coalesce and form the ordinary collapsed layers of the mature haustorium, an inward process permanently marking the point of junction. In such a mature haustorium the upper end of this collapsed layer points to the top of the nucleus or to the angle formed by the vascular strand of the axis and the base of the vascular loop. This development of the collapsed layers in *Olax* is very different from that described for the haustorium of *Santalum*. In *Santalum* the collapsed layers are formed much further out and their upper end passes well outside the whole vascular loop, and, in non-median sections, right round it. These differences are illustrated by the diagrams 2—5 on Plate IX; figs. 2 and 3 represent young and mature stages of the haustorium of *Olax*, 4 and 5 of *Santalum*. The collapsed layers are indicated by the letters *c. l.*

The gland, which is such a marked feature in the young haustorium and is apparently constantly present in haustoria of any size, leaves no trace behind it in the ordinary mature haustorium, thus again contrasting greatly with the behaviour in *Santalum*. This constant absence of traces of the gland in older sections at first caused great surprise. It was surmised that its disappearance was due to the disorganized nature of the gland in its older condition, to the great force with which penetration is effected and the hardness of the woody cylinder of the host's root against which it is pressed. Sections cut later through soft roots confirmed this view. In 12 cases distinct traces of a former gland have been met with, and these are all or almost all in attacks on soft-tissued hosts, *Azima tetracantha* and *Asparagus racemosus* being typical examples. Every section cut of haustoria penetrating these roots shows traces of the gland (Plate VII, figs. 1 and 2). The part of the gland left is presumably the last remaining cells of the cap of densely crowded cells at the top of the active gland and possibly portions of the duct. The comparison of *Olax* and *Santalum* in this respect will be rendered clear by a reference to the diagrams 3 and 5 on Plate IX, where *gl* indicates the remains of the gland after penetration.

The sucker cells in contact with the host's root are similar to those in *Santalum.* Those at the ends of the lobes are secreting, pouring out the characteristic (yellow) mucilaginous substance in which the cells are seen to radiate (Plate X, fig. 2). After the secreting edge of the lobe has passed and connection has been established between the cells of haustorium and host, the organ becomes absorptive, and reticulated vessels are formed along the main lines of transport. The cells in contact with the host's root are elongated and form a palisade-like layer which is specially distinct in old haustoria which have lost their contents (Plate X, fig. 1). In all these respects the resemblance between the suckers of *Olax* and *Santalum* is very close.

15. It will have already been noted that the vascular tract in the lower part of the haustorium in *Olax* differs from that in *Santalum* in the absence of a pith or median parenchymatous tissue. There is a single, median plate of vessels in place of two parallel ones. The absence of this parenchyma is perhaps one of the chief peculiarities in *Olax*, as it is present in all the other haustoria of the series examined, and it is accompanied by great differences in the early stages of development of the haustorium.

In *Santalum* the nucleus is seen to project upwards between the two diverging arms of the vascular loop (Plate IX, fig. 4, dotted line) and, in older stages, its upper limit is marked by a transverse collapsed layer (fig. 5). The vascular loop is open below and, in young stages, its two arms pass downwards into procambial strands on either side of the nucleus. In *Olax*, on the other hand, the vascular loop is closed below by a transverse plate of vessels and the nucleus is separately formed below this region (fig. 2). The procambial strand is formed above the gland in the median line and the vessels are not developed until the gland has been pushed down against the woody cylinder of the host's root (fig. 3).

Figure 1 on Plate VIII shows a very young stage of the vascular tract in *Olax* haustorium, the vascular loop passing down into a single vertical plate with a delicate layer of cambium on each side. In figure 1 on Plate VII a median section is shown through an older haustorium. Secondary thickening has commenced in the vertical strand, and it is interesting to note that this usually commences some way below the vascular loop, in fact, at a point about opposite to the lacunæ inside the middle parts of the collapsed layers. These two and subsequent thickenings are illustrated by a series of diagrams 6—10 on Plate IX, each one of which is taken from an individual haustorium which has been chosen as the type of a class. Figures 6 and 7 show the early stages already described; figure 8 corresponds with the haustorium shown in figure 1 on this Plate. The thickest part of the strand gradually passes upwards in succeeding stages until it embraces the base of the vascular loop (figs. 9 and 10). At this the final stage, the whole vascular mass assumes a wavy outline due, to all appearance, to its being penetrated by broad medullary rays.

The elements of this vascular mass are mainly narrow tracheide-like vessels with simple circular perforations at their ends, and of remarkably uniform character (Plate X, fig. 3). The following differences have been noted in various parts of the axis. In the region of greatest thickening, at the base of the vascular loop, the elements are short and arranged in rows derived from the same cambial mother-cell, with medullary rays here and there between them. There is little difference in the inner and outer vessels unless it be a slightly greater width in the outer ones. Passing down the axis, the medullary rays are less conspicuous, the vessels become longer and, if anything, narrower, until they separate near the host's root to isolated strands of elongated elements. The vessels in the region of the loop show greater differences. Those in the lower half are very long and narrow, but remain uniform among themselves. Above the middle, as might be expected, this regularity is disturbed and broader elements make their first appearance. The vessels increase in diameter upwards until, in the mother root, ones are found with many rows of pits. The number of pits met with across the walls of the various vessels forms a convenient mode of comparing their width. Those of the protoxylem, those in the end of the sucker and those in the lower half of the vascular loop usually have 1—3 rows of pits. The somewhat wider, outer vessels formed by the cambium of the axis show 3—4 rows, while the vessels of the transitional region (above the middle of the vascular loop) and the mother root may have as many as 6 to 10.

The sections thus far dealt with in the present paper have all been transverse, that is, cut across the root attacked. Sections in this direction, as we have seen in *Santalum,* include more of the tissues of both host and haustorium than those cut in any other plane. To understand the vascular system of the axis, however, horizontal sections will be necessary (*i.e.*, cutting the haustorium across its axis and the root attacked, if in the section, tangentially). Such sections are shown on Plate XII (figs. 1 and 1a), and the arrangement of the parts can be readily made out. Note in these figures *px*, the protoxylem, with scattered parenchymatous elements, *x* the secondary xylem with its numerous medullary rays *mr*, and the cambium *c.* The uniformity and small size of the vessels is clearly shown in transverse and horizontal sections, and on a comparison with a section of the mother root, it is seen that the haustorial vessels correspond best with those found in young roots. The larger vessels found in older roots are not met with in the axis of *Olax* haustoria attacking other plants. Those on *Olax* itself will be referred to in paragraph 18.

The section drawn on Plate IX (fig. 1) being cut in the plane of the medullary rays, the latter are not seen. The vascular strand bifurcates above and passes with its various elements upwards round the vascular loop into the transitional region. In *Santalum* attention was drawn to the fact that, in the upper part of the vascular loop, the vessels became indistinct, hyaline and filled with gum, and this region, occurring in all older haustoria, was called the "interrupted zone." There is no trace of this feature in the vascular loop of *Olax scandens*, although it is markedly present in sections of *Thesium*, *Osyris*, *Opilia* and especially *Cansjera.*

An examination of the diagrams on Plate IX will show that in the haustoria examined there is no great development of secondary thickening (see for instance the case of *Santalum* in *Santalum*, Part II, Plate IX) and, from the frequent clearness of the tissues in the older stages, it is probable that the life of these organs is comparatively short. A certain number of references to the age of haustoria are scattered through the literature on root-parasites. Thus Granel[1] remarks that the haustoria even of perennials do not usually last longer than one year. Leclerc du Sablon[2] noted that older plants of *Pedicularis* form new suckers each year. Heinricher[3] showed that the haustoria of *Lathræa* can live for more than a year and asserts that Krause has proved the same for *Bartschia alpina*. Kusano, in his studies of the haustoria of *Buckleya Quadriala* in Japan, speaks of the growth of the haustorium keeping pace with that of the root to which it is attached, and of haustorium and root growing thus together for as many as a dozen years with cambiums in contact. In the tropics we have no means of determining the age of haustoria by means of annual rings as did Kusano, for these are not developed with any distinctness. But we have, on the other hand, some reason to believe that the activity of the haustoria is short-lived, because of the regular decay of the vascular system at a certain point, the interrupted zone. On the whole one is led to believe, from the haustoria so far examined, that the functional activity of haustoria in the *Santalaceæ* and *Olacaceæ* in the tropics is not long continued, may indeed cease long before the actual growth of the haustorium does.

In older haustoria of *Santalum*, where much secondary thickening has taken place, it was noted that the inner layers of secondary wood in the axis became discoloured and filled with gum, the protoxylem, curiously enough, not suffering this change

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[1] Granel, Note sur l'Origin des suçoirs de quelques Phanerogames Parasites. Bull. d. l. Soc. Bot. de Fr. XXXIV, 2. IX. 313—321. 1887.

[2] Leclerc du Sablon, *ib.*

[3] E. Heinricher, Die grünen Halb-schmarotzer. III. *Bartschia* und *Tozzia*. Jahrb. f. wiss. Bot. XXXVI. 665—752. 1901.

but remaining white and clear. A much more pronounced duramen is to be seen in the haustoria of *Buckleya* described by Kusano attached to various Coniferous roots, the duramen of the haustorium keeping pace in growth with that of the host, as does the cambium. In *Olax* the protoxylem at an early stage becomes discoloured in like manner and a few cases have been noted in which the inner layers of the secondary wood are also thus discoloured. This discolouration is partly due to brown substance filling the lumina of the parenchyma between the vessels (Plate IX, fig. 1 and diagrams 6—10).

16. An old stage of *Olax* haustorium is shown in fig. 1 of Plate X, the host being *Casuarina equisetifolia*. The sucker lobes, working along the cambial line, have almost completely surrounded the vascular cylinder of the attacked root. Nevertheless its abundant development of new secondary bundles, both in the centre and in the cortical wings, suggests that the *Casuarina* root has as a whole suffered comparatively little injury. The haustorium, on the other hand, as is usual in such old stages, has cells emptied of all contents, the layer of cells in contact with the vascular cylinder is pronounced and the remaining tissue remarkably clear. This clearness of tissues has been regarded as a sign of waning activity of the whole organ in *Santalum* and it has been assumed that such haustoria are moribund, a point of view adopted by Solms-Laubach[1] in his study of *Thesium*. The section now being studied is of further interest in that it shows the connection between haustorium and mother root and the development of the upper part of the collapsed layers.

The collapsed layers have in this case reached their utmost development and extend upwards for a short distance on either side of the vascular loop. The lower and middle portions have already been described in detail in paragraph 13 ; the upper portion is, like them, developed entirely from cells of the cortex.

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[1] H. Graf zu Solms-Laubach, Ueber den Bau u.Entwickelung der Ernährungsorgane Parasitischer Phanerogamen. Jahrb. f. wiss. Bot. VI. 1867-68.

A small inward projection sometimes, as in this case, marks the junction of upper and middle portions, and it is easy by this means to distinguish the three parts of the collapsed layer. There is no marked differentiation here of the cells which are about to become crushed and added to the layer, but this is not the case always, as is seen from a study of Plate IX, fig. 1, where the clearing of the cells for the formation of the uppermost part of the collapsed layers is well shown (*u. c. l.*). This portion of the collapsed layers may be regarded as directly due to the increase in thickness of the axis of the haustorium by secondary thickening. As the thickest part moves upwards, it is followed by an upward extension of the collapsed layers on each side. We see then that the collapsed layers in *Olax* consists of three parts formed at different times and in different ways, all, however, arising entirely from the collapse of cortical cells which have lost their contents.

The zone of radiating cells outside the collapsed layers, so closely connected in former stages with the deposition of large starch grains, has entered on its last phase. The radial arrangement is still visible, but the starch has all gone and, in its place, masses of calcium oxalate crystals have been deposited. Thus, throughout the life of the haustorium the curves of growth have been retained in this part of the cortex, an additional proof that it takes little or no part in the penetration of the host's root. Such was not the case in *Santalum ;* but in certain cases, notably in attacks on *Pithecolobium Saman* and *P. dulce*, a narrow band of similarly arranged cells was found on the outer sides of the collapsed layers, having all the appearance of cells derived from a secondary meristem (*Santalum*, Part II, para. 7). From a consideration of the sections of *Olax scandens* haustoria examined it appears possible that this group of cells in *Santalum* is rather a remnant of the former curves of growth than a new formation.

We saw in our study of the earliest stage of *Olax* haustoria met with (Plate III) that the rows of cells forming the body of the haustorium were separated from the older, irregularly arranged cells outside them by a lacunar band of crushed cells.

This separating layer is constantly present and may be regarded as an *outer collapsed layer*. It is clearly seen in the figure under discussion (Plate X, fig. 1). Such outer collapsed layers are not infrequently found in *Santalum* (cf. *Santalum*, Part II, para. 7) and those in *Olax* are, as in that case, probably due to the shrinkage of the outer cells of the cortex. We shall refer to these outer collapsed layers in dealing with the connection between haustorium and mother root.

The deposition of crystals of calcium oxalate has been referred to on several occasions and has been regarded as evidence of a complete cessation of activity in the tissues bearing them. At first present only in the outer layers of cells under the corky surface, later on they appear in masses in the radiating cells. They are also frequently met with in the parenchymatous cells inside the vascular loop and in the little nest of cells opposite the ends of the cortical wings of the host, tissues clearly of no further use to the haustorium. Their occurrence in the clear zone is rare. Within the collapsed layers, that is, in the original nuclear area, they are also rarely found. In the few cases observed, they form, in this region, long strings of minute black crystals passing through a series of cells in a long line.

The mother root from which the haustorium was developed is seen cut across on the right hand of the top of the section (Plate X, fig. 1). The space traversed by the vascular bundles uniting it to the haustorium has been termed the transitional region. The strands of vessels in the axis of the haustorium are continuous with similar elements right up into the mother root. They are thus accompanied by the cambium. But the vascular strand of the axis is devoid of bast. The phlöem elements of the mother root are continued some way down, but cease in the transitional region. By observing their lower limit we shall have another means of judging the position of the line of separation between the haustorium proper and the region above it. The bast in *Olax* roots is distinguished as a layer of thin-walled cells densely filled with contents which are coloured light brown in spirit material. In this brown, undefined layer isolated groups of sclerotic cells of peculiar appearance occur, always accompanied by long rows of square cells with single crystals. We may term these "fibro-crystal" groups and their form is seen in Plate X, figures 4 a—f. These fibro-crystal masses are frequently found in the transitional region of the haustorium but do not (with the exception to be mentioned below) appear lower down than the middle of the vascular loop.

Although there is no distinct endodermis visible in the *Olax* roots examined, many sections show in the upper parts of the transitional region isolated brown cells of great distinctness, their position being in general outside the bast. It is not possible to connect these cells with the endodermis, and all that can be said is that they occur in the endodermal region. They are traceable from the mother root into the transitional region and, as might be expected, the outer collapsed layer is seen frequently to be in direct continuation with them. They are not found lower down than the middle of the vascular loop.

Cork is a constant feature outside the haustorium, being much more commonly found than in sandal haustoria. It usually ceases at the ends of the cortical folds, but, in not a few cases, has been traced inside the latter as far as the upper ends of the cortical wings of the host's root. In one or two cases it has been met with further in, aborted sucker lobes are seen sometimes to be surrounded by it and, in one case, the whole sucker has been cut off by its own cork formed in thick layers.

17. The relation between haustorium and host need not be dealt with so fully as it has been in *Santalum.* To do so would entail much repetition. An attempt is rather made to compare the haustoria of *Olax* with those of *Santalum* in their action on the root attacked.

Penetration follows closely the lines indicated in *Santalum.* The sucker is tongue-like at the commencement, excepting where very dense bands of sclerenchymatous cells bar its way. This form is retained in certain roots where the tissues are soft and watery, as in *Boerhaavia repens,* where a broad tongue passes right into the woody cylinder without any division into lobes. In monocotyledons like *Asparagus* the sucker proceeds thus as far as the sheath of the woody cylinder and undergoes no further differentiation, actual entry into the woody cylinder not having been observed (Plate VII, fig. 1). In *Azima tetracantha* the rule is that the sucker, after passing through the soft cortex, passes down one or more of the broad medullary rays in tongue-like branches. Such cases are rare and are obviously determined by the structure of root attacked. In ordinary dicotyledons with a fairly solid central cylinder the sucker, on reaching it, divides into two broad lobes, one on each side, which follow the cambial line, destroying it as they proceed.

The following variations may be noted. In a few species the sucker lobes, before reaching the woody cylinder, have strayed tangentially in the cortex. Such cases appear to be common in *Acacia arabica*, *Casuarina equisetifolia*, *Streblus asper*, and have been noted in one or two other species. In most of these, however, the sucker has ultimately reached the cambium by one or both lobes or by a new development of the tissue in the middle of the sucker. Where a sucker lobe has thus wandered in the cortex, the cells become after a while clear and moribund, like those of haustoria in contact with the woody cylinder. A very distinct palisade-like tissue is thus sometimes developed and this is especially well seen in sections of haustoria attacking *Casuarina equisetifolia* (Plate VII, fig. 3). One-sided entry, largely connected with this wandering in the cortex, is rare, indicating great regularity in the penetration of ordinary dicotyledonous roots, and the form figured (Plates VIII, IX and X) is by far the commonest and hardly deviated from. In the same way the woody cylinder is rarely entered. *Azima tetracantha* is an exception and is apparently always pierced along the broad medullary rays till the woody cylinder is divided up into sections. This species, with the soft *Boerhaavia repens* are practically the only cases noted.

The wings of the cortex of the host are occasionally attacked and destroyed. These wings are then in most cases cut off by the formation of cork below the injured places. Corky layers surrounding the wings appear with great frequency, thus protecting them from further injury. Cork is also found as with *Santalum* in a number of cases in the tissues opposite to the ends of the sucker lobes.

Secondary thickening in the root attacked is far more general than in the attacks of *Santalum*, and the cortical wings in a great number of cases join in this secondary wood formation. Such wood, formed after the attack has reached the cambium, deviates at first from the normal, having thinner elements, less sclerotic cells and fewer vessels in the wood (cf. *Santalum*, Part II, para. 19, *Note*). The formation of gum or thyloses in the cavities of the vessels opposite the cells of the sucker occurs as under the attacks of *Santalum* haustoria, and in many cases this formation is markedly confined to the region between the ends of the lobes of the sucker.

On the whole, the haustoria of *Olax scandens* rarely fail to enter a root attacked, possibly thanks to the complicated and long-lived gland. Moribund haustoria have been much more rarely met with than in *Santalum*, but the tracts of country from which the collections were made were very different and no definite conclusion can be drawn from this. The test for full activity or waning power is the relative absence of contents in the cells. In *Olax* it is chiefly the older haustoria which are thus emptied, such as have developed secondary thickening. The entry, as we have seen, is regular and usually along the cambial line. But when this has been effected, the haustorium does not appear to be so destructive of the host's tissues as that of *Santalum*, whether in the wings or in the woody cylinder.

The action of the sucker cells upon the tissues of the host opposite to them seems to be similar to that noted in *Santalum*. In places, the influence can be seen at a distance by the formation of new bands of sclerenchyma or cork opposite the point of attack, the formation of gum or thyloses in the vessels or the yellowing of bands of sclerotic fibre in the cortex. But there is no clearing of starch in the host's root opposite the haustorium as has been described by Fraisse in attacks by *Osyris alba.*[1]

The effect of the secretions on starch appears to be rather slow. In not a few cases starch grains have been found in the layer of secretion and disorganized cells of the host after all traces of the cell-walls have disappeared (Plate VIII, figs. 4 and 5). This seems to suggest that the ferment secreted by the sucker cell is chiefly cyto-hydrolytic and, when we consider the abundant assimilating foliage of the parasite and its need before all things of water and salts, this does not appear strange. A somewhat similar state of affairs was observed in *Santalum* (Part II, para. 33) where Peirce's[2] observations on *Cuscuta* were alluded to. Brown and Morris[3] report that in the germination of barley the tarch is not acted on until a certain amount of solution has been effected and the cells have been isolated. Newcombe[4] has given an extreme case in the ferments of germinating seeds of *Lupinus* and *Phœnix*, the ferments dissolving the cell-walls being hardly at all diastatic. It is all the more interesting to note Fraisse's observation quoted above that, opposite to the sucker cells of the haustorium of *Osyris*, a zone of cells free of starch indicates the region of its activity.

18. It was noted in *Santalum* that self-attached haustoria, that is, such as were fixed on other sandal roots, differed in certain respects from those attacking foreign roots. The relations between host and parasite in these cases varied. In several instances it was difficult to separate the tissues of the two where

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[1] Fraisse Sur le Parasitisme de l' *Osyris alba*. Comptes Rendus Acad. Sc. Paris, 30 Jan. 1905. Fraisse states that every root attacked, whether perforated or not. shows a region devoid of starch, "qui délimite le zone d'action du mamelon haustorial."

[2] G. J. Peirce, on the Structure of the Haustoria of Some Phanerogamic Parasites. Annals of Botany, VII, 1893. Peirce describes the action of the sucker cells of *Cuscuta glomerata* upon the mesophyll of balsam leaves. He states that the large thin-walled papillate cells dissolve and bore the walls of the cells they are in contact with, making perforations little wider than their own diameter. They dissolve the contents rather slowly, starchy substances first, protoplasmic later.

[3] J. R. Green, On Vegetable Ferments. Annals of Botany, VII, 1893.

[4] F. C. Newcombe, Cellulose Enzymes Annals of Botany, XIII, 1899.

they touched one another. In others considerable resistance was offered by the root attacked. The sucker was carefully cut off in the usual manner and fresh growths took place in the cortical wings, by which the sucker as a whole was squeezed, the host acting as if engaged in occluding a wound (*Santalum*, Part II, Plate XVI).

In self-attached haustoria in *Olax* fusion of the tissues is the rule (Plate XI, figs. 1, 2 and 6). This is not however all, for the difference between such and ordinary haustoria is much greater than in *Santalum*. All the vascular tissues of the mother root are continued down the entire length of the haustorium and, at the end, are in connection with the similar tissues of the host's root.

We saw in paragraph 15 that the vessels of the axial strand of the *Olax* haustorium are uniform and narrow. In self-attached haustoria wider elements make their appearance, giving the whole strand an entirely different appearance (Plate XI, figs. 1, 3 and 6 ; Plate XII, figs. 2, 2a and $2a^1$.) These wider vessels are identical in structure with the broader vessels of the secondary wood in *Olax* roots. Bast also is formed throughout the haustorium (Plate XI, fig. 1, and Plate XII, fig. 2). Not only are the fibro-crystal bodies found all along the outer edge of the cambium in the axis, but well marked sieve-tubes with callus-plates are readily distinguishable, and staining with water-blue shows that they are present in very large numbers (Plate XI, figs. 3 and 4). From an inspection of this Plate, where these facts are illustrated, it is evident that a thorough fusion of host and parasite has taken place and that the cambium passes from one to the other so as to place the wood and bast in organic connection (fig 6), the formation of wood and bast in the haustorium keeping pace with that formed in the woody cylinder of the host (fig. 1). This has not been observed elsewhere in *Olax* or *Sandal* haustoria, but the description of *Buckleya* by Kusano indicates that in older haustoria the wood formation keeps pace with that of the host. Another point of interest is that, in self-attached haustoria, the vessels at the end of the sucker lobes before secondary thickening has commenced, swell up considerably and become shorter and even globular (figs. 2 and 5).

The occurrence of sieve-tubes in the haustoria of green hemi-parasites has not been, it is believed, observed before. Peirce,[1] who investigated a number of cases, found that in *Lathræa*, *Brugmannsia* and *Cuscuta*, colourless parasites, sieve-tubes were abundant, while they were absent in *Viscum*, a green hemi-parasite, a result which is in agreement with what has been noted in *Santalum* and *Olax* and was also proved for *Buckleya* by Kusano. The presence of this complete vascular connection between host and parasite, usual only in cases of holo-parasitism, opens the way for interesting speculations and experiments regarding the nutrition of such plants. And a more careful examination of all the other cases of self-attached hemi-parasites is called for. It is not likely that *Olax* will be singular in this respect.

Botany School, Cambridge,

June 1907.

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[1] G. J. Peirce, *ib.*

APPENDIX.

List of hosts on whose roots haustoria were examined in the preparation of the present paper :—

Acacia arabica.
Acacia leucophloea.
Albizzia Lebbek.
Asparagus racemosus.
Azima tetracantha.

Boerhaavia repens.

Cadaba indica.
Capparis sp.
Carissa spinarum.
Cassia siamea.
Casuarina equisetifolia.
Cephalandra indica.

Dichrostachys cinerea.

Feronia Elephantum.

Jasminum sessiliflorum.
Jatropha gossypifolia.

Melia Azidarachta.
Morinda tinctoria.

Ocimum sanctum.
Olax scandens.
Opuntia Dillenii.

Pentatropis microphylla.
Phaseolus ? sp.
Phyllanthus simplex.
Pithecolobium dulce.
Pongamia glabra.

Rivea hypocrateriformis.
Ruellia prostrata.

Solanum trilobatum.
Streblus asper.

Tragia involucrata.

Vitex Negundo.

Zizyphus Oenoplia.
Zizyphus Jujuba.

DESCRIPTION OF PLATES.

PLATE I.—

(All the figures excepting 4 are of natural size.)

Fig. 1. Ripe fruit of *Olax scandens*. Note the calyx fused with the pericarp to near the top.

Fig. 2. Germinating seed with primary root emerging and bending downwards. Note the catuncle-like outgrowth of the endosperm.

Fig. 3. A further stage in germination. The hypocotyl forms a delicate green loop above ground, the seed being just below the surface. The lower part of the stem and the upper part of the root are white and thickened. The root is covered with root-hairs. A section across such a root is shown in fig. 1 of Plate II.

Fig. 4. Section across the seed in such a stage as that shown in fig. 2. The cotyledons are folded in the centre of the oily endosperm, their exposed surfaces having a distinct epithelium-like layer of cells.

Fig. 5. A young seedling six weeks old. The upper part of the hypocotyl is green and above ground; the lower, subterranean part is white and swollen. The node with the scars of the cotyledons is seen at the top and a first pair of leaves has been unfolded. The whole root-system is richly covered with root-hairs.

Fig. 6. A seedling grown in pure sand for six months. The root-system is copiously branched, but the frequent swellings (due to eel-worms) show it to be in an unhealthy condition. Root-hairs are still abundantly present, but no haustoria are seen. The curious fasciated ending of the root is due to its growth round the base of the pot. A number of leaves are developed, but several have already fallen. The shoot is assuming a dorsiventral habit.

Fig. 7. A seedling one year old, also grown in pure sand. It is obviously unhealthy, most of the rootlets being dead and leaving behind them characteristic scars filled with brown mucilaginous matter. The main root is distorted by eel-worms and a few haustoria are present.

Fig. 8. A seedling of *Olax scandens,* found in nature, attached by numerous haustoria to an older plant of the same species. The specimen is interesting in that it was through its being dug up that the parasitism of *Olax* was first discovered. It is preserved in the Cambridge Botanical Museum.

PLATE II.—

Fig. 1. Transverse section through part of the root of a young seedling (see fig. 3 of Plate I), showing the development of root-hairs.

Fig. 2. Part of a small rootlet of *Olax* found in nature (natural size and magnified). Numerous haustoria are being formed, and it is to be noted that, while the rootlet is covered with root-hairs, the haustoria are smooth and free from them.

Fig. 3. Root-endings of *Olax scandens* found in nature (natural size and magnified).

Fig. 4. A rootlet from a pot-plant attached to a pebble by a small haustorium (natural size and magnified).

Figs. 5 to 8. Haustoria of *Olax scandens* (figs. 6 and 7 natural size and 5 and 8 magnified).

In 5 note the peculiar lobing of one haustorium: this is not uncommon. Also note the scars left by former haustoria. The root attacked is that of *Azima tetracantha* and the figures are twice natural size. In 6 a series of haustoria, apparently terminal, are applied to a root of *Albizzia Lebbek.* A comparison with a series of specimens shows that the haustoria in *Olax* as in *Santalum* are never really terminal (see fig. 8 where a small portion of the vascular cylinder is all that remains of the mother root beyond the haustorium). Fig. 7 shows two large haustoria also apparently terminal. In fig. 8 a typical haustorium is shown as well as its burrowing action into the bark of the host's root.

PLATE III.—

Fig. 1. A non-median section through a very young haustorium. The various tissues are illustrated by enlarged drawings at a, b, c and d.

Fig. 2. An older stage of development cut so as to show the entrance of the bundle of vessels from the mother root. The parts are arranged as in fig. 1, but considerable development has taken place.

Note especially the "shadow" of starchy cells, *b*, the oval light-coloured nucleus and the dark median shadow of the gland, *d*. 2d, a portion of such a stage of the gland further magnified. $2d^1$, a similar section from another, slightly older gland. The cells of the gland are elongated horizontally.

PLATE IV.—

Four stages in the development of the gland. Fig. 1 shows a stage connected with those on Plate III. At *tt* the cells of a small triangular area on each side become charged with starch. The oval area of Plate III is thus separated into two parts, an upper, the vascular loop, and a lower, the nucleus proper.

After the stage shown in fig. 2, no definite structure can be seen in the lumen of the gland. Figs. 2a and 2b show portions of such a stage magnified further. At *x* is the bed of the secreting cells which form a cap round the upper part of the gland. In fig. 3 the lower part is lobed, while in fig. 4 the gland is mature and the cells of the upper part of the nucleus have commenced actively dividing so as to press the gland downwards. Note the duct *d*.

A change may be observed in these figures in the position of the densest, starch-filled tissue of the cortex, which is found further in in succeeding stages until it is met by the zone of clear cells. The line of demarcation between the outer and inner parts of the cortex becomes more and more distinct until, when the gland is mature, it is exceedingly sharp.

PLATE V.—

Transverse section through a haustorium attached to a root of *Melia Azidarachta*, with a mature gland. The stage is similar to that in fig. 4 of the last Plate. Detailed drawings are added of the various parts. Fig. a shows the junction of nuclear and cortical cells at the top on one side, the cortical cells being filled with starch and those of the nucleus with protoplasmic contents. In fig. b the line of separation between the starchy and clear cells of the cortex is shown. The median shadow of the upper part of the nucleus is drawn in fig. c together with a few tracheides forming the base of the vascular loop, and the upper part of the cap of the gland. Fig. d shows the duct and fig. e some of the more distinct cells at the edge of the lumen in the lower part of the gland.

PLATE VI.—

A unique specimen of a haustorium immediately before penetration. The vascular loop is well developed and a number of vessels are formed. The median shadow *c* in the upper part of the nucleus is the first stage of the vascular strand of the axis. By the growth of this part the cap is being thrust down into the lumen, the tissues there being completely disorganized. When the cap is pushed down, a part of the nucleus, *b*, is left behind on each side. This portion is separated from the region of the cap by a bay of clear cells, *d.*

The clear zone of the cortex, *cl.*, is devoid of all contents and its cells are moribund. The first traces of the collapsed layers *c. l.*, are observable at the junctions of the clear and starch-filled cells of the cortex. The root attacked is one of *Zizyphus Oenoplia* and a small crack is seen in the bark, just opposite to the opening of the duct of the gland.

In fig. 3 a small portion of the cortex is figured lower down, where clear and starchy cells adjoin one another and the collapsed layer is about to be formed, at first from the crushed cells of the clear zone and, later, from the inner cells of the starch-filled zone, the cells having meantime lost their contents.

PLATE VII.—

Fig. 1. A transverse section through an *Olax* haustorium penetrating a root of *Asparagus racemosus.* The sucker is tongue-like and has reached the woody cylinder of the host, *x*. Note *lac*, lacuna, *gl*, traces of a former gland.

Fig. 2. A part of the gland trace from another section through the same haustorium. *x*, woody cylinder of the host's root. A portion of the lumen remains and it is bounded by the mucilaginous secretion poured out by the cells. The indistinct lines show successive layers of this secretion.

Fig. 3. The end of the lobe of a haustorium which has wandered in the cortex of a root of *Casuarina equisetifolia* and has not succeeded in reaching the wood of the host. The sucker cells are moribund and, as in all such cases in *Casuarina*, form a very pronounced palisade tissue. They are embedded in brown substance largely produced from sucker cells when in a state of activity.

Fig. 4. The edge of a haustorium, the central part of which has succeeded in penetrating a root of *Vitex Negundo* as far as the cambium. It is presumed that the figure represents in some

sort the manner in which penetration takes place in the first instance. The cambium, *c*, with the layer of phlöem, *ph*, outside it, has been destroyed opposite the point of attack, but the host's root has developed a protective layer of cork, *ck*, at this point in place of the phlöem.

Plate VIII.—

Figs. 1 to 3. Transverse section through a young haustorium which has penetrated a root of *Albizzia Lebbek*. The sucker is lobed and follows the line of the cambium in the host's root. Portions are magnified further in figures 2 and 3.

Note in fig. 2, *a*, the cells of the upper part of the nucleus which have become elongated in penetration, the adjoining cells of the cortex remaining unaltered: *lac*, the lacunar region not very well developed in this case: *b*, the nest of cells: *x*, the sharp line of separation between the starchy cells of the cortex and those which are about to be added to the collapsed layer.

Fig. 3. A portion of the lower part of the collapsed layer. It is being formed by the addition of crushed cells both from the clear zone within and the cortical cells without, *cl*, clear zone *c. l.*, collapsed layers, *co*, cortex.

Fig. 4. A portion of one of the wings of the bark of *Azima tetracantha*, showing the comparatively slow solution of the starch grains, *s*, sucker cells, *scl*, sclerotic cells of the bark, *st*, starch grains, the cell walls containing them having been dissolved away, *ck*, cork being formed on the inner face of the wing. *st* and *scl* are indistinct and imbedded in yellow secretion from the sucker cells.

Fig. 5. A portion of the woody cylinder of the same root of *Azima tetracantha* showing the persistence of the starch grains in a medullary ray. *s*, sucker cells, *v*, vessel, *m. r.*, medullary ray of the host. The starch grains are lying in the yellow secretion after the cells which contained them have been dissolved away.

Plate IX.—

Fig. 1. Transverse section through a haustorium fixed on a root of *Capparis* sp., which has developed secondary thickening. Note a couple of fibro-crystal masses at the top of the loop. The lacunar region of the nucleus is well seen, as also the nest of cells below the lacuna. The lower and middle parts of the collapsed layers are well shown as also the cells becoming clear for the formation of the upper part *u. c. l.* Note the protective

cork formed in the host's root round the edge of each lobe of the sucker, and the continued formation of wood in the part of the cylinder thus protected.

Figs. 2 and 3. Diagrams of *Olax scandens* haustoria in the gland stage and after penetration. *c. l.*, collapsed layer. The dotted line signifies the outline of the nucleus *n. gl*, remains of a gland.

Figs. 4 and 5. A similar pair of diagrams for *Santalum album.*

Figs. 6 to 10. Diagrams of successive stages of secondary thickening in the haustorium. The darker, inner portion signifies older vessels breaking down and resembling duramen, although this layer is not usually pronounced.

PLATE X.—

Fig. 1. An old, moribund haustorium fixed on a root of *Casuarina equisetifolia*, for a description of which see the text (paragraph 16).

Fig. 2. The end of a sucker lobe in a haustorium fixed on a root of *Jasminum sessiliflorum.* The sucker cells are seen to spread out in a mass of dark brown substance which bathes the tissues of the host. The colouring matter is probably developed from the host, but the bulk of the matrix is secretion. Note the latest addition from the secreting cells as a clear border outside the ends of some of the cells.

Fig. 3. A small portion of the vascular strand of the axis of the haustorium with secondary thickening taking place. The vessels are uniform and bear from two to three rows of pits. The cambium passes outwards almost directly into the irregular parenchyma and there is no trace of bast formed from it.

Note the circular perforations of the vessels where they meet one another.

Fig. 4, a—f. A series of drawings of the fibro-crystal masses such as are seen cut across in various directions at the top of fig. 1. Fig. 4 a is taken from a transverse section of a young root of *Olax scandens.*

PLATE XI.—

Self-attached haustoria of *Olax scandens* (see the text, paragraph 18).

Fig. 1. Shows such an attachment under low power. The vascular strand of the axis is much developed and accompanied by bast (as indicated by the fibro-crystal masses and the medullary rays) right down to the end of the sucker. At the latter point the xylem, cambium and phlöem are seen to be in direct continuation of those of the host's root.

Fig. 2 shows the end of the sucker of another self-attached haustorium. It is difficult to state where the sucker ends and the host begins. The vessels are enlarged at their ends (see fig. 5).

Fig. 3. A portion of the vascular system of the axis in the section shown in fig. 1, further enlarged. It should be compared with fig. 3 of the last Plate which, however, has been inadvertently drawn on a larger scale.

In haustoria fixed on *Olax*, large and small vessels occur as well as fibro-crystal masses and well-developed sieve-tubes. These are absent in all other cases examined.

Fig. 4. Sieve-tubes from fig. 3 magnified further.

Fig. 5. The endings of the vessels in the sucker lobes before secondary thickening has commenced. They are almost globular in form (see fig. 2).

Fig. 6. A small portion of fig. 1 magnified to show the junction of the xylem of haustorium and host. *p*, vessels and parenchyma of haustorium, *h*, medullary ray and vessel of the host. *p* is cut longitudinally and *n* transversely.

PLATE XII.—

Horizontal sections through *Olax* haustoria (1) on *Albizzia Lebbek* and (2) on *Olax scandens* itself.

Fig. 1. *px*, protoxylem, *x*, xylem, *c*, cambium, *lac*, lacuna, *c. l.*, collapsed layer.

Fig. 1a. Portion of the last figure more highly magnified, *mr*, medullary ray.

The section shown in fig. 1 is cut so that one side (the left) is higher up in the haustorium than the other. The right-hand portion shows a section through the axis opposite the lacuna. That on the left traverses the base of the vascular loop, shows the lattice-work of vessels in longitudinal section, and again cuts across the vessels transversely as they pass upwards. Traces of bast are discernible outside the cambium in this latter part.

Fig. 2. The haustorium cut is a good deal older than that in fig. 1.

A great development of bast with fibro-crystal masses, *cr*, is seen in the axis.

Figs. 2a, 2a^1. Parts of the vascular system showing the great vessels, as compared with the small uniform ones shown in fig. 1a.

PLATE I.

Fig. 1. Terminal rootlets of *Cansjera Rheedii* with young haustoria (natural size and magnified). The rootlets are practically bare of root hairs, but the young haustoria are somewhat thickly coated with them (*h*, *h*).

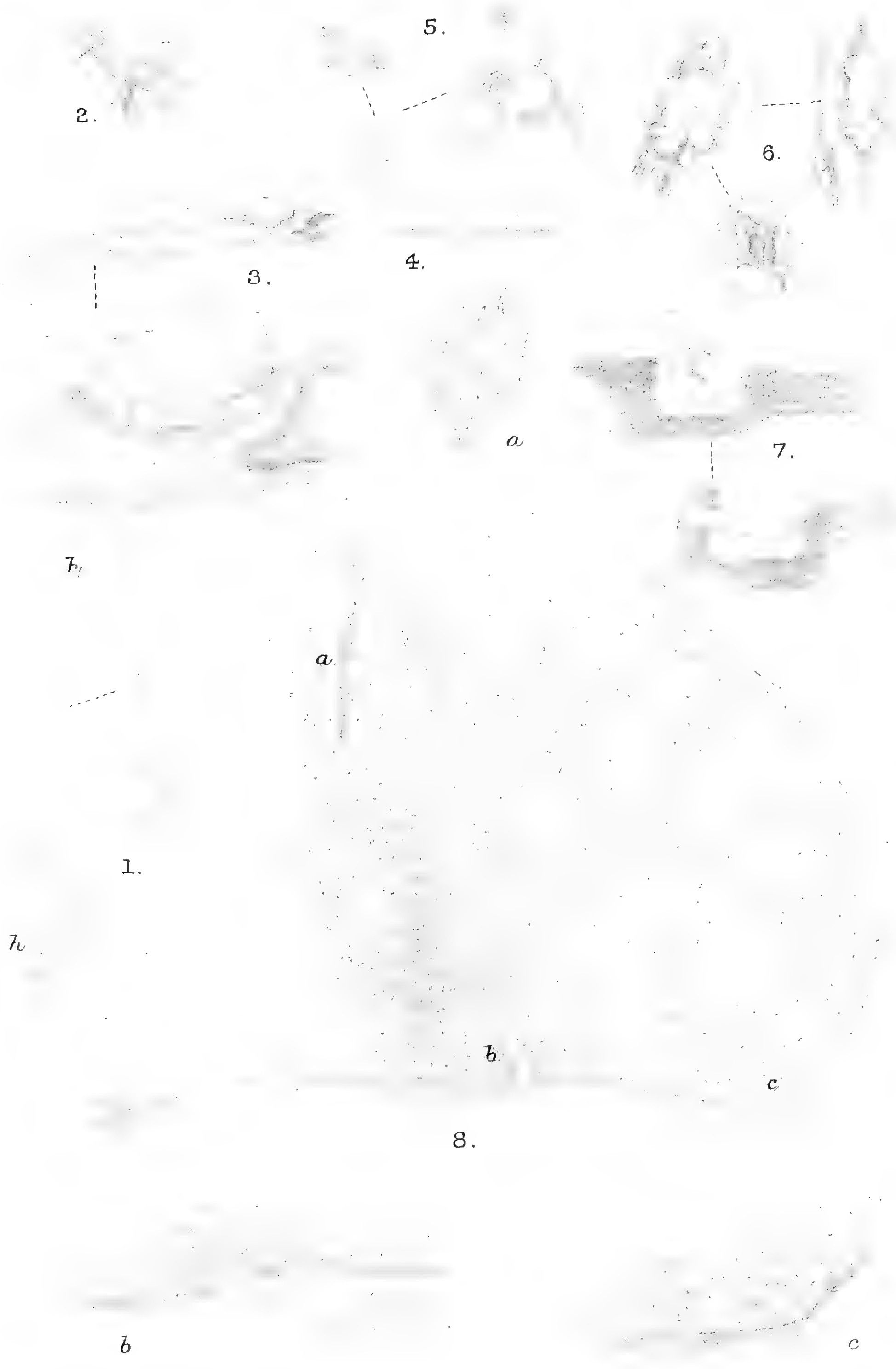
Fig. 2. Young haustoria (natural size). Their surface is still smooth.

Fig. 3. Older haustoria (natural size and magnified). These are becoming wrinkled and warty and are covered with lenticels.

Figs. 4-7. Old, irregularly-lobed haustoria (natural size, No. 5 also magnified). The sucker is shown in 5 and 6 and, in the latter case, a piece of the host's bark is attached. The haustoria are seen to be much broader above than at the point of their attachment.

Fig. 8. An early stage of haustorial development, cut transversely. Cut with the microtome, stained with Delafield's hæmatoxylin and mounted in Canada balsam. The haustorium is fixed on a root of *Abrus precatorius.* The nucleus is developing as a median, oval area. *a*, part of the procambial strand magnified further : *b* and *c*, the surface of attachment to the host's bark.

Plate I.



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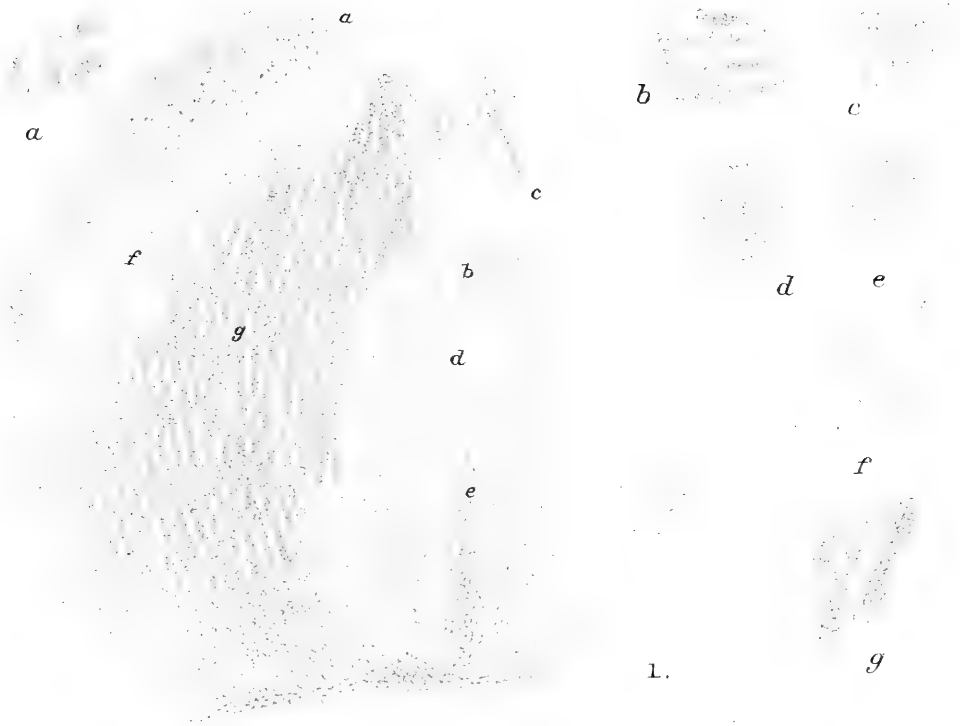
Huth, Lith^r London

Plate II.

Fig. 1. A second stage in haustorial development, this haustorium also being fixed on a root of *Abrus precatorius.* Cut by hand and mounted in dilute glycerine. The gland is appearing as a median shadow, *e* ; *a* to *g* show the various tissues as described in the text, further enlarged.

Fig. 2. A further stage in development in which the gland is formed. The haustorium is fixed to a root of *Capparis zeylanica.* The distinction between nucleus and cortex is clear, as also the vascular loop and the collapsed layers. The enlarged drawing of the lumen of the gland (*a*) shows that the secreting cells are behaving exactly as in *Santalum.* The cell contents of the cortex are not inserted in the drawing. *a*, gland : *bb*, collapsed layer.

Plate II.



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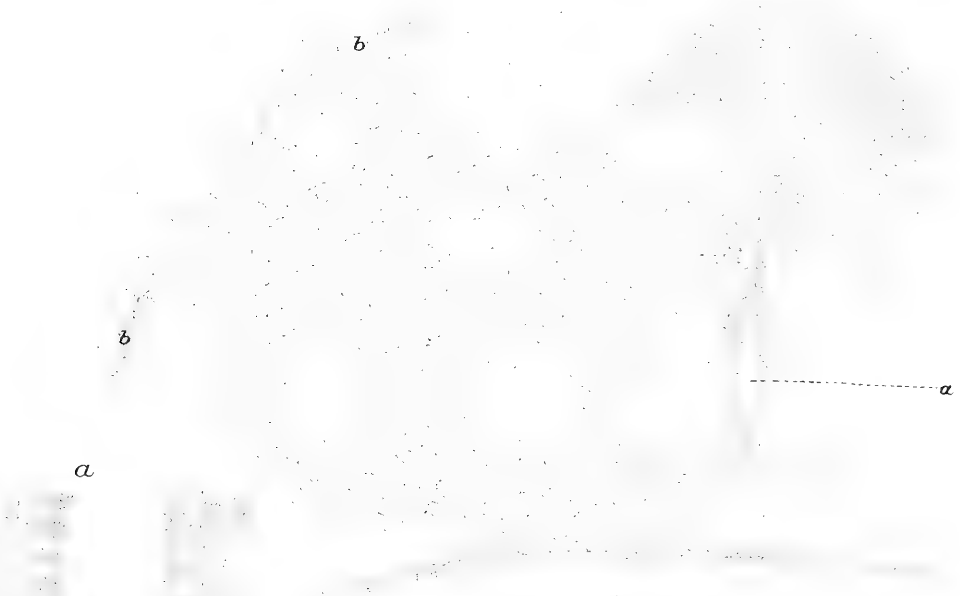

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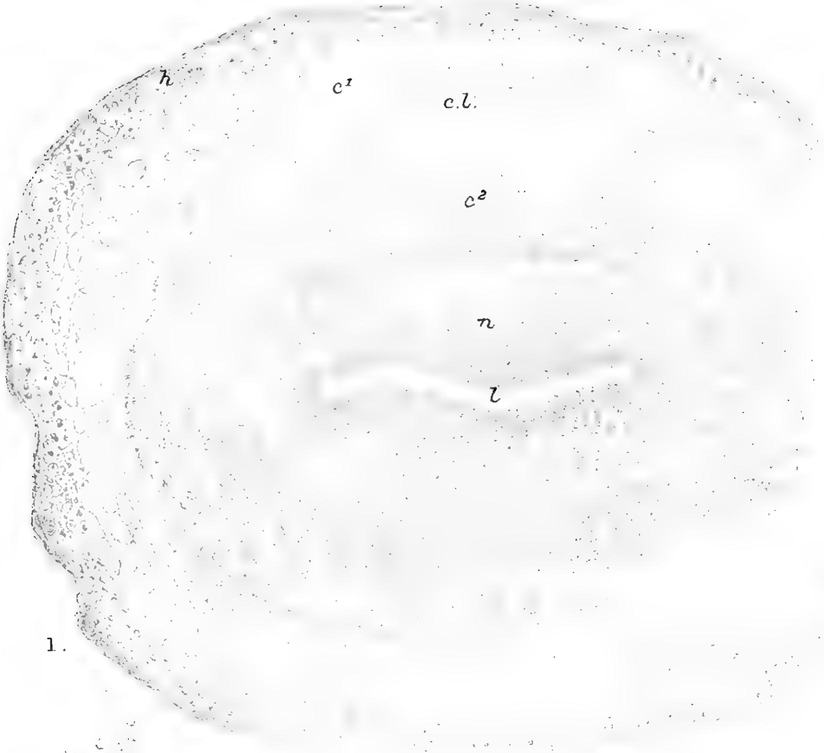
PLATE III.

Fig. 1. Horizontal section through a young haustorium fixed on a root of *Hemidesmus indicus*. The hypoderm (*h*), outer and inner cortex and collapsed layers (*c.l.*) separating them, clear (c^1) and starchy (c^2) cells of the cortex, protoplasmic cells of the nucleus (*n*), secreting cells and lumen of the gland (*l*) are clearly shown.

Fig. 2. The secreting cells from another gland, showing the rods of mucilaginous substance extruded into the lumen of the gland (cf. *Sant. I*, fig. 25).

Fig. 3. Transverse section through a diseased haustorium fixed on a root of *Abrus precatorius*. The stage is somewhat older than the last two, as shown by the gland trace (*a*) in the middle. The tissues of the nucleus are decomposed down one side and the cavity thus formed is lined with yellow substance. *a-c* show the parts magnified. *c*, lignified pitted cells.

Fig. 4. A portion of another haustorium of about the same age, also found on *Abrus precatorius*, showing the cells of the sucker in contact with the wood of the vascular cylinder.



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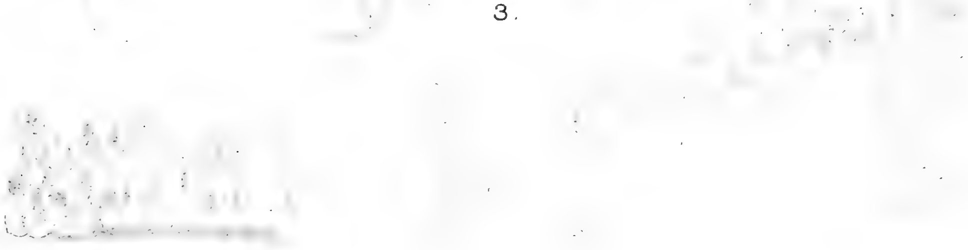

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PLATE IV.

Transverse section through a haustorium in the act of penetrating a small root of *Abrus precatorius*, the diameter of the haustorium being one-sixteenth of an inch. A microtome section, stained with hæmatoxylin and mounted in Canada balsam. The interest centres in the nucleus (*d*). The upper part of this shows cells greatly enlarged and furnished with granular protoplasm, great nuclei and nucleoli. At d^1 cells of a slightly younger haustorium are figured. The lower part of the nucleus merges into the sucker and contains the gland which is narrow and duct-like (*i*). At *j* the thick-walled, lignified, pitted cells are seen in the thickness of the end of the cortical fold. For the description of this plate see paragraph 6 of the text. The smaller drawings, with the exception of *d'*, are enlargements of different parts of the haustorium.

Plate IV.

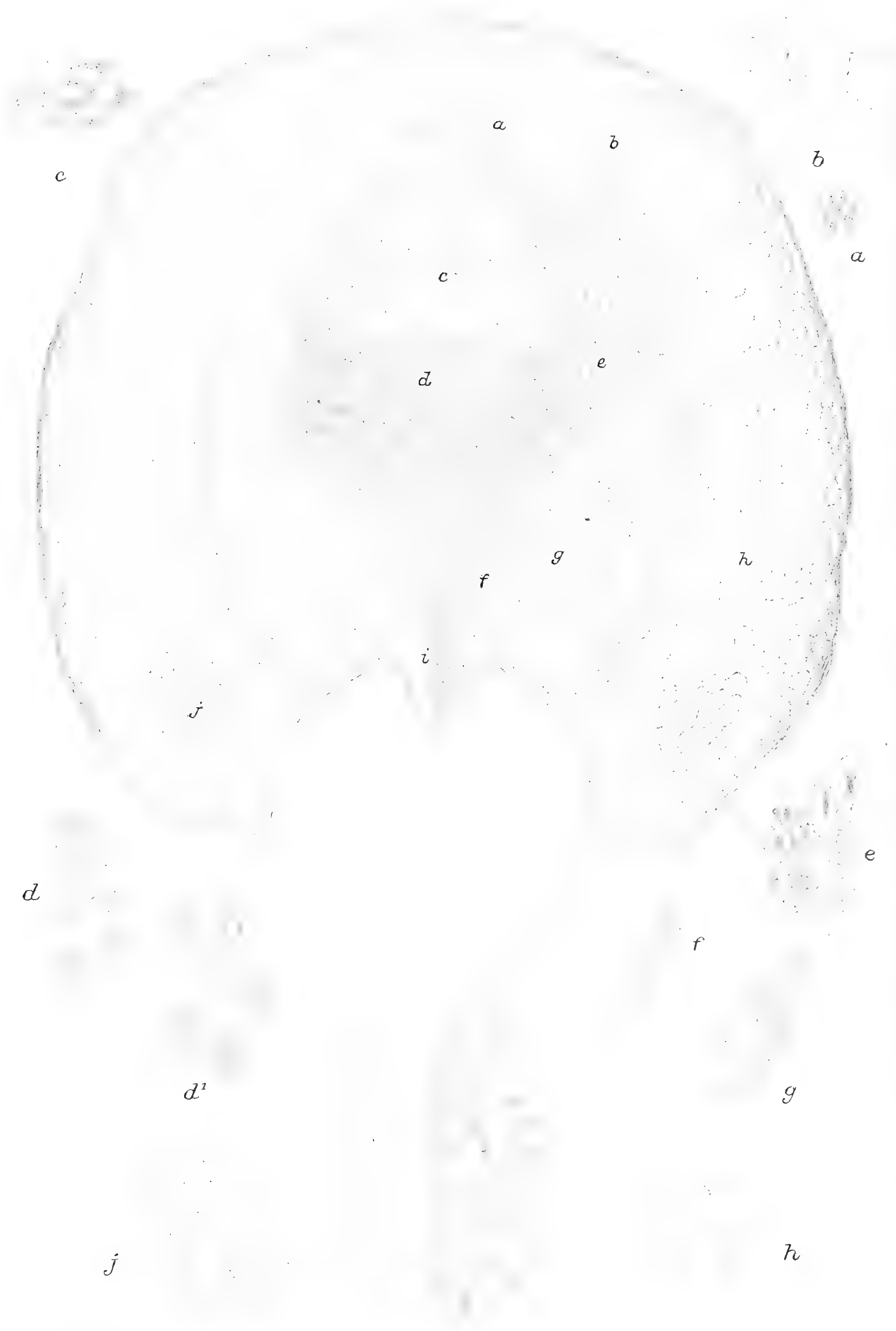

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PLATE V.

Fig. 1. Transverse section through a haustorium which has entered a root of *Pavetta indica.* The parts are still young and no vessels are formed. The nuclear cells are more vacuolated and less regular (*a*). At (*a*¹) the cells from a slightly older nucleus are shown. In the inner cortex there is a sharp distinction between the starchy (*b*) and protoplasmic cells (*c*), the latter being elongated and taking part in the formation of the sucker. Secondary thickening is taking place in the cortical fold (*d*).

Fig. 2. A haustorium fixed on a root of *Santalum album.* This may be taken as the type of the mature organ, as the vascular connection between host and haustorium is complete and the various tissues are becoming emptied of their contents. This is especially noteworthy in the breaking down of the cells at the top of the nucleus (*a*). Note also the endodermis (*e*) and the medullary rays (*m. r.*) in the transitional region, the cambium (*c*), collapsed layers and low-lying lacunæ (*lac*) inside them; also the bright cap of transparent yellow substance (*x*) at the end of each of the host's cortical wings. The structure of this is shown in fig. 4 of Plate VII. *b*, hypoderm.

C.A.B. del.

Huth, Lith.r London.

Plate VI.

Fig. 1. Part of the periphery of a haustorium attacking a root of *Hemidesmus indicus.* In this the layer of cork is seen, the hypoderm (*h*) with contents collected into drops, the starchy cells and the thick-walled, pitted, sclerotic cells of the cortex (*scl*).

Fig. 2. Masses of tabular crystals of calcium carbonate from the inner cortex of a haustorium on *Lantana Camara.* The cell contents in the cell on the right hand side (*x*) show the delicate reticulation in a crystal cell which has lain for some months in dilute glycerine and from which the crystals have been dissolved.

Fig. 3. Mulberry-like masses of calcium carbonate from the cortex of a haustorium on *Capparis horrida.*

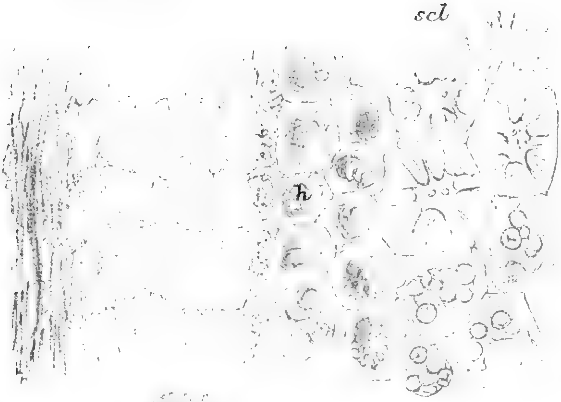
Fig. 4. Radiating crystal masses found in the outer cortex of another such haustorium.

Fig. 5. Thick-walled cortical cells as in fig. 1, from a haustorium on *Vernonia travancorica.* In one of these a mass of calcium carbonate crystals is to be seen.

Fig. 6. A section through a part of a haustorium on a root of *Toddalea aculeata.* Note the masses of calcium carbonate crystals in the usual place, in the elongating part of the inner cortex. Also note that the collapsed layer (*c.l.*) is broken down to a uniform mass of yellow substance and that this is continuous right down round the end of the wing of the host's cortex to the angle opposite the edge of the sucker lobe (*l*). *lac,* lacunar region.

Fig. 7. A section through the cortical fold of a haustorium on *Capparis horrida.* The darker cells (*d*) are lignified and thickened and are not only found in the end of the fold but run up beneath the hypoderm for a considerable distance (*d,d'*). An enlarged drawing of such cells is seen in fig. 5 of Plate VII. *lac,* lacunar region.

Plate VI.



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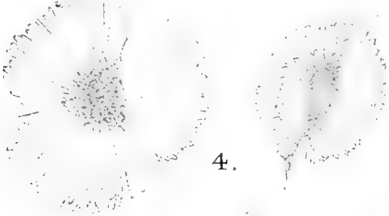

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PLATE VII.

Fig. 1. One side of the vascular loop in a haustorium attached to a root of *Alangium Lamarckii*. This shows one of the bundles in the transitional region with its endodermis (*e*), the interrupted zone (*i.z.*) and the vascular loop below it, the upper ending of the collapsed layer (*c.l.*) and the upper part of the disintegrated nucleus (*n*).

Fig. 2. Part of the same further magnified. The bast is shown under the endodermis (*e*) and contains the callus-plate of a sieve tube (*s.t.*). The isolated rows of vessels in the interrupted zone have lost their markings excepting a few in the outermost vessels, and have become filled with a yellow gummy mass. Their downward branching into white-walled, pitted vessels is well seen, as well as the thin-walled parenchyma between them.

Fig. 3. Part of the interrupted zone in a haustorium fixed on a root of *Capparis horrida*. Here the disintegration of the vessels has proceeded centrifugally and only the outer ones retain any of their markings. The vessels in the outer, latest formed row (*o*) retain their white walls and are indistinguishable from those of the main axis. All the rest are yellow.

Fig. 4. One of the caps of clear yellow substance shown at the end of the host's cortical wings (as at *x* in fig. 2 of Plate V) further magnified. It is evident that this clear yellow substance is made up of broken-down cells of the haustorium, apparently compressed by the host's bark (*b*) below.

Fig. 5. A portion of the haustorium shown in fig. 7 of Plate VI, further magnified. Note the cork, hypoderm (*h*) and the lignified, pitted cells below it.

Plate VII.

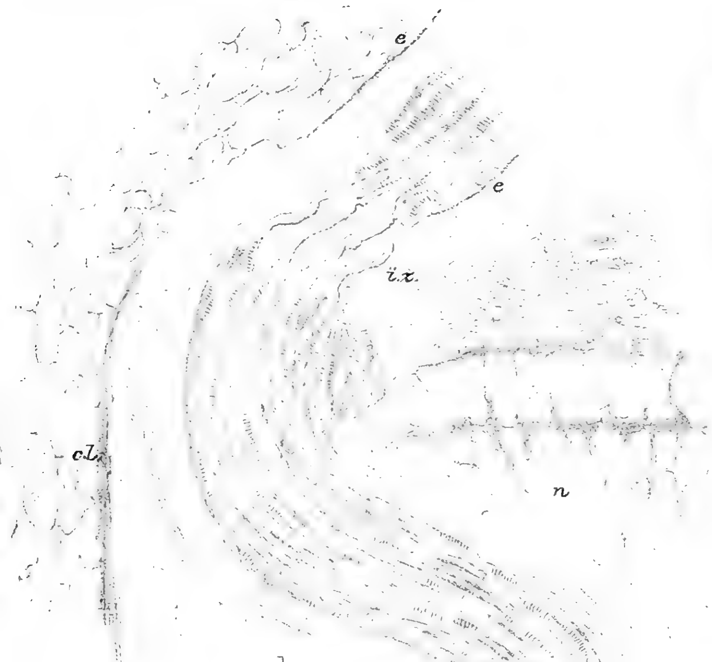

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PLATE VIII.

Fig. 1. A portion of the axial vascular strand in a haustorium attacking a root of *Plumbago rosea.* Proceeding from left to right, note, in succession, the cells of the pith with delicate protoplasmic sacs (*p*), the vessels (*v*) with long, irregular pits, the cambium (*c*) of nucleated protoplasm, and the starch-filled cells of the inner cortex (*co*). The contents of the outermost rows of the latter are not drawn. There is no trace of bast.

Figs. 2 and 3. The upper part of the axis of a haustorium on *Alangium Lamarckii.* Note the square vessels on the inner side (*sq*). In fig. 3 the pits are drawn on only one of the ordinary vessels (*v*) whose outlines are shown. They are altogether similar to those in fig. 1.

Figs. 4 and 5. Small portions of the vascular strands in different parts of the same haustorium on an unknown root. Fig. 4 is drawn from the mother root of the haustorium itself and shows the broad vessels with small, regular, oval pits and a sieve-tube (*s.t.*) in the bast. Fig. 5 shows the narrow elements of the sucker with irregular, long pits, frequently extending right across the vessels.

Plate VIII.

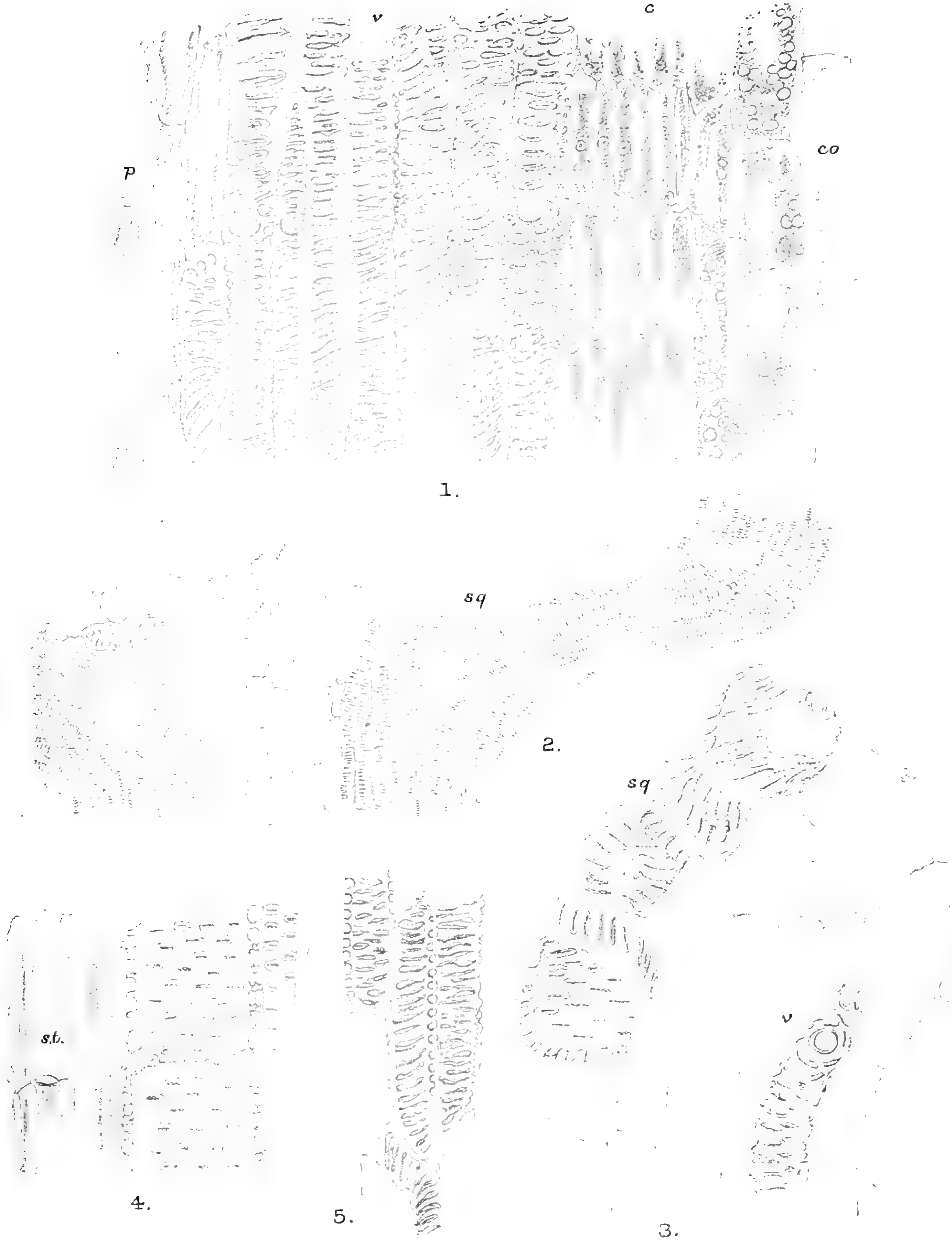

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PLATE IX.

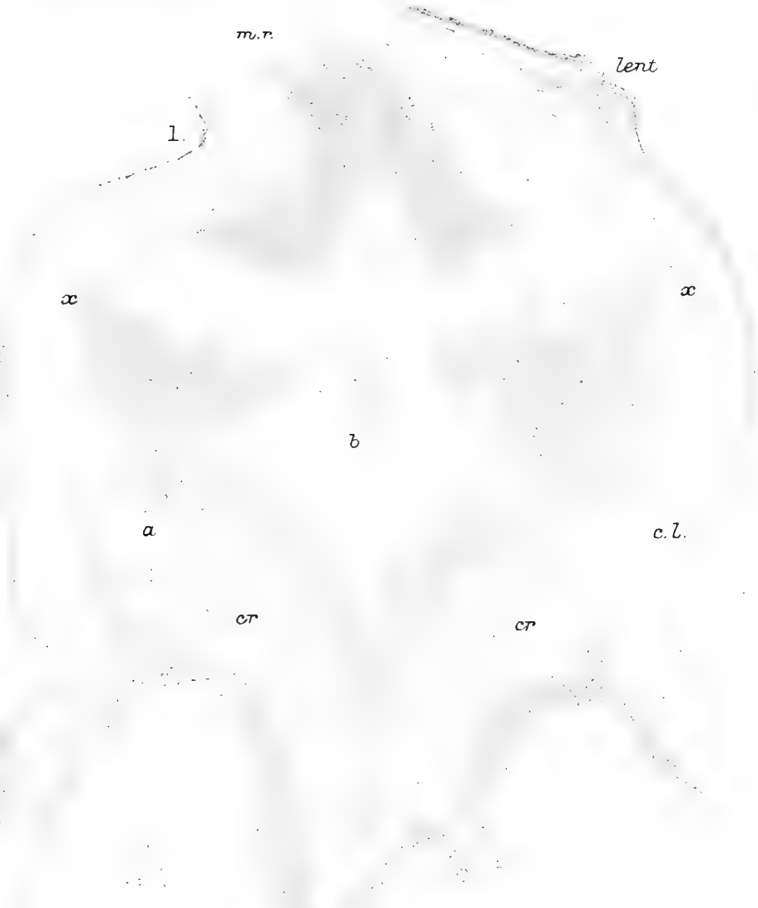
Fig. 1. An older haustorium fixed on *Argyreia speciosa.* The vascular system has undergone considerable growth in thickness. Note the place where most thickening takes place (*x*), just below the interrupted zone. The bundle from the mother root (*m r.*) is seen, as also its two divisions in the transitional region. A dark yellow mass (*b*) marks the upper limit of the nucleus. The cambium in the axis, while forming little secondary wood, has given rise to a series of rows of cells (*a*) simulating a secondary cortex. Some of these cells are enlarged at *a* and do not at all present the appearance of bast. The inner cortex is charged with calcium carbonate crystals (*cr*) and the collapsed layers (*c.l.*) are small and converge downwards.

Figs. 2 and 3. Thyloses from an invaded root of *Vernonia travancorica* showing calcium oxalate crystals and thick-walled, pitted cells inside them.

Fig. 4 A thylose from the same root of *Argyreia speciosa* with thickened and pitted cells inside it.

Fig. 5. A very old haustorium attached to a root of *Cansjera Rheedii,* cut in the middle and therefore appearing to be more regular than most (see figs. 4-7 of Plate I, where haustoria of the same age are shown). The haustorium now consists practically of only the vascular system. The root attached has been broken up and the point of attachment is minute. The collapsed layers (*c.l.*) are still visible but quite inconspicuous : they are so far disturbed by the secondary growth in thickness that they are almost in the same horizontal line. Masses of calcium carbonate crystals (*cr*) are found in both inner and outer cortex, the whole of this tissue now assuming the appearance of bark. The secondary cortex (co^2), formed by the cambium outwards, is broad and clear of contents. The greatest development of the xylem is in the upper part of the vascular loop (*x*) and this dominates the form of the haustorium which is now turbinate. The interrupted zone (*i.z.*) is bridged over by about forty strands of decomposed vessels. The upper end of the nucleus (*n*) is still discernible and the cells of the ground tissue above it are charged with crystals.

Plate IX.



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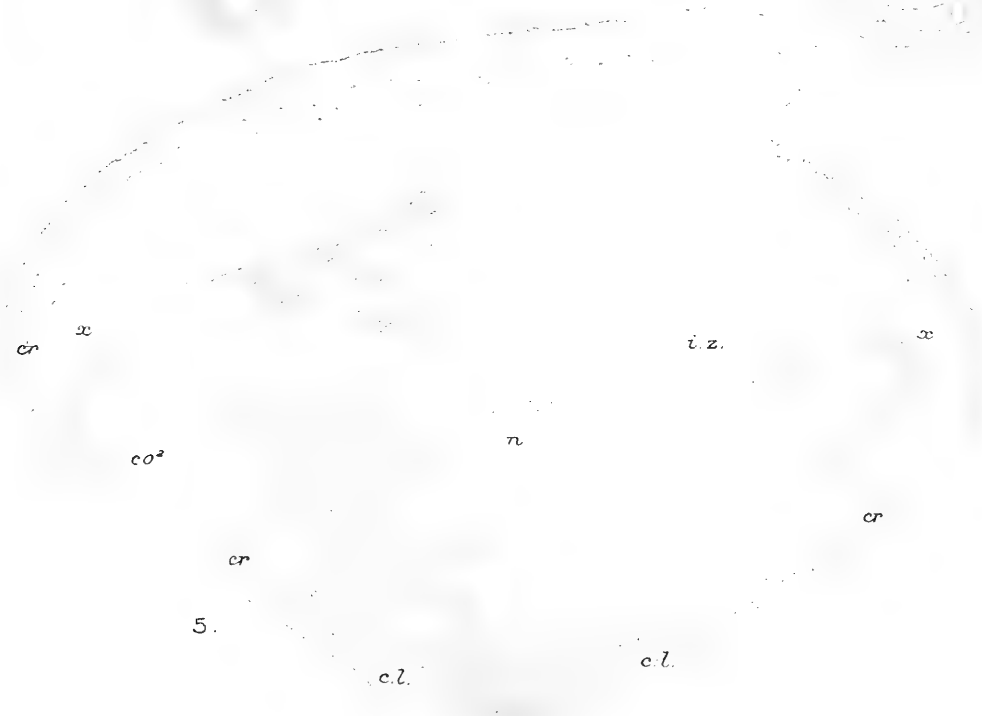

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PLATE X.

Fig. 1. Part of the sucker, including the edge of one lobe, in a haustorium attacking the root of *Plumbago rosea*. The contents are only drawn in some of the cells. Strands of vessels are formed in the sucker opposite to the vessels in the host's xylem, and the cells adjoining these vessels are fuller of protoplasmic contents than the rest (*pp*). The cells at the side of the sucker (*a*) have ceased actively secreting and are cut off by a collapsed layer (*c.l.*) from the rest of the haustorium. Cork (*ck*) is formed opposite to these in the host's wing.

Fig. 2. A similar portion of an older haustorium attached to a root of *Santalum album*. The strand of vessels (*v*) in the haustorium is not formed opposite to the vessels in the host's root. The cells at the side of the sucker (*a*) are cut off by a collapsed layer (*c.l.*), and they are moribund and crammed with starch. Between these cells and the inside of the wing of the host's bark there extends a broad layer of clear yellow substance (*b*). Near the sucker, this layer is striated and is apparently formed by the breaking down of the cells of the sucker: further out, the cells of the host evidently take part. The cells of the host's wood are filled with dark brown substance.

Fig. 3. A young haustorium on *Abrus precatorius*, which has successfully entered the host's root and yet has withdrawn itself from the woody cylinder. The whole surface (*a*) of this part of the haustorium is composed of glandular cells filled with typical, dense, granular protoplasm, a structure usually confined to the cells lining the lumen of the gland. This specimen, which is unique among those examined, recalls those met with in the haustoria of *Santalum album* on *Pterolobium indicum* (*Sant. I*, fig. 34). Some of the cells are enlarged at *a* and *b* and show the position of the glairy secretion below the cuticle.

Fig. 4. A haustorium attacking a root of *Aerua lanata*. The xylem (*x*) in this root is arranged in concentric bands separated by thin-walled parenchyma (*p*). A black "secretion" separates the sucker from the host, but the section is interesting in showing that this layer is absent where the passage of fluids is taking place (*a*). The point of junction of the vascular systems of host and haustorium is drawn on a larger scale at *a*.

Plate X.

C.A.B. del.

Huth, Lith^{r} London.

PLATE XI.

Fig. 1. An attack of *Cansjera* upon a root of *Capparis horrida.* A portion of the sucker and the end of one of the host's cortical wings are shown. The cells of the wing are completely isolated from the rest of the host's tissues by a thick layer of cork (*ck*), and yet they are crammed with starch while the rest of the root has little or none. In 1*a* the tissues are further magnified. The cells at the side of the sucker (*x*) are cut off by a collapsed layer and are filled with minutely granular starch (the original contents apparently suffering fragmentation). The cells of the wing are dead and browned but filled with clear and large starch grains.

Fig. 2. The sucker of a haustorium imbedded in a root of *Capparis horrida.* The parts within the dotted lines are full of starch (*st*) and this substance is absent from the rest of the section. Starch, it will be seen, is only deposited where the layer of secretion is formed, that is, presumably, where the passage of fluids has ceased. The remains of a former gland (*gl*) are seen.

Fig. 3. A haustorium of *Cansjera Rheedii* penetrating another *Cansjera* root. The haustorium which, in many respects, is typical, has fused in various places (*f*) with the host's tissues. Note the bundle from the mother root (*m.r.*) with its bast and endodermis (*e*). These are absent in the haustorium, but a thick layer of cambiform tissue (*c*) is met with. The distribution of the masses of calcium carbonate crystals (*cr*) in host and haustorium is instructive. Broad bands of cork are formed where the cortical folds are in contact with the host's bark, the discoloured portions being old cork (*ck*) and the white lines young cork and phellogen (*ph*).

Plate XI.

C.A.B del.
Huth, Lith^r London.

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SOME EXPERIMENTS IN THE HYBRIDISING OF INDIAN COTTONS

BY

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Professor of Botany at the Presidency College, Madras

AGRICULTURAL RESEARCH INSTITUTE, PUSA

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MEMOIRS OF THE DEPARTMENT OF AGRICULTURE IN INDIA.

STUDIES IN ROOT-PARASITISM.

IV—THE HAUSTORIUM OF CANSJERA RHEEDII.

BY

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3. Comparatively few young stages have been found in the numerous sections examined. In attempting to remedy this defect, a number of minute haustoria fixed to the roots of *Abrus precatorius* were imbedded in paraffin and cut with the microtome. But, unfortunately, some of the very smallest showed complete penetration, and most were fairly mature. The few cases of young haustoria met with show that the early stages have slight peculiarities which separate them both from *Olax* and *Santalum*, and it will, on that account, be necessary to describe the development of the haustorium.

No haustorium has been cut in which the nucleus is not already indicated. The earliest is a microtome section, and the cells are not altogether suited for the study of their contents. In this haustorium (Plate I, fig. 8), there is a median area of small cells in the act of rapid division, and around this the cells are arranged in definite order. This is the first appearance of the nucleus and the curves of growth in the ground tissue around it.

The haustorium is firmly attached to the root of the host (*Abrus precatorius*) and is fitted into all the unevennesses of its surface. This firm attachment of the haustorium to the objects it meets requires a moment's attention, as it does not seem to be merely a pressure phenomenon. It appears probable that a gummy substance is secreted, as in *Ampelopsis* or the climbing roots of ivy and pepper, but as yet no definite proof of the existence of such a substance has been obtained.

From a study of the tissues along the line of contact we learn several things. In the first place, a very distinct growing edge is distinguishable (as in *Santalum*) on each side of the haustorium. The haustorium is thus seen to be growing tangentially to the surface of the host's root. But, besides this growth at the edges, there is considerable increase in size in the middle part, resulting in a spreading movement of the tissues of the haustorium in contact with the root attacked. This is shown in the figure (8 *b*) by the doubling up of a piece of cork which is being rolled over in much the same manner as we noted in our study of *Santalum album* (*Sant. II*, Plate V, fig. 2).

4. In the next stage of development considerable differentiation of tissues has taken place (Plate II, fig. 1). The sections were mounted in dilute glycerine, and it is thus possible to study the cell contents more carefully. The first point of importance is the presence of a well-marked hypodermal layer (*a*). This is characteristic of *Cansjera* haustoria. Starch, although sometimes present here, is hidden by dense granular contents which in later stages assume the form of oily (?) drops. Immediately within the hypoderm the cortex (*f*) becomes early cleared of contents and the deeper, starch-laden cells (*g*) are arranged much as in the earlier stages of the *Olax* haustorium (Olax, Plate III, fig. 2). The densest part of the shadow of starch grains is met with outside the upper part of the nucleus, and the tissues become clearer along the lines of growth towards the host's root. The lines of growth are well defined and the cortex is distinctly separable from the nucleus. The development of the vascular system is, as usual, the vessels in the transitional region appearing long before those lower down. A downward extension of the vascular system is also commencing on each side of the nucleus, the cells of these procambial strands being densely filled with protoplasm and actively dividing by longitudinal walls (*c*).

The upper limit of the nucleus is clearly shown at this early stage, in this respect differing markedly from the haustorium of *Olax*. The cells immediately above the nucleus (*b*), really ground tissue and therefore of a similar origin to those of the cortex, but separated from it by the procambial strands, have become elongated tangentially and form a distinct mass of tissue. The cells of the nucleus, on the other hand, remain at first isodiametrical and divide rapidly in all directions (*d*).

In the lower part of the nucleus a median strand of tissue is traceable, the contents of whose cells become applied to their walls, giving them an appearance of thickening (*e*). This median strand is continued almost to the surface of the host's root. It would appear that this is the first stage in the development of the gland.

5. In the next stage figured, the gland is already well formed (Plate II, fig. 2). The arrangement of the outer, clear and inner, starch-laden cells of the cortex closely resembles that in *Olax*, but the cell contents have not been drawn in the figure. At the line of separation between these two parts of the cortex, however, the collapsed layers are becoming apparent (*bb*). And here we meet with another marked disagreement with the course of development in *Olax*. The collapsed layers in *Cansjera* are developed like those in *Santalum*.

The curved lines of growth are well seen. The nucleus is sharply separated off from the tissue outside it, and the vascular loop is indicated. The portion of ground tissue above the nucleus and between the arms of the vascular loop has cells yet more elongated horizontally than in the preceding stage, and there is evidence of pressure from the expanding nucleus below.

In the lower part of the nucleus the gland is well seen. In the few examples obtained this organ is extremely simple in structure, consisting of a median split in the nuclear tissue, lined by secreting cells. The gland in *Cansjera* is totally different from that in *Olax*. It resembles that in *Santalum* in being lined by a well-marked epithelium, but it is doubtful whether a duct is present, as in that case. The lumen is narrow and uniform in all the cases met with. The glandular cells themselves are like those already described for *Santalum* (*Sant. I*, para. 14). They have a dense mass of granular protoplasm at the base, while the upper part of the cell is clear (fig. *a*). The secretion, formed in this upper part of the cell, exudes in granular mucilaginous rods which fill the cavity of the lumen. These rods are better shown in the section drawn on Plate III (fig. 2). In the horizontal section through a slightly older haustorium (fig. 1) the various tissues referred to above may be followed. The hypoderm, clear and starch-laden cells of the cortex, the collapsed layers, the protoplasmic cells of the nucleus and the grandular epithelium are clearly separable.

6. Cases of haustoria in the act of entering the host's root are extremely rare. This fact was noted in both *Santalum* and *Olax*, and it was suggested that the cause was to be sought in the rapidity with which the sucker penetrates the cortex. Among the numerous sections of haustoria examined in the preparation of this paper, only one such case has been met with, and that is an exceedingly minute haustorium, less than one-sixteenth of an inch in diameter. The sections were cut with the microtome, stained with Delafield's hæmatoxylin and mounted in Canada balsam. They prove to be of much interest, and a detailed study of one of them is made on Plate IV.

In the transitional region the vascular strands are well seen, but no vessels are yet formed, and the strands are thus procambial (*a*, *e*). A distinct hypodermal layer is visible in the upper part of the haustorium, although its contents are not well shown. The cortical cells within it are devoid of contents with the exception of delicate protoplasmic sacs (*b*). The cells of the ground tissue in the vascular loop are sharply separated from the nucleus: they are, as usual, elongated horizontally and have well marked nuclei but little protoplasm (*c*). In the haustorium proper, below the transitional region, the collapsed layers are clearly shown, although still very thin. The cortical cells outside them (*h*) are moribund and empty and have merely a trace of protoplasm here and there. The cells of the inner cortex have distinct protoplasm and nuclei (*g*), but, from the mode of preparation, the distribution of the starch grains is not easy to make out. It is to be noted that the collapsed layers in *Cansjera* do not proceed down the whole length of the cortical folds. They turn inwards and terminate at a point half-way between the edge of the fold and the sucker. This is characteristic of *Cansjera* and forms another distinction between its haustorium and those of *Olax* and *Santalum*.

The cortical folds have ceased to grow at their edges and a growing point can no longer be traced. But a well-marked group of cells is found in the thickness of the fold, whose walls have evidently undergone some change (*j*). These walls are not stained by hæmatoxylin and thus present a yellowish patch of tissue in the surrounding violet. The addition of anilin sulphate causes them to assume a bright yellow colour, with chloroiodide of zinc they turn brown and with phloroglucin and hydrochloric acid they become pink. These and other tests show them to be lignified. The walls are thickened and pitted and their presence in this region is typical of most *Cansjera* haustoria.

The nucleus, as might be expected from the important part played by it in penetration, shows the greatest changes. The cells in the upper part have enormously increased in size, so as to greatly exceed those of the ground tissue above them, and have become distinctly elongated in the direction of the sucker. They form a striking feature in all sections of haustoria at this stage, and have large nuclei and nucleoli imbedded in deeply staining granular protoplasm. Their cell-walls, on the other hand, are extremely thin and difficult to distinguish. The appearance of these nucleated cells is so remarkable that a question as to their function naturally arises. It does not seem sufficient to assign to them a merely nutritive or mechanical action in forcing the sucker downwards into the host. The cell contents are very like those of glandular organs. A study of the drawings in Plates IV and V (d^1, *d*, *a*, a^1, and *a*) will indicate successive stages in their development, and it may be noted that they appear most like glandular cells at the moment of penetration. We have seen that the nucleus of the haustorium in *Olax* is practically all taken up in the formation of the gland, and it appears probable that the same is the case, although in a different manner, in *Cansjera*. The slit-like "gland" (*e*) then assumes more the character of a duct, and the figure on Plate IV supports this view. There is nothing of this in the haustorium of *Santalum.* Although the upper limit of the nucleus is quite sharp there, the cells are not thus enlarged, being little if any larger than those of the ground tissue above them (*Sant. II,* Plates I—III).

On either side of the nucleus the procambial strands are clearly visible; and their cells are dividing vertically only, so as to become elongated in this direction (*e*).

The lower part of the nucleus is divided into two parts, an outer (*f*), with small elongated nucleated cells, and a median strand with dense granular protoplasm, arranged as an epithelium on both sides of a narrow slit (*i*). This is presumably the gland in a late stage.

The young sucker is formed of the extension downwards of the lower part of the nucleus, and it has penetrated half-way through the host's cortex on its way to the vascular cylinder.

Details of all these tissues may be followed on Plate IV, where enlarged drawings are made of the cells in different regions.

7. The next stage, where the sucker has reached the woody cylinder of the host's root but has itself not yet formed vessels, is frequently met with, and is very characteristic of these haustoria (Plate V, fig. 1).

The cortical folds are assuming their permanent form. Growth in length has ceased, but a considerable thickening is noticeable on the inner side. Such growth in thickness, which is frequent in *Cansjera,* has not been noticed in either *Olax* or *Santalum.*

The collapsed layers are now much thicker, and separate the outer, empty cells of the cortex from the central, more or less protoplasmic mass. As before, the collapsed layers do not pass to the ends of the cortical folds, and abut on the host's bark half-way between the edge of the fold and the point where the sucker enters. The upper limit of the nucleus is particularly sharp, the cells of this region being, as usual, prominent.

As already noted, the cells of the nucleus are elongated in a direction at right angles to those immediately above them, and the latter are now considerably crushed by the nuclear growth.

The inner cortex is seen to have separated into two distinct parts. In the outer, the cells are more or less isodiametrical and filled with starch (*b*), while, in the inner, they are free from starch, have evident, nucleated protoplasm and are elongated in the direction of the sucker (*c*). This division of the inner cortex into two parts, although sometimes very clearly shown, is not always very definite. It calls to mind very forcibly the arrangement of tissues in the penetrating haustorium of *Olax scandens* (*Olax*, Plate VIII). In the latter case, however, the inner, elongating cells belong to the nucleus and the outer, starch-laden cells to the cortex. The sucker in *Olax* is formed entirely of nuclear tissue, whereas in *Cansjera*, as in *Santalum*, the sucker is formed chiefly of nucleus, but certain of the cortical cells take part, becoming greatly elongated and entering the split in the host's bark.

The sucker has reached the host's wood and is spreading along the cambial line on each side, thus becoming lobed. There is no trace of a former "gland," as in Plates III and IV, showing that the formation of this structure is not necessary for penetration. (See however para. 5.)

8. In Plate V, fig. 2, is shown a drawing of a mature haustorium penetrating a root of *Santalum album*. The main difference from the preceding stage lies in the development of the vascular system which is now fully formed. In the transitional region two strands are seen, interrupted at intervals by broad medullary rays and separated from the surrounding tissues by a distinctly marked endodermis (*e*). A well developed interrupted zone (*i. z.*) is seen at the top of the vascular loop, where the transitional region joins the haustorium proper. Below the interrupted zone the vascular loop is well defined, curving round to become a pair of strands in the haustorial axis, here without any trace of medullary rays. Two

continuous bands of vessels pass down the axis of the sucker, separated by a well-defined pith and clothed on their outer sides by cambium(*c*).

The cortex has undergone little change beyond its loss of contents. The collapsed layers are almost vertical and end downwards in the usual position. Lacunæ (*lac*) have appeared opposite the up-turned wing of the host's cortex, and the inward projection from the collapsed layers is much lower down than in *Santalum album* (*Sant. II*, Plates XIII, XIV, etc.).

The nuclear cells are practically devoid of contents and show signs of breaking up irregularly (*a*). The sucker is distinctly lobed and it is to be noted that it is provided with secreting cells on its sides as well as at its end, the whole inner sides of the wings being coated with yellow secretion. A cap of clear yellow substance is to be found at the end of each wing (*x*) (see para. 10 and Plate VII, fig. 4, for the mode of formation of this cap).

It was stated in a recent paper (*Par. Trees*) that compound haustoria were to be met with among those of *Cansjera Rheedii*. This does not appear to be the case, and the section on which the remark was based appears, on closer examination, to be abnormal. This is one of the few characters of these haustoria in which they resemble those of *Olax* rather than *Santalum*.

In the median line, where the sucker meets the wood of the host, the traces of a former gland may be made out (*gl*).

The development of the haustorium of *Cansjera Rheedii* has thus been followed from an early stage to the mature organ, and the points of difference noted between it and the similar organs of *Olax* and *Santalum*. It will now be necessary to consider certain tissues in greater detail. In this study the arrangement followed in *Olax* will best serve our purpose. The haustorium as a whole and the various tissues of the cortex and nucleus will be first examined, after which the vascular system and the sucker will be separately dealt with. Lastly, the effects produced upon the various roots attacked and their tissues will be noted and a summary statement prepared of the characteristic features of the haustoria as contrasted with those of *Santalum* and *Olax*.

TISSUES OF THE MATURE HAUSTORIUM.

9. *Cork and Lenticels.*—Cork is very common in *Cansjera* haustoria, much more so than in *Santalum*, but its presence does not discolour the surface of the root as it does in that plant. The cork in *Cansjera* is whitish yellow, and this is the prevailing colour of both its young and old haustoria. It will be remembered that in *Santalum* the cork forms a bright red-brown layer and that the older roots as well as the haustoria assume this colour.

In *Cansjera Rheedii*, cork is frequently continued round the cortical folds as far as the top of the wings of the host's bark. In one haustorium fixed on a root of *Cansjera* itself very thick layers have been formed both by the host and parasite. In the sections of this haustorium the cork is seen by transmitted light to be of a dark colour, while the phellogen is seen on each side as a thin white band (Plate XI, fig. 3).

Lenticels are common in *Cansjera* haustoria, and it is doubtless due to them that the haustoria have so irregular and warty a surface (Plate IX, fig. 1, *lent.*).

Hypoderm.—This, as has been noted, is usually to be found in *Cansjera* haustoria, although it is more distinct in some than in others. It consists of a layer of parenchymatous cells, within the cork, whose contents are peculiar. Starch grains are not found in any great abundance and, when formed, are hidden by the granular contents. The latter persist even in old specimens and are distinguished by their tendency to assume the form of drops. The hypodermal layer is distinguishable by means of this feature after all the rest of the tissues are emptied of their contents. The shape and size of the cells are also different from those within, for, while the latter become extended with the increase in size of the haustorium, the cells of the hypoderm remain small and equal-sided to the end. The structure and appearance of the hypoderm may be studied in Plates II, III, V and, especially, Plate VI, fig. 1, and Plate VII, fig. 5.

The Collapsed Layers.—These are simple in structure and are formed as in *Santalum.* They extend upwards, when fully developed, to just outside the point where the endodermis ceases (Plate V, figs. 1 and 2, and Plate VII, fig. 1), thus differing totally from those in *Olax.* In very old haustoria, however, they are left far behind by the secondary thickening of the xylem and form an insignificant part of the haustorium (Plate IX, fig. 5). Their usual downward ending is, as stated, peculiar. Instead of passing to near the ends of the cortical folds as in *Santalum,* they end half-way between this point and the edge of the host's wings. It is possible that this position may be partly the result of the secondary thickening which so frequently takes place in the end of the fold, but, whatever its cause may be, the result is that the collapsed layers soon become vertical (Plate V, fig. 2), and, as secondary thickening proceeds, ultimately converge downwards (Plate IX, figs. 1 and 2). A few cases have been met with in which the cortical folds remain long and thin, having no secondary thickening. These extend further round the attacked root than usual, and their collapsed layers also pass towards the ends of the folds.

The lacunar region inside the collapsed layers is situated much lower down than in *Santalum* and *Olax.* The tissue within the upper parts of the collapsed layers is free from breaks, but, outside the cortical wings of the host, the cells are crushed and separated by a series of characteristic lacunæ (Plates V and VI).

The collapsed layers first appear in the cortex between the starch-laden cells and the larger, empty cells without. They are formed, as in *Olax* and *Santalum,* from the decay of masses of crushed cells in the cortex. In *Cansjera* all the additions appear to be from the inner sides. The cortical cells on the outer side thus usually retain their form and are not crushed, while those within are obviously compressed and show undulations on their radial walls. The outer part of the collapsed layer is usually the oldest and, in late stages, becomes yellow and homogeneous, while the inner parts are still white and show their manner of origin from flattened cells. This decay of the outer part of the collapsed layers is not infrequent, and the application of staining reagents shows that a change in substance is taking place and that the outer parts are always more altered than the inner.

In conclusion, the small part played by the collapsed layers and the cortex generally in old haustoria reminds somewhat of what takes place in *Buckleya Quadriala* according to Kusano.* Here cork continues to be formed at increasing depths in the cortex, until ultimately almost the whole of cortex including the collapsed layers is thrown off.

10. *Yellowing of the tissues.*—Masses of yellow, transparent substance are not uncommon in the haustoria of *Cansjera Rheedii.* These are found not only in the vascular system, as in the interrupted zone and the older secondary wood, but in many parts of the nucleus and cortex, which habitually undergo disintegration.

In young haustoria which for some reason have been arrested in their growth, large lacunæ are not infrequent (Plate III, fig. 3). These are lined with yellow, transparent substance, formed by the breaking down of the cells whose places the lacunæ occupy.

In cases where the cortical folds have failed to grasp the object attacked and are thus brought into contact with the sides of the sucker, the space between these parts is filled with a similar yellow substance. This is also not uncommon in *Santalum* (*Sant. I*, figs. 14 and 15, *gl*). The lumen of the gland, again, after it has ceased its activity, is usually filled with yellow substance.

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* Kusano, S., Studies in the Parasitism of *Bukleya Quadriala* B. et H., a Santalaceous Parasite, etc. Journ. Coll. Sc. Imp. Univ. Tokyo, XVII, No. 10. 1902.

In older haustoria of *Santalum* the cells along the top of the nucleus become crushed and form a well-marked collapsed layer (*Sant. II*, Plate XI, fig. 2), and this is sometimes the case in *Cansjera*. But in the latter case the transverse band of cells more frequently becomes separated irregularly and disintegrated to a clear, yellowish brown mass (Plate IX, fig. 1, *b*).

More interesting is the presence in many sections of a small cap of brilliant yellow substance of the end of the host's disrupted cortex, and it is in most cases quite easy to see that this cap is made up of crushed haustorial cells (Plates V, fig. 2, *x*, and VII, fig. 4). In *Olax* and *Santalum* crushed masses of tissue are usual at this place, but they remain as such and are not fused into a yellow mass.

With these cases in view, it is not surprising that the collapsed layers themselves are sometimes converted into yellow bands, and haustoria have been noted in which a clear transition can be traced from the white walls of freshly added cells on the inner side of the yellow fused mass of older tissue outside. On Plate VI (fig. 6) a haustorium is drawn in which the collapsed layer has undergone complete disorganisation. The cell walls of which it was composed have become a clear yellow band. This yellow band is continuous downwards along the inward projection to the yellow cap at the end of the host's wing, and this last may be traced, through the clear, yellow substance which lines the inner side of the host's wing, to the yellow mass which is always found opposite the end of the sucker lobes. We have thus an instructive continuity between the yellowing of decaying haustorial tissues and the film of yellow "secretion" which spreads over the host's tissues wherever they are in contact with the sucker cells. This substance is again referred to in paragraph 18, where an attempt is made to trace its origin.

11. *Internal Meristems.*—The yellowing of the tissues described in the last paragraph is not infrequently accompanied by activity in the neighbouring cells which had, to all

appearance, already become permanent. A series of parallel walls are formed and a layer of cells resembling cork makes its appearance, surrounding the decayed part. Thus, in the case of the yellowed collapsed layers figured on Plate VI, the cells on both sides have developed in a meristem-like manner. Similar secondary tissue has been noted around the lacunæ in young haustoria and the yellow band of decayed cells across the upper part of the nucleus.

It is natural to assume that this cell-formation has for its object the provision of a separating layer of cork by which the dead tissues may be cut off from the living. It is to be noted in passing, that the cells thus formed are sufficiently turgid to project into the yellow mass, much as the external cells of the sucker project as papillæ into the mass of yellow secretion. It is probable that in both cases the form assumed is due to purely mechanical conditions.

The cortical cells on the outer sides of the collapsed layers soon lose their contents and become apparently moribund. There is none of the radial arrangement of the cells which forms so marked a character of the old haustoria of *Olax scandens*, and the cells of this part are similar to those of *Santalum album*. And this similarity is emphasised by the occasional appearance in this place of meristematic cells resembling those found in haustoria of *Santalum album* attacking the roots of *Pithecolobium dulce* (*Sant. II*, Plate V, fig. 1, *me*).

A much more striking feature is the occurrence of secondary thickening in the ends of the cortical folds, mentioned in para. 7 (Plate V, fig. 1). This appears to be independent of the lignification of a small patch of cells in the end of the cortical fold noted in para. 6 (Plate IV, *j*). There is a tendency in certain plants for this lignification to extend upwards as a narrow band, three or four cells broad, immediately below the hypoderm (Plates VI, fig. 7, and VII, fig. 5). It is thus not infrequent for the outer layers of the haustorium to assume some complexity, and this has been noted especially in the case of certain hosts. For instance, while no trace of the lignified cells appears in the folds of haustoria clasping the roots of *Commelina fruticosa,* it is present in most if not all of the dozen or so examined which were attached to *Hemidesmus indicus* and *Capparis horrida.*

12. *Crystals of Calcium Carbonate.*—As has been pointed out by Edelhoff* and Valeton† there are no calcium oxalate crystals in the tissues of *Cansjera,* their place being taken by crystalline cystoliths of calcium carbonate. Masses of cal cium carbonate crystals, although rare in young haustoria, are abundant in older ones, being presumably only formed in cells whose activity is on the wane. Thus, certain tracts of cells which are no longer required by the haustorium are noted for their frequent appearance. The crystals occur in the elongating portion of the inner cortex, inside the collapsed layers near the lacunar tissue, in the cortex outside the collapsed layers and, especially, in the ground tissue immediately above the nucleus (Plates VI, IX and XI). They are rarer in the hypoderm and are not formed in the nuclear tissues. The distribution of these crystal masses is thus mainly cortical, and follows with remarkable fidelity that of the calcium oxalate crystals in the haustoria of *Olax scandens* (*Olax,* para. 16). The presence of these bodies has been noted in some forty haustoria, but was probably more widely spread in the original material because many of the sections were mounted in dilute glycerine and lay for some time before examination. In some sections, at least, the crystals have been noted gradually to disappear in this medium. In these cases no definite structure was left behind and no residual basis has been found giving callose reactions (see Plate VI, fig. 2, x, and the description of this figure). Fresh material has not been available for the examination of these bodies, but, from the spirit material at

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* Edelhoff, E., Vergl. Anat. des Blattes der Familie der *Olacineen.* Engler, Botan. Jahrb. VIII, 1886-7.

† Valeton, Crit. Overz. d. *Olacineen,* Groeningen, 1886. (I have not been able to see this paper.)

command, they do not appear to resemble the double cystoliths described for *Cansjera* by van Tieghem.*

They occur in isolated cells and the manner of deposition appears to be rather that of ordinary calcium oxalate crystals than of normal cystoliths. They form masses of clearly defined tabular crystals of calcium carbonate *or* a mulberry-like mass with blunt and frequently branching projections (Plate VI, figs. 2 and 3). In one case a quite different form is assumed. In the outer cortex of some sections the crystals of calcium carbonate have taken on the appearance of sphærocrystals (Plate VI, fig. 4). Such crystal masses, instead of belonging to one cell, project into two or three from their common angle. At the place of junction a substance is found which stains deeply with methylene blue. In the haustoria where these occur, the radiating crystals were found in the outer cortex, while the crystal masses in the inner cortex had the normal form described above.†

In a few cases the walls of the cells in which the crystal masses occur have become sclerotic (Plate VI, fig. 5). These thick-walled cells call to mind the sclerotic cystoliths found in Champereia.‡

Isolated thick-walled cells are found scattered throughout the cortex of *Cansjera* haustoria. Their usual position is

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* Van Tieghem, Recherches sur la Structure et les Affinités des *Thymeleacées* et des *Peneacées*. Ann. d. Sc. Nat. Ser. VII, Bot., T. XVII, 1893: pp. 249-257, *Cansjera, Champereia* et la Famille des *Opiliacées*.

† The facts concerning these supposed radiating crystals of calcium carbonate are as follows. They were found in sections of several haustoria attacking *Capparis horrida* roots. In these haustoria the ordinary crystal masses were present in abundance in the usual places and the radiating crystals were confined to the ends of the cortical folds. Upon the addition of dilute acetic acid all the crystals disappeared rapidly, with the evolution of bubbles of gas, but it was not possible to assert that any of this gas came from the masses of radiating crystals, because it made its appearance at points of the sections far removed from any crystals.

The radiating crystals do not exhibit the true structure of sphærocrystals as described by Hansen. They are simply groups of crystals projecting into several cells from a basis of amorphous substance which was readily stained. There was no outer shell or skin visible. It is possible that they do not occur in fresh material, but have been slowly formed, like sphærocrystals, in the alcoholic material. (See Ad. Hansen, Ueber Sphærocrystalle, Arb. Bot. Inst. Würzburg, III, 1888.)

‡ Solereder, Syst. Anat. d. Dicotyledonen, 1899.

outside the collapsed layers (Plate VI, figs. 1 and 5), but they are sometimes found along with crystals of calcium carbonate in the elongating cells of the inner cortex In a few cases, as stated above, the crystals are found inside them.

The Vascular System.

13. The *general arrangement of the vascular system* in the haustorium of *Cansjera Rheedii* is similar to that described already for *Santalum* and *Olax.* A branch from the vascular cylinder of the mother root spreads out to form a widening circle of bundles in the transitional region. At a certain point these bundles are broken up, and isolated rows of vessels, separated by parenchyma, are uniformly distributed over a broad circle round the central mass of ground tissue. This has been regarded as the region where the mother root joins the haustorium proper. Below it, the vessels are seen to branch repeatedly so that their number increases greatly. They are, moreover, no longer separated, but fuse to a dense mass of xylem arranged in a broad oval ring. This ring rapidly flattens downwards, at the same time becoming discontinuous at two opposite points, so that, ultimately, two parallel lamellæ are formed which pass down the axis of the haustorium. This is the arrangement in *Santalum:* it will be remembered that in *Olax* only one plate of vessels is found in the axis of the haustorium. Lastly, the bundles become broken up again and the vessels form separate rows in the sucker as it approaches the host's root. A closer study of this general arrangement need not detain us longer, as it has been fully dealt with in previous papers (*Sant. II,* Plates IV and VI—VIII)

Certain parts of the vascular system are, however, peculiar in *Cansjera* haustoria. The endodermis, occasionally noted in *Santalum,* but of so problematical a nature in *Olax,* is very clearly defined. The interrupted zone described in *Santalum,* but totally absent in *Olax,* has its greatest development in *Cansjera.* As in *Santalum,* no bast is found in the haustorium, even in cases of self-attack: in *Olax*, it will be remembered, the presence of masses of sieve-tubes and other bast elements was a surprising but well-marked feature in cases of self-attachment. In older haustoria with much secondary thickening, a mass of cambiform tissue filled with contents is found outside the cambium, forming, as in *Santalum*, a sort of secondary cortex. Secondary thickening is practically confined to the upper part of the vascular loop, and this fact gives a peculiar and characteristic appearance to sections of old haustoria. Lastly, there is a marked difference in the size and pitting of the vessels of the sucker and those of the mother root. These points of interest will be dealt with in order.

14. The *Endodermis* is extremely clearly shown in the upper part of the haustorium of *Cansjera Rheedii.* It is, however, confined to the mother root and transitional region and stops short at the interrupted zone (Plates V, fig. 2, and VII, fig. 1). In ordinary haustoria it is seen to consist of a layer of crushed cells whose walls are much darker in transmitted light than those of the cells around them. Here and there, in sections of young parts, there are shadows on the walls, and in rare cases this is seen to be due to undulations similar to those in the endodermis of many roots. An endodermal layer appears to surround each bundle where they are separated in the transitional region, but good figures of this are not easy to obtain.

The *Interrupted Zone* is very well developed in these haustoria. The change undergone by the vessels of this region is exactly that described for *Santalum album* (*Sant. II*, para. 9). The walls lose their characteristic markings and assume a yellow colour and, in later stages, the whole vessel becomes filled with yellow substance, the lumen being entirely obliterated. The interrupted zone occurs at the point of junction of the transitional region and the haustorium proper, just above the place of greatest width of the vascular loop and in the place (mentioned above) where the bundles of the transitional region separate to isolated rows (*Sant. II*, Plate VI, fig. 2, *a*, *a*). They are here separated by thin-walled, small-coated parenchyma (Plate VII). A curious circumstance about this interrupted zone is its extremely early appearance, some of the first stages of vascular development met with showing complete disorganisation at this point and, presumably, a complete dislocation of the vascular system. In other cases, however, it has been observed that the outermost strands are still normal while the inner ones are yellowed. The yellowing is centrifugal, and passes outwards in much the same manner as the duramen in the secondary wood, only it is much more rapidly completed. In the figures on Plate VII these points are illustrated. In the first two figures yellowing is complete, mere traces of pitting alone being found on the outermost row of vessels. In figure 3, however, the outer row is apparently still intact, while all the rest are filled with gummy substance. It should be noted that the last mentioned case is not very common and the appearance shown in figures 1 and 2 is more usual.

As already remarked (*Sant. II*, para. 9), it is difficult to understand the utility of this arrangement, for it would appear that interruption occurs very shortly after the sucker has reached the woody cylinder of the host and soon after the fusion of the vascular systems of the two plants. The conclusion at present arrived at is that the activity of the haustorium is extremely short and that, as in ordinary plants, the absorbing portion of the root-system in these parasites functions only for a short time, and this absorbing power is passed onwards as the roots grow in length, branch and encounter new foreign systems to which to attach themselves. According to this view, the parasite is brought into contact with new roots in rapid succession and the old suckers are practically closed. If this be true, on the other hand, it is difficult to understand the amount of secondary thickening which takes place in some haustoria, the new vessels being apparently closed in succession almost as fast as they are formed (Plate IX, fig. 5).

To learn what really happens in these organs will, however, have to be left until they can be studied in the field. We shall there perhaps be able to test whether there is any passage of fluids in the older haustoria and, if so, by what path they pass upwards. Such experiments have not been possible up to the present.

Before leaving the interrupted zone, it may be remarked that the rows of vessels in this region are fairly equidistant. The number of strands varies according to the amount of secondary thickening which has taken place, and, in general, a fair idea may be obtained of the age of a haustorium by counting the number of strands present. In very early cases a single strand is seen, while, in old, distorted haustoria, it is not infrequent to count as many as 40 in the section on each side (Plate IX, fig 5).

15. The *Cambium* is distinctly seen in all parts of the vascular system, although it is less marked towards the sucker than in *Olax* and *Santalum*. Its activity and length of life, however, seem to vary in different parts of the haustorium and, in this respect, *Cansjera* differs from both the haustoria already described. Speaking generally, the cambium is short-lived in the axial region and it probably very soon ceases to produce wood there, while, passing upwards, its activity increases, until, in the middle of the vascular loop, a great development takes place. This will be rendered clearer on reading the paragraph on secondary thickening.

The *vessels* are uniform in character in the haustorium proper, long and narrow, richly perforated with wide, irregular pits which frequently extend right across the width of the vessel (Plate VIII, figs. 1, 2 and 5). In this latter character they differ remarkably from the vessels of the transitional region and mother root. Here the pits are small and oval and are arranged in regular lines over the surface of the wide vessel (fig. 4). Just as in *Olax*, while the vessels of the sucker present one extreme and those of the mother root another, numerous transitional cases occur in the body of the haustorium (*Olax*, 28 & 29). The vessels of the mother root are, as might be expected, much wider than those of the haustorium proper.

In one place the vessels are peculiar, and it is doubtful if they have much to do with the transmission of fluids. This is at the top of the axis, where the two bands of vessels separate outwards to curve round the loop. On the inner edge of the vascular loop at this point the vessels are broad and short, have in fact much the shape and size of the neighbouring cells of the nuclear "pith" (Plate VIII, figs. 2 and 3, *sq.*).

Bast has not been met with in the haustorium proper of *Cansjera.* The sieve-tubes of the mother root are very small and difficult to locate, and little callus-formation has been met with in the sections, although the haustoria were collected at different times of the year. As far as can be seen, the sieve-tubes are found as far down as the end of the endodermis (Plate VII, fig. 2), but no trace of them has been met with lower down, even in cases of self-attachment. It will be remembered that, in *Olax scandens*, an abundant development of bast occurred throughout the haustorium in the latter case.

In certain sections, especially in old haustoria (Plate IX, figs. 1 and 5, and Plate XI, fig. 3), a well-defined mass of tissue in regular layers is found outside the cambium. It is possible that a store of material is here laid up for the formation of further vessels in secondary thickening. On the other hand, it is just here that fewest vessels are formed. The tissue has much the appearance of secondary cortex, the latter being usually crushed and dead in old haustoria, especially in the lower parts. A protection would thus be afforded to the cambial cells within.

16. *Secondary thickening* of the vascular system differs considerably in *Cansjera* haustoria from that in *Olax* and *Santalum.* In the latter (*Sant. II*, Plate IX), wood is developed equally throughout the haustorium, as much in the sucker and axis as in the vascular loop. In *Olax*, however (*Olax*, Plate

IX, figs. 6—10), we see that the increase in thickness of the vascular strands assumes its maximum in the lower part of the vascular loop. In *Cansjera* this tendency is increased to such an extent that comparatively little thickening takes place in the sucker or axis, and the addition of secondary wood is chiefly in the middle of the vascular loop, immediately below the interrupted zone. This feature gives the old haustoria a very characteristic appearance. In them there is a curious bell-shaped expansion of the wood on each side of the loop, terminating upwards in the isolated strands of the interrupted zone. The haustorium thus becomes broader at the top with increasing age and the collapsed layers assume a vertical position (Plate IX, fig. 1). In very old haustoria the effect is still more striking. The whole haustorium assumes a turbinate form, the upper part being very broad and the point of attachment frequently minute (Plate I, figs. 5 and 6), like the peg of a top. The collapsed layers in such haustoria are inconspicuous and ultimately become almost horizontal, the cambiform tissue is broad and the cortex is reduced to a narrow strip charged with calcium carbonate crystals (Plate IX, fig. 5).

Yellowing of the old wood is not a very marked character in *Cansjera* haustoria, but it is met with here and there. It is interesting to note that, in this matter, as in so many others, *Cansjera* resembles *Santalum* rather than *Olax*. In the latter the yellowing commences in the primary xylem and gradually extends outwards through the secondary wood. In *Santalum* and *Cansjera*, while the inner layers of secondary wood become yellowed with age, the primary xylem remains white in colour like the younger part of the secondary wood.

THE SUCKER.

17. *Penetration.*—It is assumed that the chief reason for the penetration, by green hemi-parasites, of the roots of other plants is to form a connection through the haustorium between the vascular systems of the host and parasite. By

this means the stream of water and salts will be tapped and the deficiency in root-hairs will be rectified. Let us consider the difficulties in the way of such penetration. Roots are protected externally by a bark largely composed of cork. Added to this, there are frequently thick-walled cells in the cortex, which vary from isolated bundles to uninterrupted bands of considerable thickness. The rest of the cortex consists of parenchyma, frequently starch-laden, and there may or may not be a sheath of sclerotic cells around the central vascular cylinder. On the whole, the roots of monocotyledons, and especially palms, appear to be better provided with such protective layers than those of dicotyledons, a fact that may be connected with the looser structure of their vascular cylinder.

The first obstacle to be overcome is the cork. It is improbable that the ferment secreted by the haustorium has any great power of dissolving cuticularised membranes, cork indeed being, usually, a successful protection of the invaded tissues of the host from further attack, and some other way of removing the cork is needed. In paragraph 3 of this paper it was suggested that the firm adhesion of the young haustorium to a host's root may be due to the secretion of a gummy substance. As the haustorium increases in width, a shearing action is thus brought into play, causing the layers of cork to be rolled apart (Plate I, figs. 8 and *b*). Compare this with *Sant. II*, Plate V, figs. 2 and 2′). In other cases strands of cork are lifted bodily away, as shown in *Sant. I*, figs. 15, 16 and 18. This action of the superficial layers of the haustorium together with the undoubted pressure exerted, is probably sufficient to account for the successful penetration of the bark, even when composed of thick layers of corky tissue.

The sclerotic bands appear to be more difficult to negotiate, especially when they are lignified. We have seen that, when they are discontinuous, the sucker, passing along the line of least resistance, avoids them and finds its way through the parenchymatous tissue between (Plate X, fig. 4, and *Sant. II*,

Plate XI, fig. 2). But where the bands are at all continuous, great difficulty is experienced. This is shown in *Santalum* by the formation of compound haustoria and, in some cases, such as *Zizyphus* and various monocotyledons, the haustorium is frequently defeated in its attempts at penetration. The same applies to continuous sclerotic sheaths round the vascular cylinder. Progress is very slow and the haustorium is often found to be shrunken and moribund before entrance has been effected (*Sant. I*, Plate VI, fig. 29).

In an ordinary attack on a dicotyledon root we may thus assume that the cork is lifted piece-meal, while the sclerenchymatous bands are either very slowly dissolved or, more frequently, avoided altogether. The main work left for the secreting cells is the dissolution of the cortex and bast, and this is done with great rapidity and success by the ferments in the haustorium. It has been pointed out that, in *Cansjera*, as in *Santalum*, the presence of a gland is not necessary for penetration, this work being accomplished by secretions from the ordinary surface cells, probably aided by the cells of the nucleus.

The mode of penetration varies in character in *Cansjera*, as in the other haustoria examined, according to the hardness of the root attacked and the distribution of its thick-walled protective cells. In soft roots, with loose or lightly lignified woody cylinder, the latter is penetrated by the sucker, either all over or down the medullary rays. Occasionally the sucker wanders between the sclerenchymatous bands in the cortex, but, on the whole, these irregularities are much less frequently met with than in *Santalum* and *Olax*.

18. *The Sucker.*—This part of the haustorium, as we have seen, is formed chiefly of nuclear cells in *Cansjera Rheedii*, and the cause of its rapid entry is to be put down to the great accumulation of such cells inside the young haustorium and their sudden expansion the moment a split is formed in the bark. Some of the inner cortex, distinguished by the absence of starch

in its cells, also takes part in the formation of the sucker (Plates IV and V). As in *Santalum*, the sucker of *Cansjera* consists partly of nuclear and partly of cortical cells : that of *Olax* is purely nuclear.

The further development of the sucker in *Cansjera* is extremely limited as compared with that in *Santalum* and *Olax*. Having reached the woody cylinder, and being prevented from further progress in this direction, it spreads along the cambial line and thus becomes bilobed. But the lobing in *Cansjera* is very slight and sometimes altogether absent. In not a few cases the sucker remains plug-like or columnar (Plate IX, figs. 1 and 5). This is in marked contrast with the long-continued growth of the sucker lobes in the other haustoria. Besides this, the sucker does not greatly increase in thickness, and, as a consequence, the wings of host's bark thrust aside by its entry are comparatively small. It may be noted, in passing, that the haustoria of *Ximenia americana*, although not yet fully examined, appear to present the opposite extreme, as well in the growth of the sucker lobes as in that of the cortical folds. Both of these grow right round the opposing root until they completely envelope it. One result of the meagre development of the sucker in *Cansjera* is that the whole haustorium, from the start almost, is much broader above than below, a character which becomes intensified when secondary thickening takes place in the vascular system.

On the other hand, the sucker is not active only at its end where it touches the woody cylinder of the host's root, but also at its sides where it is in contact with the cortex and bark. A thick layer of yellow substance lines the inner sides of each wing, and the cells of the sucker extend as papillæ into this layer just as they do at the edges of the lobes. At some later period the active cells at the sides are usually cut off from the main body of the sucker by a collapsed layer, and when this happens, they rapidly become permanent and are ultimately crushed (Plates X, figs. 1 & 2, *a*, and XI, fig. 1). A similar state of things has been occasionally met with in *Santalum*.

The vessels in the axis and the sucker behave much as in *Santalum* and *Olax*, with the exception already noted that there is comparatively little secondary thickening. As the host's tissue is approached, they form separate rows and apply themselves to different parts of the woody tissue. As in the other haustoria, there is no special tendency for these rows to apply themselves to the vessels of the host and, in most cases, no definite connection can be noted between the vessels of host and parasite. Occasionally, however, we find vessels formed in the sucker accurately opposite to the vessels of the host. Two such cases are figured on Plate X (figs. 1 and 4) and call to mind a similar example mentioned in our study of *Santalum* (*Sant. II*, 29).

A few lines, in conclusion, may be devoted to the yellow "secretion" so often referred to as occurring between the sucker and the host's tissues, for some additional light has been thrown on its origin and structure by the examination of *Cansjera* sections (Compare Plate X, fig. 2, with *Sant. II*, page 31, and Plate X, figs. 1—3, and *Olax*, Plate X, fig. 2). In the purely glandular cells and the lumen of the gland the yellow transparent substance is obviously the direct product of the protoplasm accumulating beneath the cuticle and being discharged at intervals. A yellowish colour is not infrequently assumed by discharges of this kind (Marshall Ward, for instance, noted this colour in the secretion from *Botrytis* hyphæ on *Lilium candidum*). In the more diffused action of the general haustorial surface, the yellow substance has not infrequently traces of structure, many instances of striation or lamination having been noted. This lamination appears to be caused by the breaking down of successive cells (refer also to paragraph 10 where the yellow substance formed by the breaking down of the cells of the collapsed layer are clearly continuous with the yellow secretion at the end of the sucker). In some cases these cells belong to the sucker, and it is natural to suppose that they have been dissolved by the action of the cells behind them. In other cases the yellow layer is evidently formed in part by the crushed cells of the host. The whole mass is probably filled with ferment formed in the haustorial cells, and, while the remains of haustorial cells are added on the one side, those of the host may sometimes also be seen on the other, and the mass thus assumes a considerable thickness (Plate X, fig. 2, *b*). Long after the secreting cells have lost their activity, it would thus be possible for the yellow mass to continue its action on the host's tissues, until the latter are effectively protected by the formation of a layer of cork. Sooner or later various pigments are added to the mass and it assumes colours characteristic of different hosts. All stages from clear yellow (*Citrus*), through reds and browns (*Acacias and Albizzias*) are met with, until, in such plants as *Diospyros* and *Strychnos*, the colour becomes an inky black.

It is interesting to note that this coloured separating substance is always wanting opposite to the rows of vessels in the sucker (Plate X, figs. 1 and 4), a fact tending to show that absorption no longer takes place where the yellow substance is formed. A study of fig. 2 on Plate XI leads to the same conclusion. In staining for starch, the tissues of host and haustorium were coloured blue wherever the dark secretion layer separated them (*st*). In other places no coloration was observed. It is obvious that no active flow of nutriment takes place where the cells are full of starch.

EFFECT ON THE HOST'S TISSUES.

19. The general effect of the haustorial action on the host's tissues is similar in *Cansjera* to that in *Santalum* and *Olax*, but the sucker is smaller, and this seems to cause certain differences.

The wings of the host's bark are uniformly attacked, as we have seen, by the active sides of the sucker. The attacked parts are generally cut off by a layer of cork from the living cells of the host's root. The wings are, however, small, probably on account of the poor development of the sucker. And this poor development will also probably account for the fact that the secondary growths, which form so marked a feature in the attacks of *Olax scandens*, are almost entirely absent in the roots entered by *Cansjera*. Secondary growth of any kind (excepting of course the formation of corky separating layers) is very rare in the wings of the cortex, and the formation of secondary wood there is practically unknown.

The formation of cork in the angle opposite the edge of the sucker lobe is frequently met with, and this is usually sufficient to bar further progress. The origin of this cork is well seen in one section through the root of *Plumbago rosea*. The phellogen appears to arise from a row of cells derived from the cambium. Instead of becoming lignified in the usual way, these cells divide by radial walls and thus form tangential rows of cork. In certain cases noted, this corky protection of the cambium is neglected or insufficient, the action of the sucker cells extending far beyond the place occupied by them. Thus, in a couple of haustoria fixed on *Alangium Lamarckii*, the destruction of the cambium passes nearly all round the root, although the lobing of the sucker is, as usual, small.

Secondary thickening of the woody cylinder of the host, after attack, occurs in a few cases, but it is rare. Is this because of the smallness of the haustorium or its comparatively short duration ? Or is it due to the fact that these haustoria have been collected in a dry region where growth of any kind is slow ?

Some of the roots attacked have abnormal structure. Considering the differences noted in the structure of haustoria attacking monocotyledon and dicotyledon roots (*Sant. I*, 14), it is interesting to mark their behaviour in these cases. In *Ærua lanata* the wood occurs in concentric, more or less continuous bands, and these are mainly composed of thick-walled elements. Where these bands extend right across the area of contact, the sucker treats them as ordinary woody cylinder and spreads along the cambium. If there is any gap, however, the sucker passes through it and attacks the band within, the outer layer of wood with its layer of cambium being treated exactly as if it were a sclerotic band (Plate X, fig. 4). The scattered bast bundles in the wood of the root of *Strychnos Nux-Vomica* do not appear to materially affect the course of the sucker.

The vessels opposite to the sucker are, for the most part, filled with gummy substance of varying colour. In a few cases a dense black pigment is present.—*Azima tetracantha, Mallotus distans, Strychnos Nux-Vomica, Barleria buxifolia.* Thyloses occur in the vessels of certain species and are of special interest in two cases. In *Vernonia travancorica* and *Argyreia speciosa* they become thick-walled and pitted (Plate IX, figs. 3 and 4), a single thylose sometimes filling up a vessel so as to present the appearance of one vessel inside another. In *Vernonia travancorica*, some of the thyloses are filled with crystals of calcium oxalate (fig. 2).

20. *Action of the Secretion on Starch.*—This has already been referred to (*Sant. II*, 33 and *Olax*, para. 17), and it was demonstrated from a study of many sections that the ferment was more active in the destruction of cellulose cell walls than of their starchy contents. The study of the sections of *Cansjera Rheedii* haustoria leads to the same conclusion, and the following remarks may be added to those already made.

In the rapid progress of the sucker through the cortex the starch grains are of minor importance, the object being presumably to penetrate the tissues as soon as possible by the solution of the cell-walls. Starch grains are thus not infrequently found in the yellow mass of substance formed by the outpouring of secretion from the glandular cells and the breaking down of the cell-walls. But this is not all. In not a few cases there appears to be a definite accumulation of starch in this layer when no such substance is to be found in the neighbouring cells. In other cases, there is a dense mass of starch in the woody cylinder exactly opposite the sucker end, while there is none in the rest of the root attacked. This is the case in several sections cut through the roots of *Capparis zeylanica* and *horrida.* Further, in the wings of the host's bark cut off by cork, the cells of which are browned and evidently decomposed, it is not uncommon to find masses of starch grains while the rest of the cortex is almost quite clear of contents (Plate XI, figs. 1 and 1*a*). How are we to explain the presence of such quantities of stored carbohydrate in these places ?

It might be suggested that, while the transverse connection of parts in the attacked roots has been interrupted, a passage of substances might take place lengthwise. But longitudinal sections show that the dead cells of the wing are cut off in this direction by cork as well as across the section. It is, again, possible that the cortical cells were cut off at a time when all the tissues were charged with starch which has been subsequently translocated in the free tissues, but blocked by the cork in those cut off, or, indeed, that this very formation of cork or the formation of thyloses and gum in the vessels has taken up the superfluous starch. But a careful study of the sections does not incline one to this view, and this explanation could hardly be offered for the accumulation of starch in the yellow substance.

It looks very much as if, in these cases, the last act of the protoplasm, before or after the destruction of the cell-wall, was the deposition of starch from the excess of carbohydrates available from the action of the ferment in dissolving the cell-walls. We learn from Peirce's observations on *Cuscuta glomerata* attacking balsam leaves,* that the ferments act first on the cell-wall and last on the protoplasm, and that the mesophyll cells are capable of forming fresh starch for a considerable period after they have been attacked by the sucker cells. It may be noted in passing that this accumulation of starch is only characteristic of attacks on certain plants. Thus in *Morinda tinctoria*, penetrated by *Olax* haustoria, it is almost invariably

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* Peirce, G. J., On the Structure of some Phanerogamic Parasites, Annals of Botany, Vol. VII, 1893.

present in the yellow layer at the sides and ends of the wings. In *Capparis horrida* and *Azima tetracantha*, on the other hand, the wings themselves are almost always gorged with starch grains, even when they are old, browned and collapsed, while the neighbouring tissues are empty (Plate XI, figs. 1 and 1*a*).

If the explanation offered, namely, that the formation of starch in these places is due to the last act of the moribund protoplasm, is insufficient, one is tempted to refer to the reverse action of ferments demonstrated by Cross Hill in concentrated solutions of glucose.* The building up of starch by such reverse action has not been observed at present, but the presence of these masses of starch in the sections is very striking and, until a more satisfactory explanation can be arrived at, this suggestion may be recorded.

The physical effect of the secretion on the starch in the host's tissues appears to be that it swells up considerably and ultimately disappears (*Olax*, Plate VIII, figs. 4 and 5, and *Sant. II*, Plate II, fig. 2). It is interesting to note that starch in the haustorial cells is acted on in a different manner when about to be translocated, the grains in this case becoming minutely subdivided and suffering fragmentation (Plate XI, fig. 1*a*, *x*, and *Olax*, Plate VIII, fig. 3).

COMPARISON OF THE HAUSTORIA OF CANSJERA, OLAX AND SANTALUM.

21. It may be useful to conclude our study of the structure of the haustorium of *Cansjera* with a summary of the points of difference between it and the haustoria already familiar to us, those of *Olax* and *Santalum*. As might be expected from the remarks in paragraph 1, *Cansjera* haustoria are very similar to those of *Santalum:* in fact, to determine the points of difference has necessitated a much more detailed study than was at first contemplated. Many of these points are of

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* Cross Hill's work on reverse action of maltase in excess of glucose is referred to in Green, J. R., Fermentation, 1899, p. 436.

very minor importance, as will be seen directly. The differences from *Olax* haustoria, on the other hand, are so many and great that their mere enumeration would mean a recapitulation of much of this and the preceding paper in this series. In only three particulars has the haustorium of *Cansjera* been found to resemble that of *Olax* rather than that of *Santalum:* the haustorium is whitish and not coloured brown with age, no compound haustoria have been met with and secondary thickening in the wood is greater in the vascular loop than in the axis. In the characters now to be mentioned the haustoria of *Cansjera* differ as much from *Olax* as they do from *Santalum.*

The haustorium of *Cansjera* is smaller and less regular than that of *Santalum,* the early irregularities being apparently due to the abundance of lenticels which are not found in *Santalum.* In extreme age the haustorium frequently becomes fantastically lobed, the attachment to the host's root being small if not minute. The general shape of the haustorium thus becomes broad above and narrow below : the case in *Santalum* is the reverse, some of the oldest and largest haustoria collected being smooth and conical or limpet-shaped.

The development of the young haustorium is very similar to that in both the haustoria thus far considered, but when the nucleus is formed, its cells are sharply separated off from those above, the latter being elongated in a direction at right angles to the axis. When entrance is being effected, the cells of the upper part of the nucleus assume a striking appearance. They become much enlarged, develop dense, granular protoplasm and large nuclei and nucleoli—assume in fact the structure of glandular cells. The gland proper is small and slit-like and there is no duct. It thus would appear that, in *Cansjera,* the whole of the nucleus forms a gland, the so-called "gland" perhaps acting as its lumen and duct. In *Santalum,* the cells of the upper part of the nucleus do not take on any peculiar form and, although sharply marked off from those above, remain small. The gland, on the other hand, is well developed. It is divided into an upper, broader part with distinct lumen and a lower, narrow portion, while the tissues between it and the host's root are traversed by a distinct duct.

Cork is much commoner in *Cansjera* haustoria and lenticels are frequent. A layer of tissue below the epidermis or cork remains smaller celled and has peculiar contents which persist in the form of drops. Such a hypodermal tissue is absent from *Santalum*. Sclerotic pitted cells are found in the cortex. In place of the calcium oxalate crystals found in *Santalum* there are similar crystals of calcium carbonate.

The cortical folds soon cease to grow round the root of the host and become thickened instead. They are thus usually short and thick, and do not envelope much of the host's circumference. In advanced stages the folds are small and functionless. The folds in *Santalum* continue to grow round the root attacked for a considerable time and distance, and there is no secondary growth in thickness. In *Cansjera* a small group of cells in the end of the fold become thick-walled, pitted and lignified: there is nothing of the kind in *Santalum*. The collapsed layers terminate upwards more or less as in *Santalum*, but, downwards, they end at a point half-way between the edge of the fold and the side of the sucker. Taking into consideration the shortness of the folds, the result of this is that the collapsed layers are much more erect and frequently vertical. With secondary thickening they soon become vertical, if not so before, then converge downwards and finally lie almost in one line pointing towards each other. There is a similar movement in *Santalum*, but, even in the extreme case figured in *Sant. I*, Plate IX, the collapsed layers are far from this position. These layers in old *Cansjera* haustoria dwindle into insignificance.

The inner cortex is separated in *Cansjera* into two more or less distinct parts at the time of penetration: an upper and outer where the cells become filled with starch and remain equal-sided, and an inner and lower where the cells are protoplasmic, become elongated and take part in the formation of the sucker. It is probable that something of this kind also takes place in *Santalum*, but at present it has only been noted that a few of the cortical cells near the sucker are dragged in with the penetrating nucleus. In *Olax* a similar subdivision into starchy and protoplasmic cells takes place, but these cells belong to the cortex and nucleus respectively.

An endodermis is very clearly seen in most haustoria. It accompanies the branch of bundles from the mother root and is found round each of its subdivisions in the transitional region, and ceases at the interrupted zone. The latter zone is especially clear in *Cansjera* and is evidently centrifugal in its development.

The activity of the cambium varies in different parts of the haustorium. In the axis it soon ceases to form wood, but for a long time forms layers of cells outwards which may be regarded as secondary cortex. In the vascular loop a great development of xylem takes place, with the result that the vascular strands assume a characteristic and peculiar shape. The older haustoria are chiefly composed of xylem, and it is chiefly due to its development that the form of such old haustoria is turbinate. In *Santalum*, although there is a similar development of secondary cortex, the formation of wood takes place equally in the axis and the loop.

The sucker is narrow in *Cansjera* and little lobed, resembling the cortical folds in this limited growth. An abundance of yellow "gummy" substance is found in different parts of the haustorium from the decomposition of its cells. This extends to the collapsed layers whose decay is seen to be centripetal and sometimes complete. Such decayed tissues are frequently surrounded by meristematic divisions in the neighbouring cells. A brilliant cap of clear yellow substance is found over the end of each of the host's wings. This formation of yellow substance and internal meristems is much rarer in *Santalum*.

BOTANY SCHOOL, CAMBRIDGE;
30th December, 1907.

APPENDIX.

List of Plants attacked by *Cansjera*, whose roots have been examined in the preparation of this paper.

Abrus precatorius.[2]
Acalypha paniculata.
Aerua lanata.
Alangium Lamarckii.[2]
Argyreia speciosa.
Azima tetracantha.
Barleria buxifolia.
Calophanes vagans.
Cansjera Rheedii.[2]
Capparis horrida.
,, zeylanica.[2]
Carissa spinarum.
Celastrus paniculata.
Commelina suffruticosa.
Curculigo orchioides.
Diospyros Chloroxylon.
Grewia hirsuta.
Hardwickia binata.
Helicteres Isora.
Hemidesmus indicus.[3]
Hippocratea obtusifolia.
Ichnocarpus frutescens.
Jasminum auriculatum
Lantana Camara.
Mallotus distans.
Pavetta indica.
Phyllanthus debilis.
Plumbago rosea.
Premna tomentosa.
Pupalia atropurpurea.
Randia malabarica.
Santalum album.
Sida humilis.
Streblus asper.
Strobilanthes consanguineus.
Strychnos Nux-Vomica.
Tamarindus indicus.
Toddalea aculeata.
Vernonia travancorica.
Webera corymbosa.[2]
Zizyphus Oenoplia.
,, Xylopyrus.
And a few others.

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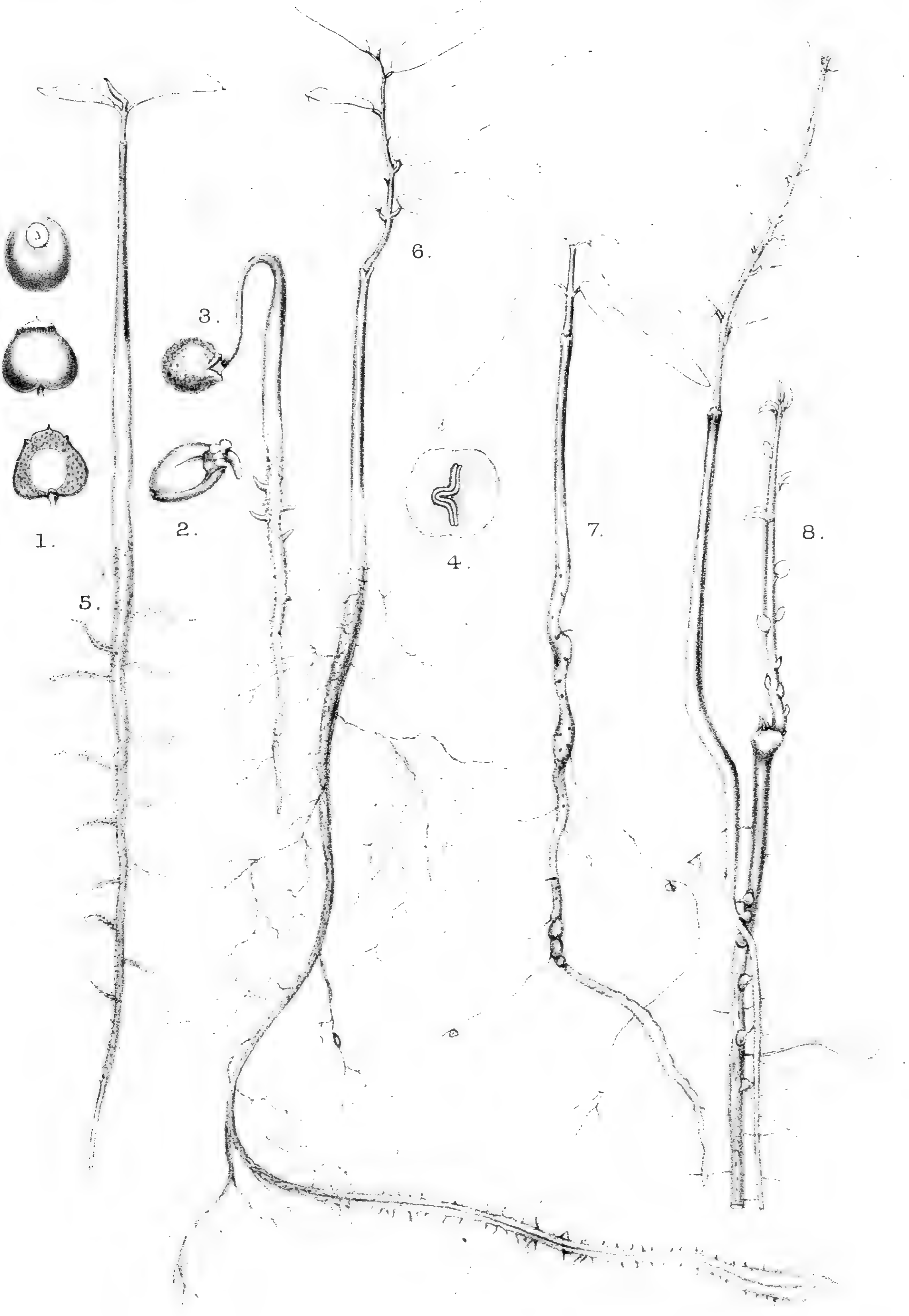
[2], [3] The figures appended signify the number of localities from which the collections were made. The three regions examined were over 500 miles from each other. In each of these *Hemidesmus indicus* and in two of them *Abrus precatorius*, etc., were not only associates but actually hosts.

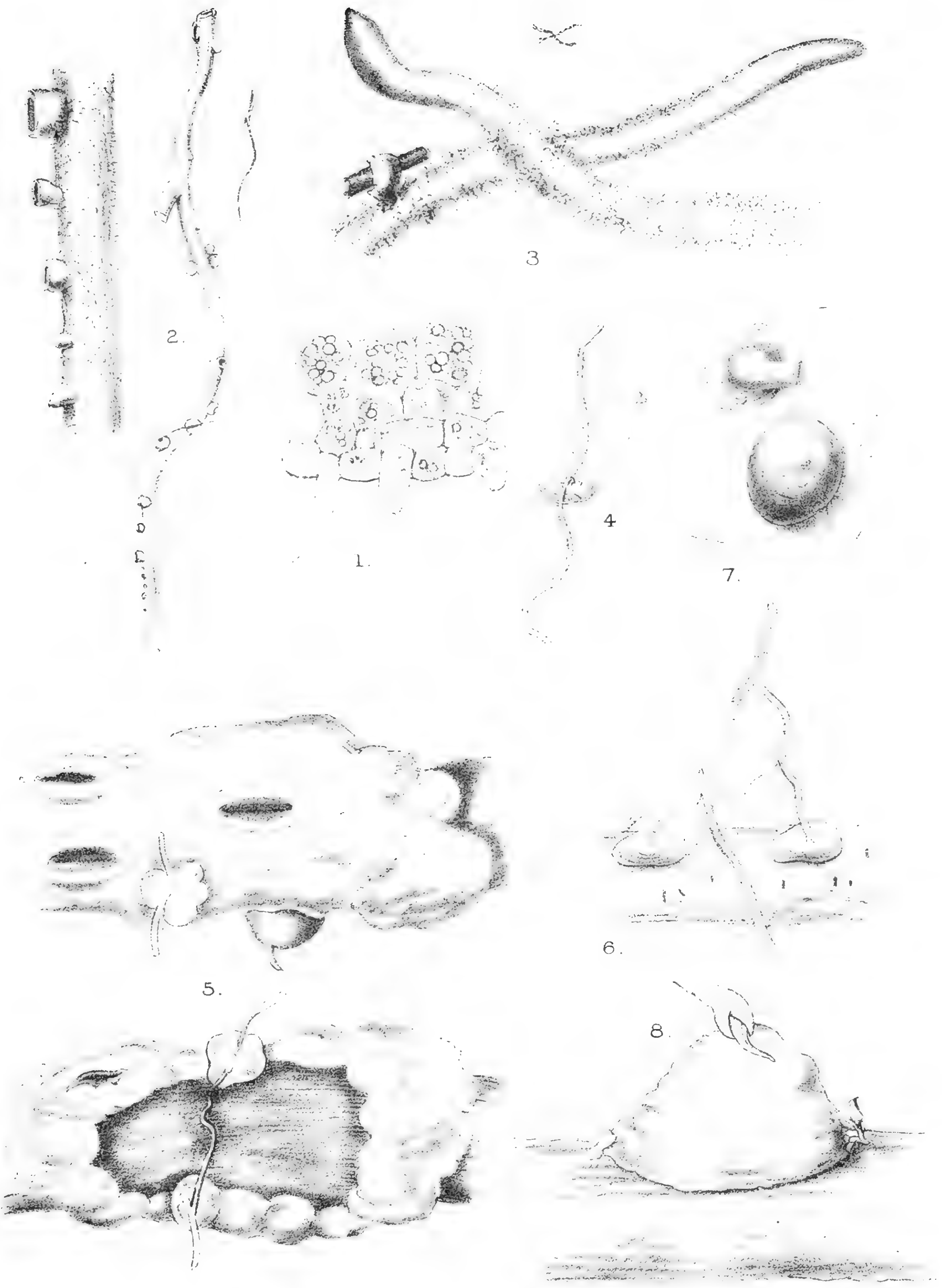
Plate I.



C.A.B. del.

Huth, Lith^r London.

Plate II

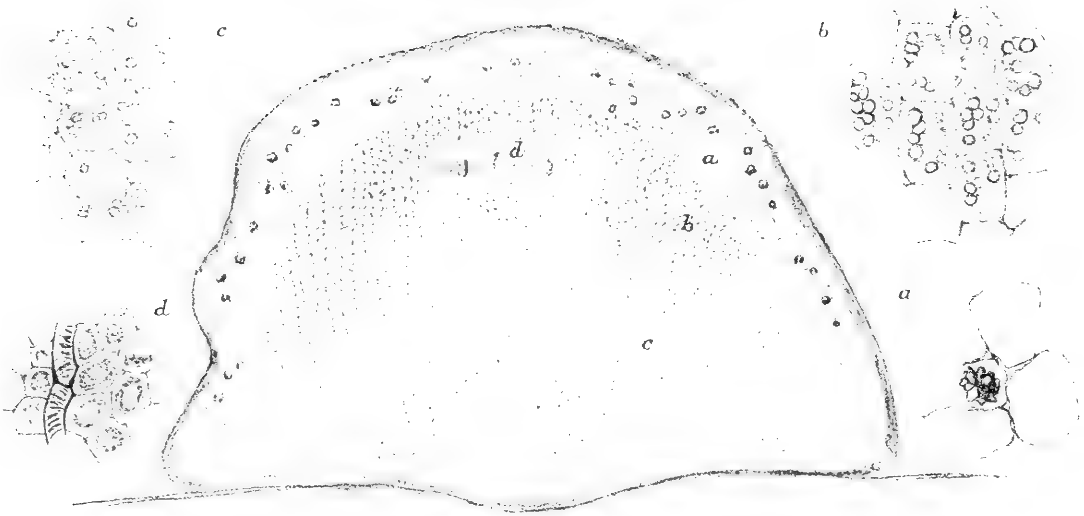


C.A.B. del.

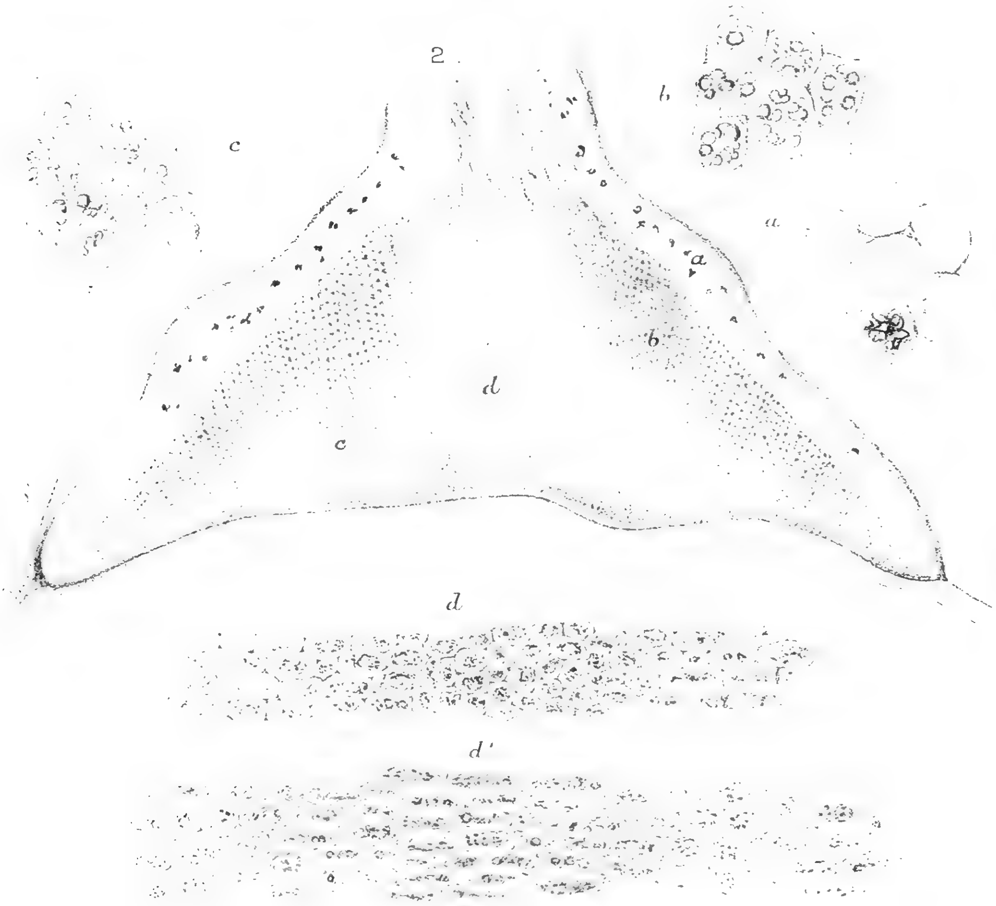
Huth, Lith? London

Plate III.

1



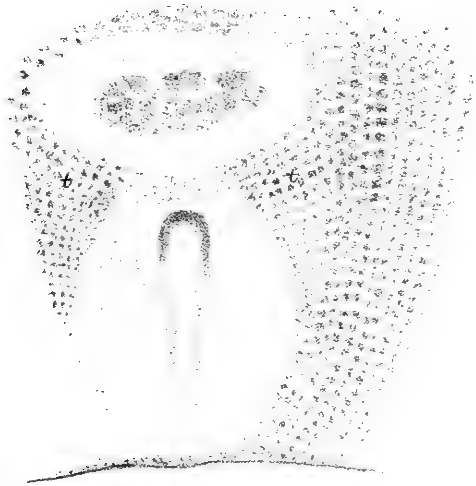
2



C. A. B. del.

Huth Lithʳ London

Plate IV.



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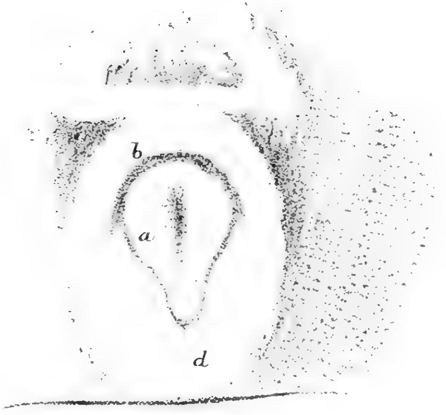

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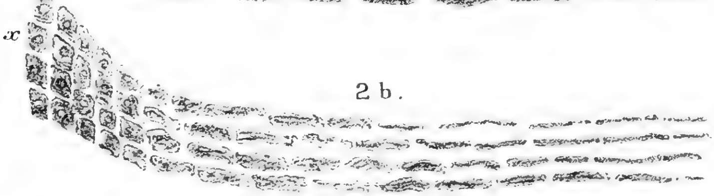

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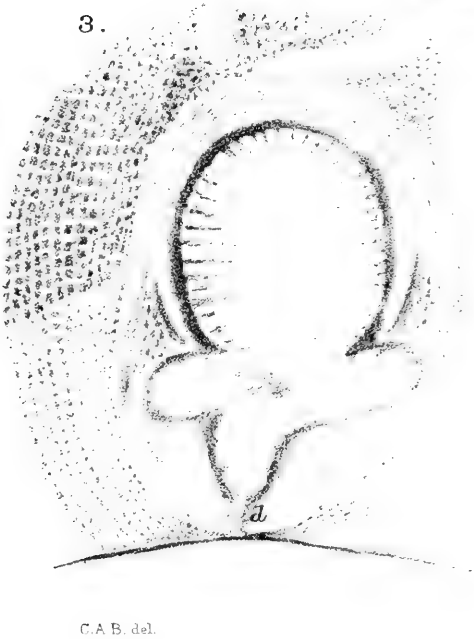

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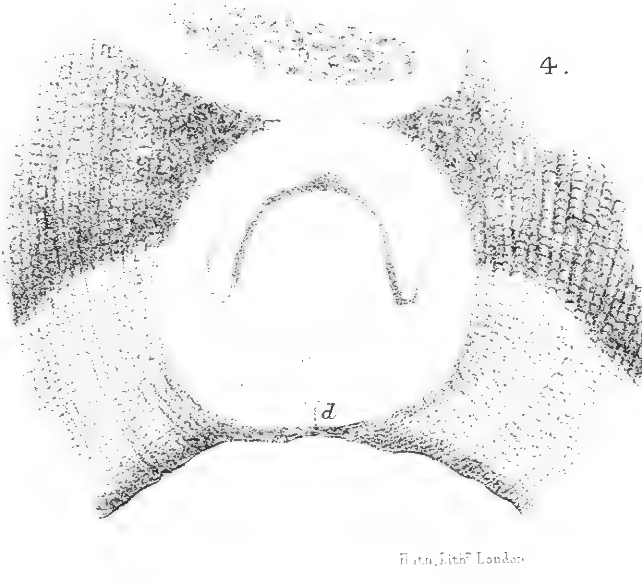

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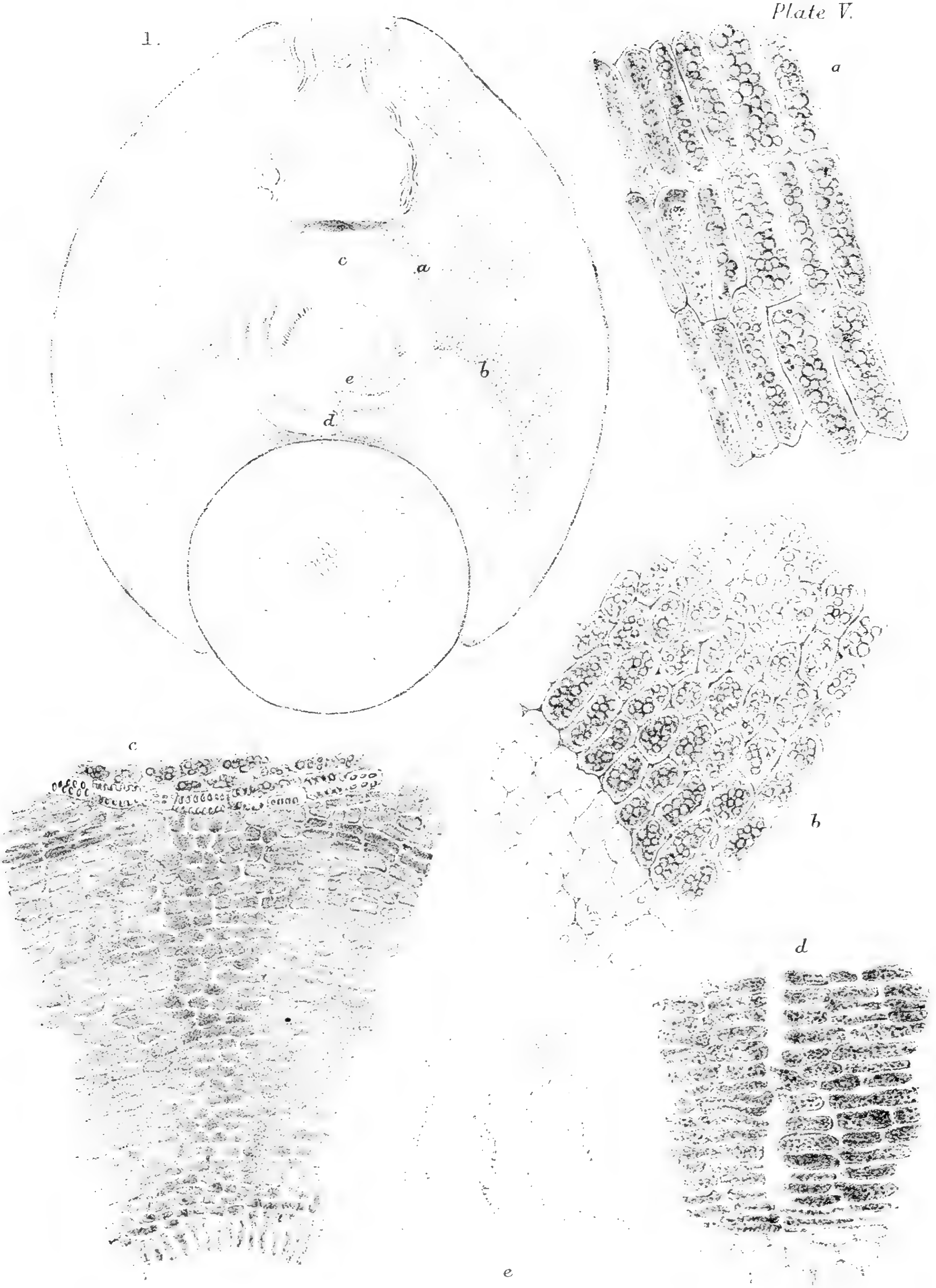
Plate V.



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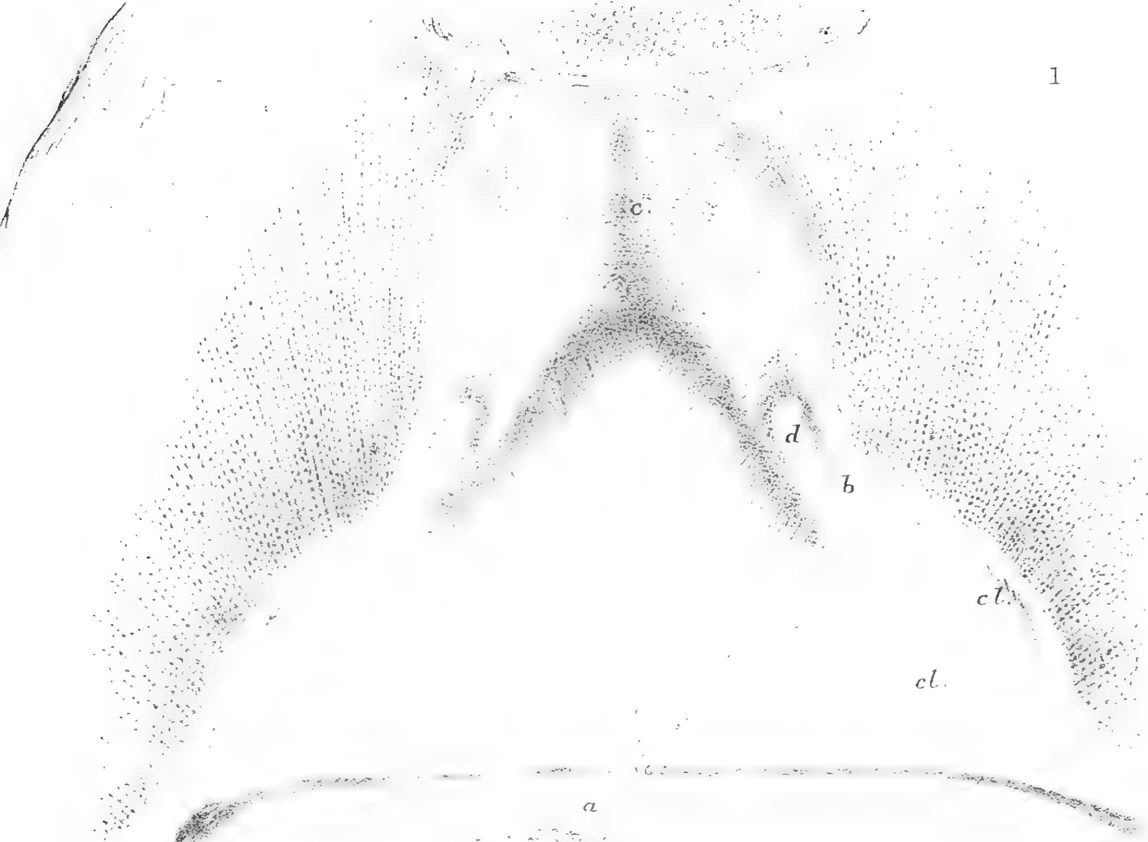

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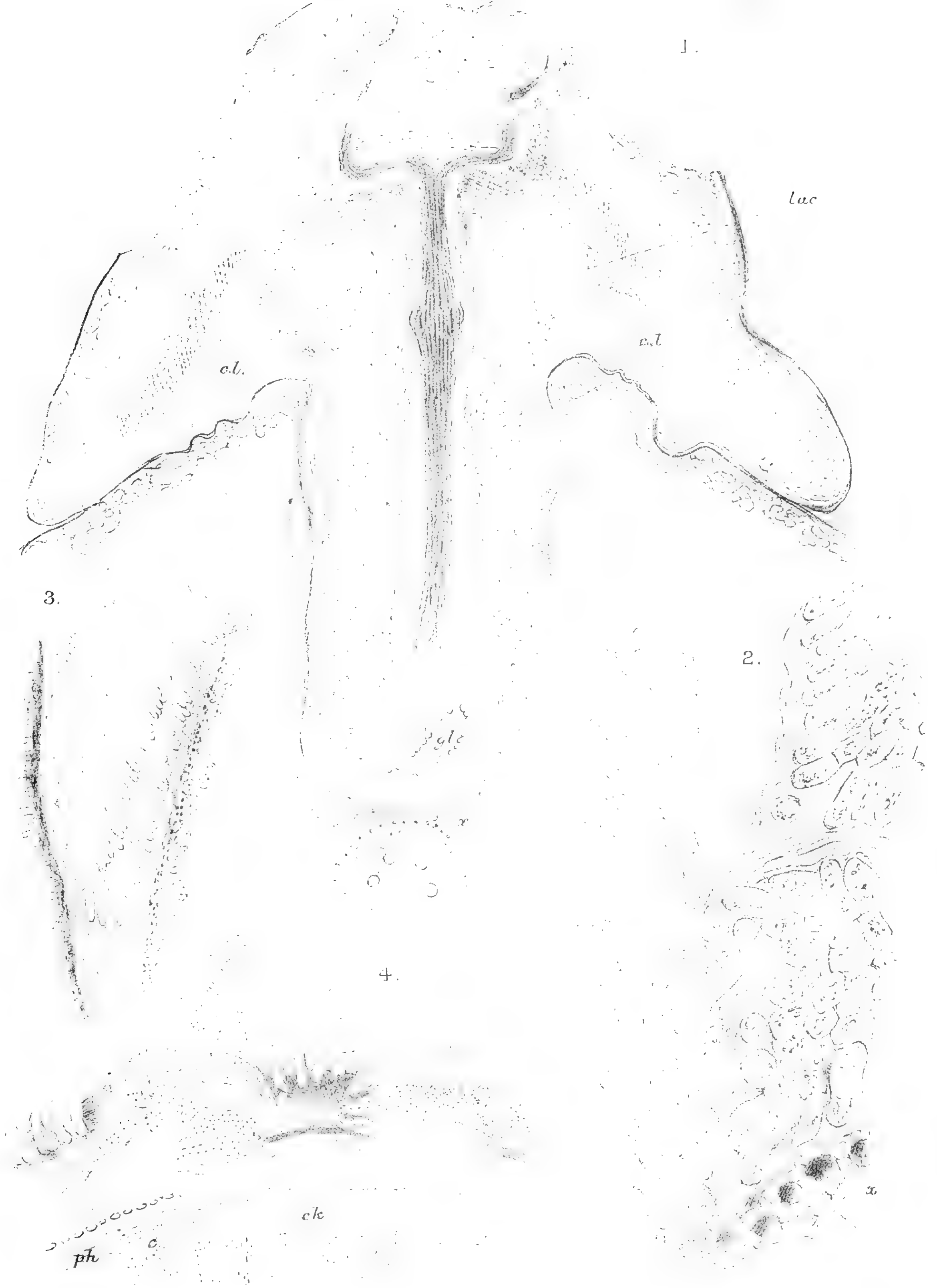
Plate VII.



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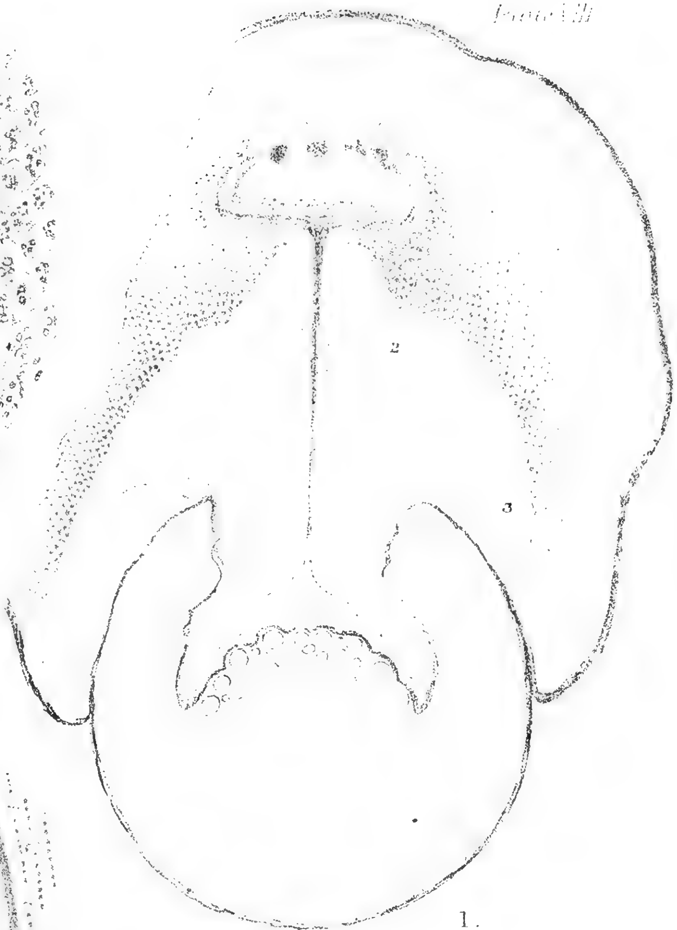

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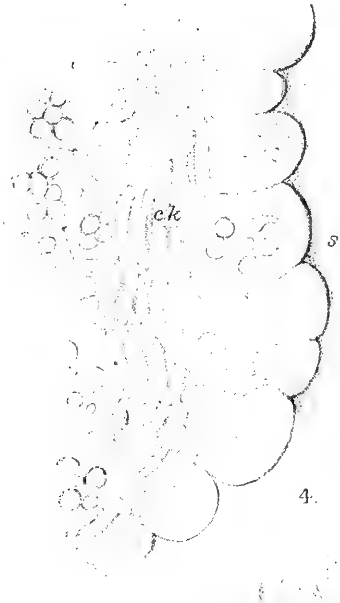

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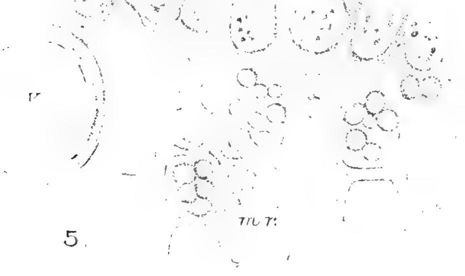

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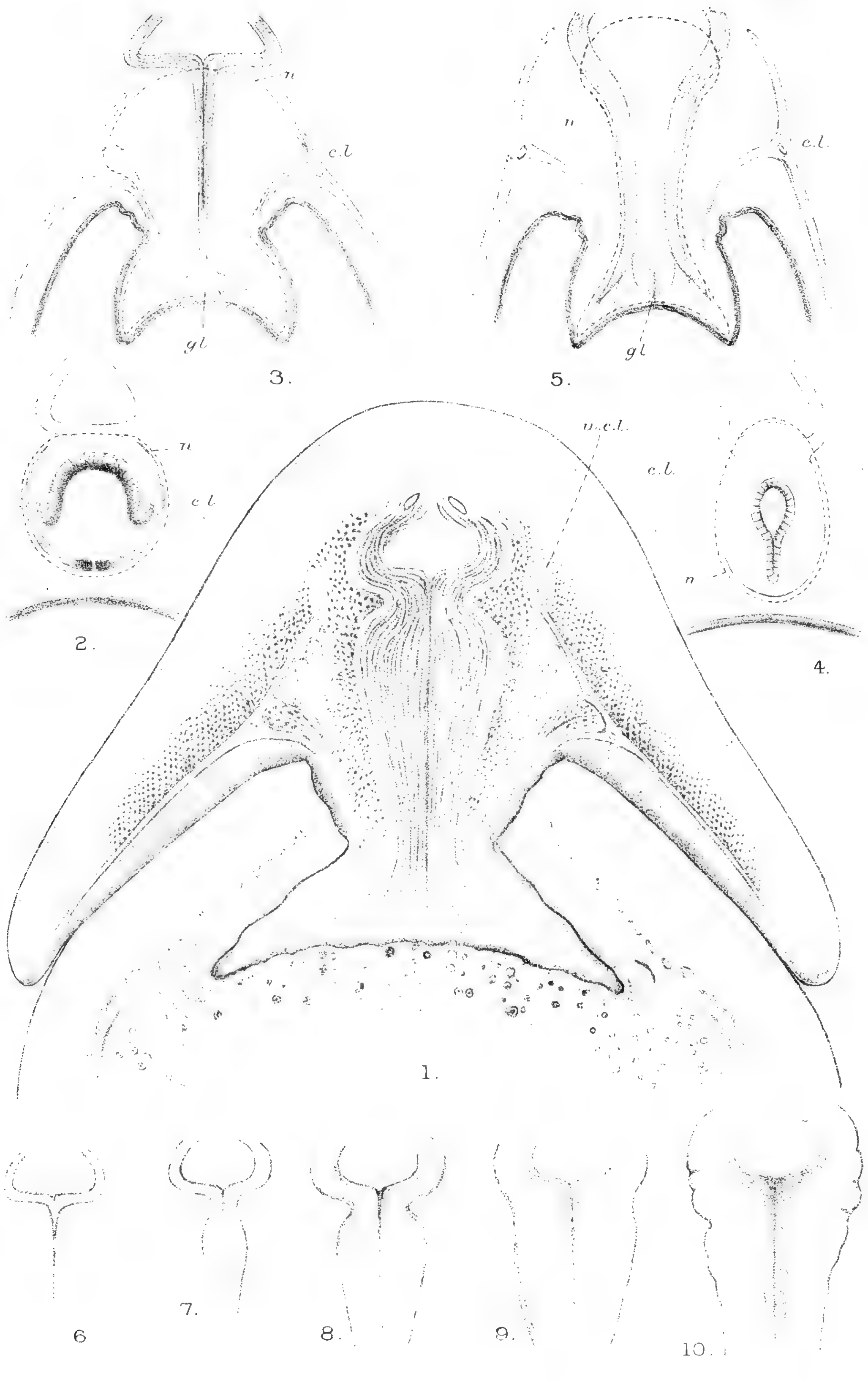

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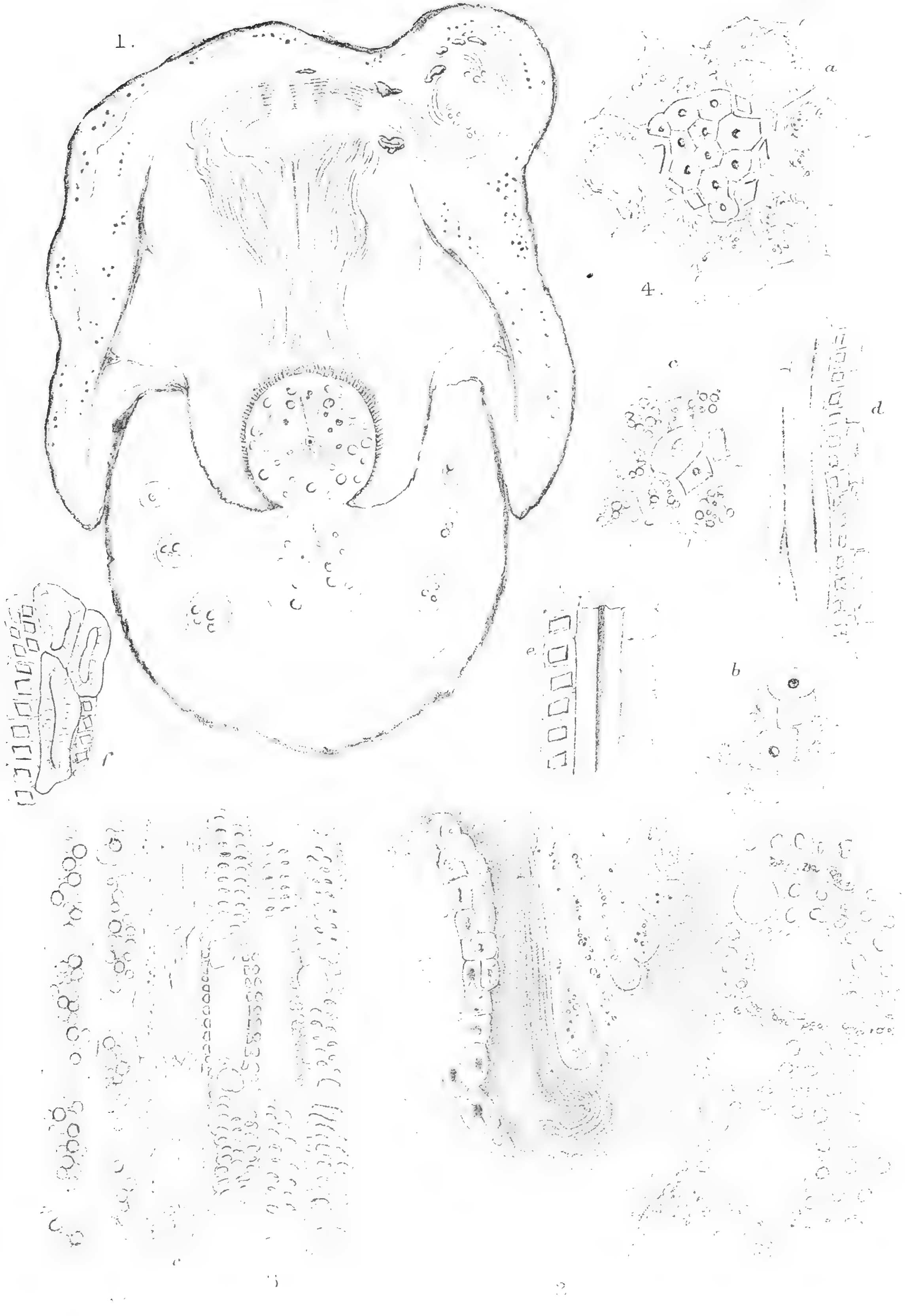
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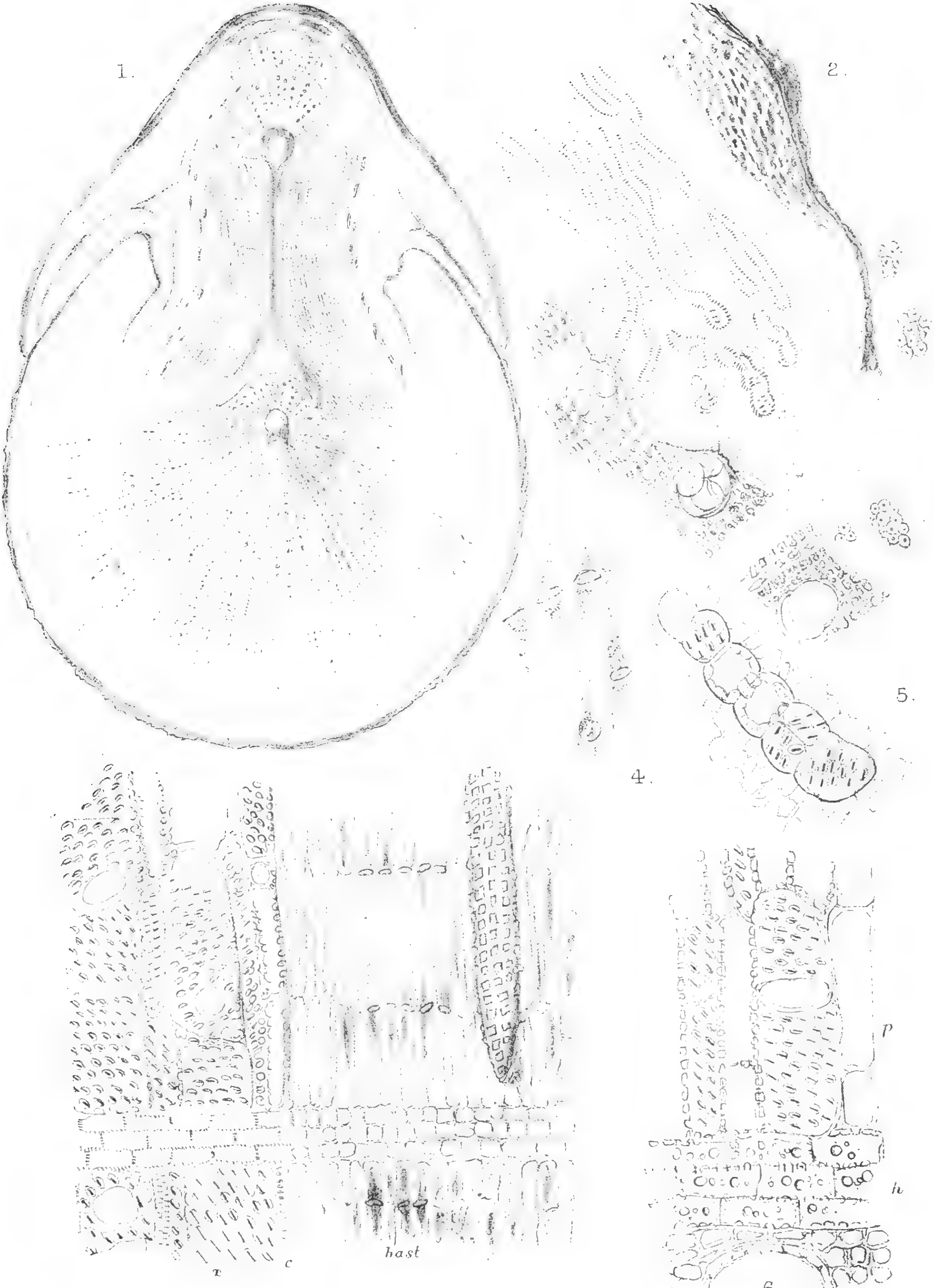
Plate XI.



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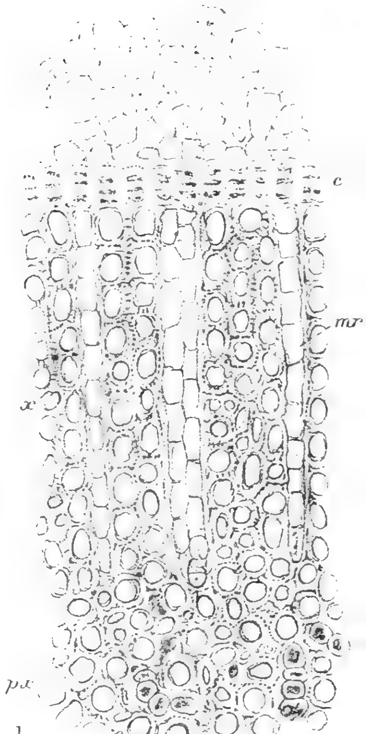

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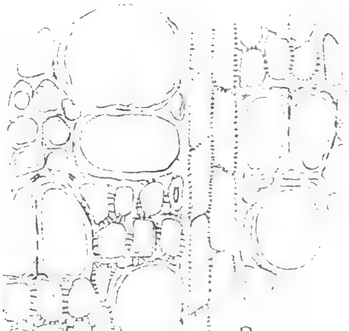

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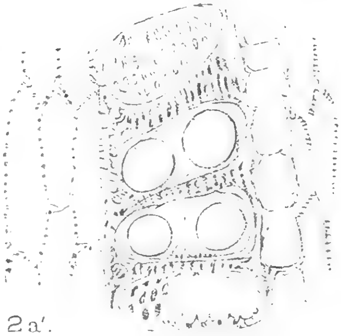

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Memoirs of the Department of Agriculture in India

STUDIES IN ROOT-PARASITISM

IV.—THE HAUSTORIUM OF CANSJERA RHEEDII

BY

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AGRICULTURAL RESEARCH INSTITUTE, PUSA

PUBLISHED FOR
THE IMPERIAL DEPARTMENT OF AGRICULTURE IN INDIA,
BY
THACKER, SPINK & CO., CALCUTTA
W. THACKER & CO., 2, CREED LANE, LONDON

Price, Rs. 2-8

December 1908. BOTANICAL SERIES. Vol. II, No. 6

MEMOIRS OF THE DEPARTMENT OF AGRICULTURE IN INDIA

SOME EXPERIMENTS IN THE HYBRIDISING OF INDIAN COTTONS

BY

P. F. FYSON, B.A., F.L.S

Professor of Botany at the Presidency College, Madras

AGRICULTURAL RESEARCH INSTITUTE, PUSA

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SOME EXPERIMENTS IN THE HYBRIDISING OF INDIAN COTTONS.

By P. F. FYSON, B.A., F.L.S.,

Professor of Botany at the Presidency College, Madras.

Experiments in crossing different varieties of cotton plants have often been made with the idea of uniting into one, the good qualities of two or more strains. Some reference to these may be found in Sir George Watt's book, "The wild and cultivated cotton plants of the world." The first experiments of which records have been made, were, he says,* perhaps those by Rohr, who more than a hundred years ago crossed some American fuzzy and clean seeded species, but did not apparently experiment with Indian cottons. In 1884, however, Dr. Alexander Burns of Broach crossed *Gossypium obtusifolium* var. *wightiana* [Guzerat cotton] with the red flowered *G. arboreum*, and obtained a plant having the good qualities of both parents. "The leaves were those of Arboreum, ...the flowers were red with a yellow throat" and the plant cropped early and produced a very silky floss. But nothing seems to be known about the subsequent history of this cross and the plant apparently died out. Major Trevor Clarke was, in the sixties, experimenting with Indian varieties, but I have been not able to find any record of his results.† In 1903, Professor Gammie,‡ of Poona, published a tentative classification of Indian cottons, and with this some account of crosses that he had made of Indian cottons, *inter se*

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* Watt, Sir George, (1) "The wild and cultivated cotton plants of the world" 1907, p. 333 *et seq.*

† *Ibid*, p. 336.

‡ Gammie, G. A., (2) "Classification of the Indian cottons (tentative)" 1903, p. 15.

and also with the naturalised American "Dharwar" (*G. hirsutum*). His success in crossing the latter species with *Varadi*, with *Kumpta* and with *Nagpur* or *Kil*, varieties which belong to the great group of African-Asiatic species (Watt's section II of the genus *Gossypium*) proves that such hybrids are possible,* but they are difficult to obtain, and appear to be very unfertile, for he says of all that he obtained only one survived.† In his account too of the crosses made between Indian varieties themselves, he says nothing of the second and succeeding hybrid generations. Mr. F. Fletcher, in a Bulletin on Bombay cottons,‡ gave details of some crosses that had been made, but these like those of Prof. Gammie were with reference to the lint alone, and were not on Mendelian lines. The same worker had a note, later on, in the "*Journal of Agricultural Science*"§ on "Mendelian inheritance in cottons," in which he stated that dominance was shown in several characters, among others by the fineness, length and colour of the lint, (which I have also observed in another cross) by the yellow colour of the petals (over white) and by fuzziness of the seed over nakedness. But his figures were for the first and second generations only. That this would hold for later generations and that therefore Mendel's law was applicable was not shown. Mr. Lawrence Balls, who has been working on Egyptian cottons, has also published papers on the subject.‖ ¶ ** He believes that cross-fertilisation by insects occurs to a very considerable extent in the field, and in this he is in agreement

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* Natural hybrids are occasionally found where "Indian" and American varieties are grown together. Sir George Watt considers *jowari* "to have arisen from such a natural cross. Watt, *ibid.*, pp. 338, 339.

† Gammie, G. A. (3) "The Indian Cottons," 1905.

‡ Fletcher, F. (4) Bulletin No. 26 of the Bombay Agricultural Department, 1907.

§ Fletcher, F. (5) "Mendelian Inheritance in Cottons," Journal of Agricultural Science, Vol. II, Dec. 1907, p. 281.

‖ Balls, W. Lawrence. (6) "Note on Mendelian Heredity in Cottons," *ibid.*, p. 216.

¶ (Idem). (7) "Studies of Egyptian Cotton," Year Book of the Khedival Agricultural Society, 1906.

** (Idem). (8) "Mendelian Studies of Egyptian Cotton," Journal of Agricultural Science, Vol. II, p. 347 *et seq.* (July 1908).

with Leake,* myself, and others, in regard to an entirely different set of plants, the Indian cottons. I became acquainted with his work, as also with Fletcher's and Leake's, only after the manuscript of this paper had been written, but I have referred in foot-notes to his and their results where they touch on mine. Mr. Leake published* after this was written, a note on the variation and inheritance of certain characters in cotton plants. He determined by measurement the factor $\frac{\text{length}}{\text{breadth}}$ of the lobes of a leaf, in a number of cases, and found that when a *G. indicum* having rather narrow lobes, was crossed with a *G. arboreum* with broader lobes, the hybrid was of an intermediate type. The next generation, he says, "contained, among others, plants with typical "broad"—and typical "narrow"—"lobed leaves," but he gives no statistics to show the numerical distribution of the different types, nor, as far as I know, has any full statistical account been published of experiments with cottons on Mendelian lines.

The experiments described in this paper, of which a preliminary account was sent to the "Director of Agriculture," Madras, in 1906, were begun in the autumn of 1904, soon after my arrival in India, with a view to determining whether the results of crossing Indian varieties of cotton plants, could be described by any "law," which would guide one in attempting to breed new and improved races, and whether any unit characters exist or can be found which can be passed on undiluted from one variety to another. My observations go to show that such unit characters do exist in both vegetative and floral organs. I have followed the behaviour of three such pairs, the rounded herbaceum or pointed neglectum, shape of leaf, the white or yellow colour of the flower, and the white fuzzy or black naked seed, for five generations, and from observations of some hundreds of plants (817 in the 4th generation, 1177 in the 5th) conclude that the characters studied do really segregate on Mendelian lines. Balls (18) and Fletcher†(4)

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* Leake (9) "Studies in the Experimental Breeding of Indian Cottons," Journal of the Asiatic Society of Bengal. New Series, Vol. IV, 1908, No. 1.

† Fletcher, F. (4) Bulletin No. 26 of the Bombay Agricultural Department, 1907.

have anticipated me in the publishing of similar conclusions, with other varieties of Egyptian and Indian cottons, but these are based, as far as the published results show, on two generations only and on a much smaller number of plants.

The practical outcome of these observations appears to be that the cross-breeding of these varieties could be carried on with almost mathematical precision, and if, as seems likely, these principles apply to other characters as well, one might expect to obtain any desired type in a very few years.

As I could obtain no information as to what crosses would succeed, or would be likely to give useful or interesting results, I started with a few different kinds, the seed of which, from the Government farms at Bellary and elsewhere, was kindly given me by Mr. Charles Benson, at that time Deputy Director of Agriculture, Madras. They consisted of a red-flowered tree-cotton named *Karehathi*, *Jari* and *Bani* of the Central Provinces, *Jowari* (fuzzy and naked seeded) *Northerns Bilaihathi* and *Yerrapathi* of this Presidency. In addition, there were two races of American upland cottons, a naturalised "Kidney" tree-cotton, and another tree-cotton, related apparently to *G. peruvianum*. Hybrids were readily obtained by crossing these exotics *inter se*. From one of the American uplands (W. H. Cooke) and the tree-cotton (*G. peruvianum* were obtained a number of bushy plants very like some I saw grown from seed supplied by Messrs. Shaw, Wallace & Co. of Calcutta, as a new variety. The lint was long and silky and the plants were intermediate in size between the two parents, those from seed of bolls on the tree being slightly larger than those by the reverse cross but otherwise very similar.

As my concern was with the indigenous races, these and the other exotic hybrids were allowed to die out, but in the twenty plants of which I have notes, the red colour of the leaf stalks, and the pink spot at the base of the leaf-blade,*—characters belonging to the herbaceous parent, and the pink spot at the base of the

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* Cf. also Balls (8).

petals, and the naked surface of the seed of the tree-cotton were dominant characters. This is so far interesting as the red colour of the leaf-stalks and the nakedness of the seed, were dominant also in totally different crosses between two Indian races.

The seeds were all sown in my garden in September 1904, and the Indian varieties came into flower two months later. The local races—*Northerns Bilaihathi Jowari* and *Yerrapathi*—had been grown for some years on the Government farm at Bellary, and might be considered pure. The ten or twelve plants in each bed appeared to be very similar. But among the *Jari* and the *Bani*, from the Central Provinces, were two plants having large yellow instead of small white flowers. Attempts to cross the two kinds of *Bani*—the yellow and the white flowered—were not successful, but the yellow flowered *Jari* was crossed with other plants. (Table II, No. 4.)

I found it necessary to remove the anthers early in the morning as soon as it was light (and even before daybreak in the case of the "Americans") as they mature and shed their pollen very early. Sir George Watt quotes* Major Trevor Clarke's advice to apply the pollen overnight, "*i.e.*, just before the flower has expanded or has been attacked by pollen-bearing insects." This advice would apply more to the American varieties than to those I was dealing with. I tried removing the anthers overnight, covering the styles, and pollinating them the next day, but gave this plan up, as it was difficult to know which flowers would open the next morning, and none of my crosses so made were successful. I am inclined, however, to think that evening is the best time for removing the anthers, as in the morning they are so nearly ripe, that they are liable to burst and shed the pollen while being removed, and I had to give up a large number of flowers on that account. All who have worked at cross-pollination of flowers, are, I believe, convinced of the extreme sensitiveness of the stigma,—Charles Darwin often insisted on this—and it

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* Watt. (1) *Ibid*, p. 338.

was found almost impossible to remove grains from the stigma without injuring its receptiveness.

To emasculate a flower, the bracteoles and petals were first removed before the latter had opened, and the anthers cut off with a pair of fine pointed scissors, beginning from above and working downwards, so as to prevent them touching the stigma. It was then pollinated from some other plant and covered with a small paper bag, about 3 inches long and one inch wide, and a small label was attached to the flower-stalk, with the registered number. If not pollinated immediately it was covered and labelled and crossed later on in the day with pollen from a previously covered flower, and again covered with the paper bag. The number of the cross and of the parents were entered both on the label and in a book. My first pollinations were made in the mornings, but as the pollen did not then adhere well, I often left them till the afternoon.

The weather appears to exert a decided influence on the germination or fertility of the pollen grains. In the following table are given the numbers of cross-pollinations made, and of ripe bolls obtained from them, together with the average percentage of cloud in the sky, as determined at the Madras Observatory for the periods stated :—

TABLE 1.

Periods........ days ending.			Number of pollinated styles.	Number of bolls.	%	Average cloud.
5 days to	Nov.	9	17	2	12	40
Do.	do.	14	34	5	14·7	53
Do.	do.	22	—	—	—	30
———	do.	23 & 24	35	12	34	09
5 days to	do.	29	77	21	27·2	29
Do.	Dec.	4	20	3	15	72
Do.	do.	9	6	1	16·6	49
Do.	do.	14	22	6	27·3	37
Do.	do.	*19	15	1	6·5	53*
Do.	do.	24	—	—	—	—
Do.	do.	29	8	1	12·5	40

That fine bright days are the best for setting of flowers, is, I believe, the experience of gardeners, and these figures amply

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* Rain fell on the 18th to 21st.

bear this out. The highest % (34) of successful pollinations being when the average cloud was least (·09) and *pari passu* the more cloud the fewer fertilised bolls. Mr. Charles Benson told me that rain or even heavy dew would often cause half ripened bolls to drop, and a good many were lost, probably from this cause.

I collected the hybrid seeds myself, and after picking off the floss sowed them in pots from which the young plants were put out into beds, in February 1905. The uniformity of the crosses between *Jari* and the local "*herbaceums*" was very striking. They were all alike in having the red stems and petioles and narrow-lobed leaves of *Jari*, but had the full yellow flowers of *Jowari*, *Northerns* and *Bilai*. One lot, No. 3 in tables II and V and i. in table X came into boll in April, and by sowing seed at once, I obtained a second generation crop before the November rains. This was sown along with seed from the others on land hired near Madras, when I had, therefore, one lot a generation ahead of the others.

The plants of the first generation, with the exception of the lot just referred to (fig. 15) were all larger and more vigorous than their parents. This increased vigour was continued in the 2nd, 3rd and 4th generations, and was very marked. Those of each bed—*i.e.*, from each hybridised boll—were, as far as I could see, very much alike. In the 2nd generation, however, the utmost diversity appeared among the descendants of the *Jari* and "*herbaceum*" and *Bani* and "*herbaceum*" crosses. Some grew tall and straight, branching stiffly at right angles (fig. 16), others were low with spreading branches (fig. 17). Some had broad lobed leaves of the "*herbaceum*" or "*obtusifolium*" type, others had the long narrow pointed lobes of *Jari*. While, moreover, all in the first generation had yellow flowers, a considerable number of the 2nd generation from a white and yellow flower cross had pure white flowers. Some had short rounded bolls like those of the original *Jowari*, in others the bolls were long and pointed. Again, the short coarse nature of the lint (floss) of the *Jari* and *Bani* parents was absent in the first generation, but appeared in the second. And Mr. C. Benson drew my attention to the similarity exhibited by some plants in one lot—from a cross between Bani and *Jowari*—to "American uplands," the broad flat leaves and spreading branches reminding one of that type.

The cotton plant appears to attract a large number of insects. Large red striped beetles bit through at the base of the flowers and destroyed the style. The latter too was often damaged in the bud by caterpillars. Boll-worms destroyed the seed, but the greatest damage was, I think, done by the "scarlet cotton-bug," and the small "dusky cotton-bug," which attacked the seed as soon as a boll opened, and were never got under, though a small boy was employed to go round and shake them off into a tin of paraffin. Any seeds that were left on the bushes were quickly eaten by ground vermin. They had, therefore, to be collected almost daily, and the picking from so many separate plants was very tedious. There was the further disadvantage that the field being some way out of the town, work there was necessarily intermittent, and the flowers and seeds of some plants were on that account never seen. The next year I was given by the authorities the use of land on a Government experimental farm, where my plants were well looked after by the manager, who also, while I was unavoidably absent from the country, made many of the notes on which I base the figures of the fourth generation.

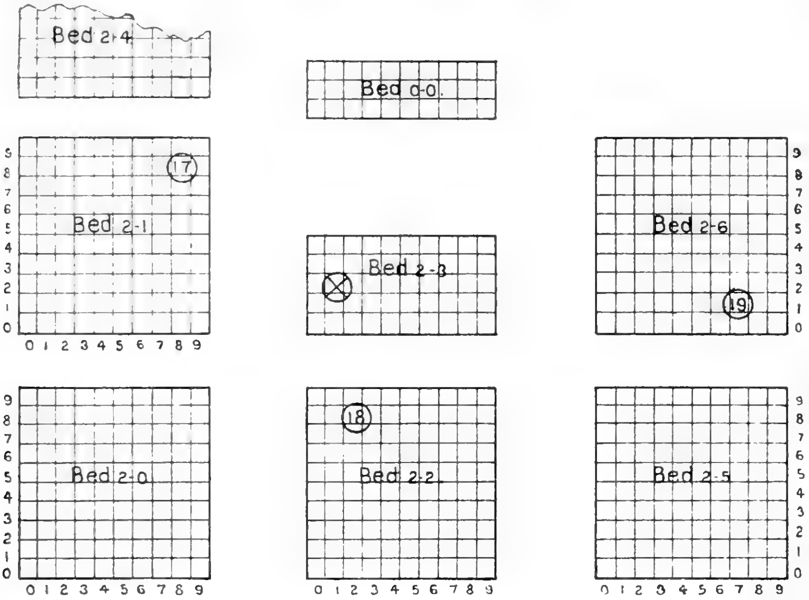
But most of the seeds sown there failed to germinate. Cotton seed is known to keep badly during the hot weather if ginned, as mine were. Or it may be that in the damp atmosphere of Madras these seeds were never properly dried, and so were particularly susceptible to heat. The local Horticultural Society has always found that imported garden seed, especially those of an oily nature, rapidly deteriorate in germinating power. In my case over 8,000 seeds from selected plants of F. 2 were sown, but those that did come up were all washed out of the light sandy soil by a heavy fall of rain which occurred soon afterwards. The whole of these on which I was relying for my third generation were therefore wiped out, and I have to fall back on the 240 plants from F. 1, No. 3, referred to above as grown the previous season near Madras. This was the more unfortunate, as the characters of the parent plants had been very carefully noted, and as these were still growing it was hoped to compare the new generation with them, while less attention had been paid to these other few plants.

I had not made a point of collecting seed from the other lot. but sufficient had been taken from a few of the plants, for the fourth hybrid generation, and on another part of the farm enough were grown to indicate the distribution of the characters (tables IV, IX and XII).

ON THE ARRANGEMENT OF THE PLANTS.

The original plants and the first hybrid generation were set out in numbered beds and named by letters of the Greek alphabet. But as the number of plants which could be so named in any bed was thus limited, by the number of letters available, and the naming was somewhat cumbersome, I adopted for the second and subsequent generations another system, which I will shortly describe, as it is so well suited for work of this kind, and I have not seen anything similar referred to in accounts of breeding experiments.

The plants were arranged in rows, about two feet apart or more. In each row were 10 plants, and 10 rows constituted a rectangular bed. The rows were numbered 0 to 9, and the plants in each row, from left to right, also 0 to 9. No labels were affixed, except here and there, if experience showed on account of overcrowding or irregular growth, a plant might be wrongly numbered. Each plant in fact has a number depending only on its position in the bed, thus the 4th plant of the 6th row would be No. 53 of that bed. The first plant of the bed is 00. The last 99. The beds of any one lot were also numbered, and by using also the registered number of the whole lot of seeds, the position and origin of any plant was defined and could be easily and shortly written down. Thus fig. 16 is from the photograph of a plant No. 2321, *i.e.*, the second plant of the 3rd row in the 4th bed of lot 2, the position of which is shown in the plan (X). Fig. 17 is of No. 2188, the 9th plant of the 9th row of the 2nd bed of the same lot. These are from photographs taken in the field. Fig. 18 is of a dried piece from No. 2282, fig. 19 of No. 2617.



Copy of part of the plan of the field to show method of numbering the plants for their identification by their position.

Bed 2—0.

9	Y	P	Y	W	Y	Y	W	Y	W	Y
8	Y	P	Y	P	Y	W	W	P	W	P
7		W	Y	Y	Y	Y	W	Y	Y	Y
6	W	W	Y	Y	Y	Y	W	W	Y	Y
5	W	P	Y	P	W	P	P	W	Y	Y
4	W	P	W	W	W	Y	P	W	W	Y
3	W	P	Y	Y	Y	W	P	Y	W	P
2	Y	Y	W	W	P	Y	Y	Y	W	W
1	Y	Y		W	W	W	Y	W	P	Y
0	Y	W	Y	Y	Y	Y	Y	W	Y	W
	0	1	2	3	4	5	6	7	8	

Yellow flowers	... ...	47
Pale ,,	... ...	17
White ,,	... ...	34
Plants died	... ...	2

The taking of notes of the plants was also very much simplified by this system. A square ruled to 100 small squares represented a bed, each small square representing a plant. It is only necessary to write in the square some letter or symbol denoting the nature of the character noted. Thus the colours of the flowers in the bed marked 2-0 in the plan were noted as in the accompanying note-book plan of the bed.

THE LEAF.

Crosses were made between all the Indian races named above, but the two species which differed most in the shape of the leaf were *Jari* (*G. arboreum* Linn. var. *neglectum* of Watt; *G. neglectum* Tod. of Gammie) and *G. obtusifolium* Roxb. (of Watt) or *G. herbaceum* Linn. (of Gammie) represented in my beds by *Northerns*, by fuzzy seeded (white) *Jowari*, by naked seeded (black) *Jowari* and by *Bilaihathi*. Figures 1, 2, 3, 4, show the characteristic shape of their leaves.

The following table gives the number of bolls and of plants obtained.

Table II.

Fig.	Seed plant.	Pollen plant.	Bolls.	Plants.	Leaves like.
1	Jowari fuzzy ...	Jari white flower ...	2	19	......
2	Jari white flower ...	Jowari fuzzy ...	1	11	Fig. 5
3	Jowari naked ...	Jari white flower ...	1	16	,, 6 & 7
4	Bilaihathi ...	,, yellow flower ...	2	16	,, 17
5	Northerns ...	,, white flower ...	4	58	,, 8
6	Jari white flower ...	Northerns	1	11	,, 9
		Total ...	11	131	

All these 131 plants were without exception like *Jari* in the shape of the leaf.* Figures 5 to 9 were drawn to scale from

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* It might appear that my observations are here at variance with those of Leake who (9 p. 15) says the hybrids he obtained were intermediate between the parents. But his crosses were between *G. arboreum* and *G. indicum*, while mine were between *G. neglectum* and *G. herbaceum*, species which are probably less closely connected. The cases are, therefore, not analogous, nor the observations necessarily contradictory.

representative leaves. The uniformity of the plants of a bed was most striking: this was particularly the case with lot No. 3, which were all small plants and sparingly branched like their *Jari* parent, with large bright yellow flowers like *Jowari* (fig. 15).

Seed was collected from these beds during the months April to August, and from lot No. 3, which were the earliest, some were sown in April. It is from this lot that the plants of the 3rd and 4th generations of this cross were raised. The others were sown in September in small seed-beds and planted out in rows and beds as explained above.

It was at once seen that the *herbaceum* (of Gammie) type of leaf, of which there was no sign in the first generation, (fig. 15) had reappeared in its original form in a large number of plants of the next.

Of those of No. 3, out of 620 plants 370 had leaves like *Jari*, 128 like *Jowari*, 121 more or less intermediate. That is to say 21% had the character which was not present in the first hybrid generation.

From No. 4, of 102 plants 54 were like *Jari* and 22 like the *herbaceum*, a percentage of 21·6. Of lot No. 5 however a larger proportion were classed as intermediate—of 163 plants 114 were like *Jari*, 33 intermediate, and 16 *herbaceums*. I refer only to the general form of the leaf. *Jari* and *Jowari* leaves differ also in texture and surface, but it was difficult in the short time available to discriminate these characters. Some classed above as like *Jari* had for instance even narrower lobes, and had the soft feel and surface of *Jowari*. In a few the margins of the leaves were waved, a strikingly exaggerated instance of this being shown in fig. 10.

Table III shows the behaviour of the plants from *neglectum* (*Jari*-like), and of the *herbaceum* or *Jowari*-like plants in the next generation.

TABLE III.

The third hybrid generation.

No.	PARENTS' LEAF.	Negl.	Herb.	TOTAL.	
				N	H.
1	neglectum	7	...	...	...
2	do.	10	...	...	...
3	do.	6	...	...	...
4	do.	6	...	...	...
5	do.	20	...	49	0
6	do.	17	5	...	...
7	do.	6	3	...	...
8	do.	12	5	...	...
9	do.	23	5	58	18
10	do.	?	?	...	...
11	do.	?	?	...	...
12	do.	?	?	...	...
13	herbaceum	...	30	...	...
14	do.	...	26	...	...
15	do.	1	20	...	...
16	do.	...	8	1	84

Nos. 1 to 5 appear to have been, as regards the shape of the leaf, pure *neglectums*; my impression is that the progeny of Nos. 10—12 were also all *neglectums*, but as it was not intended to deduce the distribution of characters from this lot,* no notes were made of their leaves. They are introduced here as notes were made of their flowers and seed.

The other '*neglectum*-leafed' parents (Nos. 6 to 9) gave out of 76 plants, noted, 18 *herbaceums*, which is almost exactly the Mendelian expectation ($\frac{1}{4}$ of $76 = 19$). Nos. 13 to 16 bred practically true to the *herbaceum* character, there being only one stray *neglectum* among 85 plants.

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* See page 8.

TABLE IV.

The fourth hybrid generation.

No.	Parent.			Negl.	Herb.	Negl.	Herb.
1	neglectum ...	...	...	13	...	...	...
2	do. ...	...	...	138	...	...	...
3	do. ...	...	...	6	...	157	0
4	do. ...	...	...	37	3	...	...
5	do. ...	...	...	67	7	...	...
6	do. ...	...	...	15	5	...	...
7	do. ...	...	...	7	6	...	...
8	do. ...	...	...	36	10	...	...
9	do. ...	...	...	94	16	...	...
10	do. ...	...	...	60	67	...	...
11	do. ...	...	...	12	7	328	121
12	do. ...	...	...	1	9*	...	...
13	do. ...	...	...	4	2	...	...
14	do. ...	...	..	8	19	...	...
15	intermediate or	herbaceum	...	5	40	...	...
16	do.	do.	...	4	20	...	...
17	do.	do.	...	3	20	...	...
18	do.	do.	...	1	53	...	...
19	do.	do.	..	3	62	16	195

In the fourth generation a similar distribution holds. Three of the *neglectums* were pure dominants. Nos. 4 to 11 gave out of 449 plants, 121 recessives. Theoretically the number of these should be 112. The last five were probably pure *herbaceums.* But they stood amongst *neglectums,* to crossing with which the 8% of *neglectums* are probably due.

TABLE V.

The fifth hybrid generation.

No.	No. in table IV.	Leaves of		Negl.	Herb.	Totals.	
		Grandparent.	Parent.			N.	H.
1	2	neglectum ...	neglectum ...	218	1	...	...
2	6	do. ...	do. ...	38	0	...	...
3	8	do. ...	do. ...	73	0	...	...
4	9	do. ...	do. ..	86	0	...	...
5	12	do. ...	do. ...	20	0	..	...
6	13	do. ...	do. ...	46	0	481	1
7	6	do. ...	do. ...	15	5	...	...
8	8	do. ...	do. ...	15	6	...	...
9	9	do. ...	do. ...	38	5	...	...
10	12	do. ...	do. ...	7	3	...	...
11	16	intermediate ...	do. ...	6	11	91	30
12	8	neglectum ...	herbaceum ...	1	10	...	...
13	16	intermediate ...	do. ...	6	135	...	...
14	18	do. ...	do. ...	1	334	...	...
15	19	do. ...	do. ...	1	181	8	639

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* These numbers are not included in the totals, as they represent only a few plants out of a much larger number of seeds sown, and no importance can therefore be properly attached to them. But some of the plants are the parents of some in the next table.

The second column of figures refers to the number of the parent in table IV.

The parents in lots 1 to 6 appear to have been pure *neglectums*, for with the exception of one stray plant in line 1, all the offspring were *neglectums*. Those of lots 6 to 11 were hybrids and the proportion of *herbaceums*—30 out of 121—is exactly the expected Mendelian ratio of one-fourth. There are a few *neglectums* among the offspring of *herbaceum* parents (lots 12 to 15), but four of them were in one bed, and the rest may perhaps safely be taken as accidental inclusions. We see therefore that among plants of the fourth generation, as of the two preceding, there were two kinds of *neglectums*—pure and hybrid. the offspring of the latter showing the dominant and recessive characters in the proportion of 3 to 1.

THE FLOWER.

Most of the Indian varieties of cotton plants have yellow flowers, marked in the centre with red or purple, which in the evening fade to a terra-cotta colour. But two of the varieties with which I began these had comparatively small white flowers, marked also with purple, but fading to a pink colour. These were the white flowered *Jari* and *Bani*. Thirteen successfully crossed bolls were obtained between white and yellow flowered indigenous races thus :—

TABLE VI.

	Seed Plant.	Pollen Plant.	Bolls.	Yellow.	White.
1	Jowari	Jari	2	19	...
2	Jari	Jowari	1	11	..
3	Jowari	Jari	1	16	...
4	Northerns ...	Do.	4	58	...
5	Jari	Northerns ...	1	11	...
6	Jowari	Bani	3	24	...
7	Bani	Jowari	1	16	...
8	......	......	...	...	...
		Total ...	13	155	0

The flowers all appeared when fresh to be of a full yellow colour and not intermediate in tint or size between those of the parents, and whether the yellow colour was supplied by pollen or by the ovule made no difference.

In the next generation, however, there were many plants with perfectly white flowers exactly like their *Jari* or *Bani* grandparents, and also some of a pale colour. In some cases these were observed to fade to a terra-cotta colour like the yellow flowers, in others to turn pink like the white flowers. The yellow and pale flowers were large and open like the "*herbaceums*," and a few of the white were also large. But nearly all the white flowers were small and like those of *Jari* in shape, and there were no small yellow flowers observed.

The following is the distribution of flowers in the next generation :—

TABLE VII.

Second hybrid generation.

No.	F.	Yellow.	Pale.	White.	% White.
1	3	287	110	178	31
2	5	25	5	27	...
3	6	182	15	85	30·2
4	6	83	10	57	...
5	6	76	8	32	...
6	6	35	0	11	...
7	6	41	8	21	...
	Total ...	729	156	411	31·6

In some beds notes were not made of the flowers of all the plants, for some did not appear to flower at all, others only seldom, and continuous work not being possible, these latter were sometimes missed.

TABLE VIII.

The third hybrid generation.

No.	Number in table III.	Parent.	Yellow.	Pale.	White.	TOTALS. Y.	P.	W.
1	10	Yellow ...	21	...	...	21	0	0
2	8	Do. ...	25	...	11			
3	12	Do. ..	25	1	2			
4	5	Do. ...	13	...	3			
5	11	Do. ...	10	...	6			
6	7	Do. ...	7	...	2	80	1	24
7	13	Do. ..	*12*	...	1*			
8	14	Do. ...	*6*	...	7*			
9	3	Do. ...	*2*	...	1*			
10	9	Pale ...	18	7	9	18	7	9
11	1	White ...	1	...	6			
12	6	Do. ...	...	...	22			
13	2	Do. ...	1	...	8			
14	15	Do. ...	...	...	9			
15	4	Do. ...	..	...	6	2	0	51
16	15	Do. ...	...	*1*	*10*			

The first plant (Table III, No. 10) was evidently a pure yellow. Nos. 2 to 6 gave 23% whites, 76% yellows. Of Nos. 7, 8 and 9 of this table, not enough plants were observed in flower to give full numbers, but they were evidently hybrid yellows.

The white-flowered plants gave nearly all whites. No. 15 (Table III, No. 4) was, as regards leaf and flower, a pure *Jari*.

TABLE IX.

The fourth hybrid generation.

No.	Grandparent.	Parent.	Yellow.	Pale.	White.	TOTALS. Y.	P.	W.
1	Yellow ...	Yellow ...	20	..	...	20	0	0
2	Do. ...	Do. ...	76	6	4			
3	Do. ...	Do. ...	11	...	4			
4	Do. ...	Do. ...	47	..	13			
5	Do. ...	Do. ...	26	...	10			
6	Do. ...	Do. ...	50	...	21			
7	Do. ...	Do. ...	5	13	1			
8	Do. ...	Do. ...	37	3	12			
9	Do. ...	Do. ...	72	...	45			
10	Pale ...	Do. ...	33	...	11			
11	Do. ...	Do. ...	82	13	37			
12	Do. ...	Do. ...	30	6	10	469	41	166
13	Do. ...	Pale ...	10	2	1			
14	Do. ..	Do. ...	3	1	2			
15	Do. ...	Do. ...	2	...	10			
16	Do. ...	Do. ...	14	2	8	29	5	21
17	Yellow ...	White ...	*5*	*0*	*2*			
18	Do. ...	Do. ...	*5*	*1*	*2*			
19	Do. ..	Do. ...	...	...	27	0	0	27

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* These were all that were observed in flower, of a much larger number of actual plants growing; they are therefore not included in the total. It is fair to point out, that if they were

No. 1 appears to have been a pure yellow, and No. 19 a pure white-flowered plant. Nos. 2 to 12 gave between them, out of a total of 676, 166 whites or 24·2% of recessives. On the Mendelian theory, the number should have been 169—a very close approximation.

TABLE X.

The fifth hybrid generation.

No.	No. in table IV.	Grandparent.	Parent.	Yellow.	White.	TOTALS.	
						Y.	W.
1	2	Yellow	Yellow	13	..	...	..
2	8	Do.	Do.	13	..	.	...
3	9	Do.	Do.	9	...	...	..
4	15	Do.	Do.	28	...	...	...
5	18	Do.	Do.	53	...	116	0
6	2	Do.	Do.	129	54	...	...
7	8	Do.	Do.	108	44	...	..
8	9	Do.	Do.	26	6	...	...
9	15	Do.	Do.	177	58	...	...
10	16	Do.	Do.	83	27	...	...
11	18	Do.	Do.	90	26	613	215
12	2	Do.	White	1	81	...	...
13	6	Do.	Do.	...	6	...	...
14	8	Do.	Do.	...	6	..	...
15	9	Do.	Do.	...	5	...	...
16	18	Do.	Do.	1	2	..	..
17	19	Do.	Do.	1	86	3	193
18	13	White	Do.	3	41	..	...
19	..	Do.	Do.	1	31	4	72

The difference between yellow and white flowered plants is again plainly shown. The first five plants were pure yellows, and gave not a single white in over a hundred plants. The next six were hybrid yellows, and from them out of 828 plants 215 or 26 % were whites, a very close approximation to the expected ratio of 25 %. Extracted whites gave of nearly 200 plants, only 1·5 % yellows. The last two plants were in small beds among yellows to vicinism with which the yellows among them are probably due.

THE SEED.

Cotton seeds differ in shape, in size, and in colour—*i.e.*, after removal of the "floss" or "lint" the surface may be

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included, the proportion of white to yellow or pale—33 to 101—would be almost exactly the expected Mendelian ratio of 1 to 3.

glabrous and black, or be covered by a more or less dense coating of short hairs, the "velvet" or "fuzz." Size is not a character easily discriminated, as it may depend on several factors. There is more real difference in the shape, the seeds of *Jowari* being for instance round, with a hard prominent beak. But attacks of seed-sucking insects, particularly of the Scarlet Bug (*Dysdercus cingulatus*), and the Dusky cotton-bug (*Oxycaraenus laetus*) so altered the shape, that attempts to discriminate between the seeds in this respect were given up. One variety—*Tellapatti* or black seeded *Jowari* differs from all the other Indian kinds, by having a smooth glabrous seed coat of a dark brown or black colour. Sir George Watt in his book (1) p. 152, says of this "There would seem little doubt that this is a naturally produced hybrid between the *uppam* and Bourbon cottons" and "the same seed on germination may produce" some or more fuzz. The possibility of its being such a hybrid had not occurred to me, for I looked upon it as a variety merely of the white or fuzzy *Jowari*. Nor, as far as I can see, does Prof. Gammie in his classification of Indian cottons (1903-1904 and 1905) give a hint of such an origin. Crosses were made of this race with the normal fuzzy *Jowari*, and with *Jari*.

Table XI shows the numbers of bolls and of plants obtained from them.

TABLE XI.

Bolls.	Seed Parent.	Pollen Parent.	Naked.	Inter.	Velvet.
a	Jowari fuzzy ...	Jowari naked ...	5	0	0
b	Do. do. ...	do. do. ...	16	0	0
c	Do. do. ...	do. do. ...	9	11	0
d	Do. do. ...	do. do. ...	0	0	10
e	Do. naked ...	do. fuzzy ...	6	0	1
f	Do. do. ...	do. do. ...	12	0	0
g	Do. do. ...	do. do. ...	0	12	0
h	Do. do. ...	do. do. ...	16	0	0
i=3	Do. do. ...	Jari	16	0	0
		Total ...	71	23	11

With the exception of boll "d," and of one plant out of boll "e," no fuzzy-seeded plants were obtained in the first generation by crossing the two kinds. These exceptions must, I think, be taken as due to self-pollination, and to be not hybrids at all. The seeds of the plants from "c" were very nearly naked, and of those from "g," I have a note that though not quite clean, they were very like those of *Tellapatti*. Leaving "c" out of account therefore 8 bolls gave between them 95 plants,—71 having perfectly naked seeds, 23 nearly naked, and 1 fuzzy seed. As "i" which was the same as Table II No. 3, in previous table, was the most interesting cross on the whole, and also the most prolific in seed, attention was mainly directed to its progeny.

In the next generation, F. 2, many of the plants again had perfectly clean black seeds, but in others it was covered with a fuzz, as dense or even denser than that of the original *Jari* parent. Most of the plants could easily be classified as having naked or "fuzzy" seeds, but there were differences in the thickness of the covering, and in some the black seed-coat could be seen through it.

A considerable number were nearly naked, having varying quantities of short fuzzy hairs - either as a tuft at one or both ends, or extending half over the surface of the seed.

I divided them therefore into four groups. Those of No. 3 (Boll i) were as follows :—

Naked	207
Nearly naked	69
Thinly fuzzy	13
Fuzzy	304

There were fewer intermediates in the plants of the third generation, the distribution being as in Table XII.

TABLE XII.

The third hybrid generation.

No.	No. in Table III.	Parent.	Naked.	Inter.	Fuzzy.	TOTALS.		
						N.	I.	F.
1	16	Naked ...	8	...	...	8	0	0
2	2	Do. ...	9	1	...	64	16	20
3	6	Do. ...	16	3	...			
4	8	Do. ...	19	6	10			
5	12	Do. ...	16	6	7			
6	1	Do. ...	4	...	3			
7	5	Do. ...	*6*	...	*11**			
8	4	Do. ...	*3*	...	...			
9	7	Intermediate ...	2	1	5	2	1	5
10	9	Fuzzy ...	...	3	31	0	5	89
11	11	Do. ...	...	1	16			
12	10	Do. ...	...	1	20			
13	4	Do. ...	...	...	6			
14	5	Do. ..	...	...	16			
15	14	Do. ...	...	...	*8*			

The first on the list was a pure clean or naked-seeded plant. Of the next five, 20% were quite fuzzy, 64% quite naked.

From the really fuzzy seed, no naked-seeded plants were got, but there were about 5% of plants whose seed had a thin fuzz with black seed coat underneath.

TABLE XIII.

The fourth hybrid generation.

No.	Grandparent.	Parent.	Naked.	Inter.	Fuzzy.	TOTALS.		
						N.	I.	F.
1	Naked ...	Naked ...	7	...	4	21	2	6
2	Do. ...	Do. ..	14	2	2			
3	Intermediate ...	Do. ..	*20*	*3*	*20*			
4	Do. ...	Do. ...	*2*	*1*	*6*			
5	Do. ...	Do. ...	1	...	4			
6	Do. ...	Intermediate ...	*3*	...	*11*			
7	Do. ...	Do. ...	31	7	36	41	12	57
8	Do. ...	Do. ...	10	5	21			
9	Naked ...	Fuzzy ..	...	...	29	2	4	249
10	Do. ..	Do. ...	...	1	55			
11	Do. ...	Do. ...	...	...	7			
12	Do. ...	Do. ...	...	...	8			
13	Do. ..	Do. ...	...	...	45			
14	Do. ...	Do. ...	2	3	105			
15	Do. ...	Do. ...	2	...	22			
16	Fuzzy ...	Do. ..	...	1	65	1	1	121
17	Do. ...	Do. ...	1	...	38			
18	Do. ...	Do. ...	...	...	6			
19	Do. ...	Do. ...	...	...	12			

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* Figures in italics mean that these were all that were observed of a much larger number.

Of Nos. 1 and 2, rather less than one quarter were fuzzy-seeded. The small proportion of naked and intermediates among those of fuzzy-seeded parents, whether extracted from naked grandparents or not, is very striking and in marked contrast to others. Intermediates appear to give about half naked and half fuzzy.

TABLE XIV.

The fifth hybrid generation.

No.	No. in table IV.	Grand parent.	Parent.	Naked.	Fuzzy.	TOTALS.	
						N.	V.
1	8	Naked	Naked	4	...		
2	9	Do.	Do.	6	...	10	0
3	2	Do.	Do.	7	4		
4	8	Do.	Do.	6	2	13	6
5	8	Do.	Fuzzy	8	25	8	25
6	8	Do.	Do.	1	135	1	135
7	2	Fuzzy	Do.	...	129		
8	2	Do.	Do.	6	122		
9	9	Do.	Do.	...	5		
10	13	Do.	Do.	...	68		
11	15	Do.	Do.	2	259		
12	16	Do.	Do.	8	97		
13	16	Do.	Do.	...	24		
14	18	Do.	Do.	1	138		
15	19	Do.	Do.	...	87	17	929

The first two were probably pure naked-seeded plants, the next two hybrids. There was apparently a certain amount of intercrossing with naked-seeded plants growing near by, but on the whole the velvet seeds came very fairly pure to their kind. Except in the case of Nos. 5, 8 and 12, there were either no naked-seeded plants at all or less than 1%.

SUMMARY AND CONCLUSIONS.

The first and most obvious result of crossing was a great increase in the size and vigour of the plants. This is in accordance with general experience. In the cross *Jowari* × *Jari* the results of which form the substance of this paper, the first hybrid generation, the immediate results of the crossing were indeed small plants (fig. 11), but the next and succeeding generations contained some which were large bushes running up to six or seven feet in height.* In other cases this increase in vigour was evident from the first. On the whole, too, the plants bolled freely and bore well, though some of the third generation of lot No. 3 were very poor. The smaller and *neglectum*-leaved plants came into bearing first, and two were especially marked in this respect, bearing heavily while the majority were still only in flower. As their seeds were naked and had long and silky staple, it was hoped that they might prove the progenitors of a useful variety, but as explained above (p. 8) none of the seeds of that lot survived.

Secondly, the plants were in some cases very variable, as is often observed with hybrids, Charles Darwin calling attention† to this in "animals and plants." According to the pure Mendelian theory, while the individual unit characters may change places, and combine in every way that chance may direct, so that the plants as a whole appear variable, each unit character should appear in itself true. In the shape of the leaf I found considerable variation, the lobes of some *neglectums* being very narrow, almost linear, and a few had wavy margins not unlike those of Assam cotton figured by Watt.‡ These might be due to different combinations § of *Allelomorphs*, but since wavy margins do not occur in the normal leaves of either *Jari* or *Jowari*, and appeared less frequently in later generations, I am inclined to consider them as monstrosities due to variation induced by hybridisation and by change of climate and soil. There is a general tendency too, for plants to approximate in character with age : in those more than twelve months old it is very difficult often to specify the nature of the leaf, or of the branching, and to this must be put down the failure to determine the characters of the lots Nos. 10, 11 and 12 of Table III. See fig. 7 and compare with figs. 11 and 12.

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* My original *Jari* plants were small. **Balls (8) notes** a similar **"intensification"** of characters.

† **Darwin, C.** Variation in Animals and Plants under Domestication, **1868,** ed. Vol. II, pp. 264, 266, 267.

‡ Watt *ibid.* (1) plate 18. Opp. p. 108.

§ Bateson and Saunders, (11) Report to the Evolution Committee of the Royal Society, p. 144.

THE INTERPRETATION OF THE RESULTS.

It is generally considered that flowers of cotton plants are habitually self-fertilised. Sir George Watt quotes the Danish colonist Rohr* as observing in 1790 that "Fecundation ordinarily takes place in *Gossypium*" before the flower has fully expanded: the same writer later on speaks hopefully of hybridising experiments with cotton,—"a plant that through the early maturity of its stamens (as in Mendel's classic experiments with *Pisum sativum*) is fully under control." † Mr. Charles Benson told me as the result of his long experience of cotton in Southern India, that it is practically always self-fertilised. Other officers of the Agricultural Department have said the same, pointing out that the ryots usually sow mixed seed, and that the absence of intermediate forms shows that crossing does not occur.

Professor Gammie, in his classification of Indian cottons, 1903 and 1905, emphasised the same point. For these reasons it was not thought necessary to cover the flowers, to make sure of obtaining self-fertilised seed for the second and subsequent generations. It would, moreover, have entailed more time and labour than I could give. A few flowers in the first hybrid generation were covered, but the plants so obtained (Bed. 0-0) did not show any less variation than those from uncovered flowers. Yet I think that a certain amount of crossing‡ did occur with my plants, the result of which was most apparent in the offspring of the first hybrid families, the latter being each of a few plants only and in beds close together. The presence of the few yellow flowers in a bed which one would expect to be all white and of *neglectum* leaves among *herbaceums* may, I think, have been due to accidental inter-crossing by the insects which visited the flowers in large numbers. Such inter-crossing almost certainly does occur even if only rarely, among cottons in the field. Mr. Sampson, the Deputy Director of Agriculture, pointed out to

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* Watt, (1)., p. 338.

† *Ibid*, p. 341.

‡ Compare also Shull (13) "On Mendelian inheritance of sunflowers." *Botanical Gazette*, Vol. XLV, No. 2, Feb. 1908, p. 106.

me several plants among Karanganis (*G. obtusifolium* Roxb. of Gammie) which showed characters belonging to Uppam (*G. herbaceum* Linn. of Gammie) and Karangani-like plants among Uppams, and there was one which seemed to be a natural cross between "American" type. If these were not natural crosses they were very remarkable instances of variation.*

THEORETICAL.

Though in some cases a considerable proportion of the seeds sown did not produce plants, one may reasonably suppose those that did, to be a fair sample of the lot. There is no *a priori* reason why seeds carrying a "*herbaceum*" leaf character should germinate better than those of the other kind, or that they should have done so, for instance in lots Nos. 13 to 16 of table 3 and not in lots Nos. 1 to 5; and when out of 676 plants (table IX) 166 or nearly 25 per cent. are of one type, this may fairly be considered to have been the proportion of all the seeds sown. Unless this is conceded no conclusion can be drawn from observations of a statistical kind, for one cannot well sow *all* the seeds of a plant, and of every batch of seeds some always fail.

Of the characters observed, two pairs, the *herbaceum* or *neglectum* shape of the leaf, and the white or yellow colour of the flowers, appear to segregate on Mendelian lines. Yellow is dominant over white, a fact which bears out C. Darwin's observation that characters common to a number of species are usually prepotent over those belonging to a few only, for nearly all species of *Gossypium* have yellow flowers.† In this connection it is also interesting to note that in crosses between coloured and white varieties of other genera, it has been found that white is in some cases dominant; in others recessive; and that this appears to depend on the way in which the colour is contained in the cells, Bateson in fact distinguishes two kinds of yellow

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* Since the above was written Leake (9) has expressed the opinion that crossing by insects is quite common.

† Balls (8) p. 363 and Fletcher (5) also find red dominant over yellow; and cf. with reference to Alex. Burn and Watt's view of the antiquity of *G. arboreum* (1) p. 86.

coloration.[*] In Stocks (*Mathiola*) yellow is recessive, as Correns also found in crosses between a white *Polemonium cœruleum* and *P. Flavum*, and in these the colour is contained in plastids.[†]

In *Verbascum blattaria* L., Shull[‡] finds yellow dominant, and here the colour is dissolved in the cell sap. Microscopic examination shows that with cottons in which, too, yellow is dominant it is a sap colour.

The *neglectum* (*arboreum*) shape of leaf is dominant over the *herbaceum*, and if we suppose that here again it is the phylogenetically older character which is dominant, this fact would confirm Sir George Watt's view that "*G. arboreum* Linn. if not an original wild stock, and therefore botanically a species, is remarkably near to what we are justified in believing, may have been one of the ancestral stocks of many of the cultivated cotton plants of the Old World[§] and that by cultivation was produced from the original *G. arbsreum*, the annual plant now known as *G. herbaceum*."[||]

The seed-coat does not appear to behave in exactly the same way: looking at a collection of seeds, from each plant of a bed, one would say at once that the "fuzzy" and "naked" characters obviously segregate. But closer observation shows that there are intermediate grades of "fuzzyness." It may be that these characters really do segregate in the same way as other varietal differences, but are influenced by external conditions, for Fletcher[¶] found that in cottons of other species irrigation tends to make the seeds naked.[**] Or it may be that these characters are "*poikilodynamic*," and while separating in the germ cells, as

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[*] Bateson (W.). Saunders (Miss E. R.) and Punnett (R. C.) Reports to the Evolution Committee of the Royal Society II and III, 1905 and 1906.

[†] Correns (C.). Weitere Beitrage zur Kenntniss der dominerenden Merkmaale und der Mosaik-bildung der "Bastarde" Ber. Dentsch. Bot. Gesells. 21 : s. 195—201. 1903, quoted by Shull (13).

[‡] Shull (13), p. 115.

[§] Watt (1), p. 86.

[||] Watt *ibid*, p. 323.

[¶] Fletcher Review of Sir George Watt's Book (1) Nature, Jan. 1908 : Vol. 77, p. 242.

[**] Among Egyptian cottons Balls finds, on the other hand, much fuzz dominant over little fuzz, and Fletcher (5) in another pair of Indian varieties that fuzz is dominant Neither worker gives details of more than two generations.

unit characters do, are of varying power, so that when combined in the hybrid, the dominance of the one (naked) is not always complete. This sort of thing occurs for instance (according to Shull) (13) in the branching of the sunflower.

Other characters also appeared to segregate, but their behaviour could not be followed after the second hybrid generation, on account of the failure of the third. But as far as the two generations showed, length and fineness of lint were dominant over the short and rough woolly nature, and the habit of the bolls opening widely as in fig. 16 and allowing the seeds to hang down freely (and so be collected cleanly) dominant over that of opening only a little.

If this be so, these important characters like the others of which this has been shown, could be bred into our Indian races of cotton plants without much difficulty.

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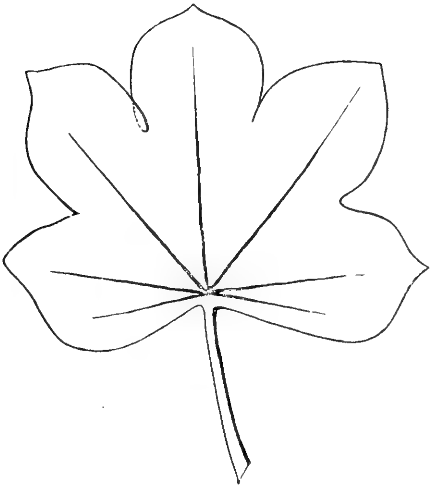
DESCRIPTION OF FIGURES.

Figs. 1 to 10 are from tracings made of normal leaves.

Fig. 1. "Jowari" (G. herbaceum).
Fig. 2. ,, ,,
Fig. 3. "Northerns" ,,
Fig. 4. Jari (G. neglectum).
Fig. 5. Cross Jari × Jowari (No. 2 of Table II).
Fig. 6. ,, Jowari × Jari (No. 3 ,, II).
Fig. 7. Leaves on young and old stems of the same cross as No. 6.
Fig. 8. Cross Northerns × Jari (No. 5 of Table II).
Fig. 9. ,, Jari × Northerns (No. 6 ,, II).
Fig. 10. Abnormal leaves in the second generation hybrid of Jowari × Jari.

Figs. 11 to 18 are from photographs 15, 16 and 17 of living plants, the others of herbarium material.

Fig. 11. Young plant of Jari.
Fig. 12. From an older plant of Jari.
Fig. 13. Northerns.
Fig. 14. Cross Bilai × Jari.
Fig. 15. A row of Jowari × Jari hybrid (No. 3). Showing the similarity of the plants in height and in their leaves, Some of the flowers have been covered by paper bags and labelled. Behind and parallel to it, is a row of cross No. 5.—(Northerns × Jari), and behind these at right angles a row of pure Jari, and two young tree cottons nearer to the right.
Fig. 16. Part of plant No. 2321. The lower branches ascend the upper are stiffly at right angles (the middle one on the left hand side was broken), the characteristic "neglectum" leaves and the opening of the bolls are clearly shown.
Fig. 17. Part of plant No. 2188, the branches are less stiff, and the leaves quite different.
Fig. 18. Part of plant No. 2282 (herbarium material).
Fig. 19. ,, ,, 2617 (,, ,,).



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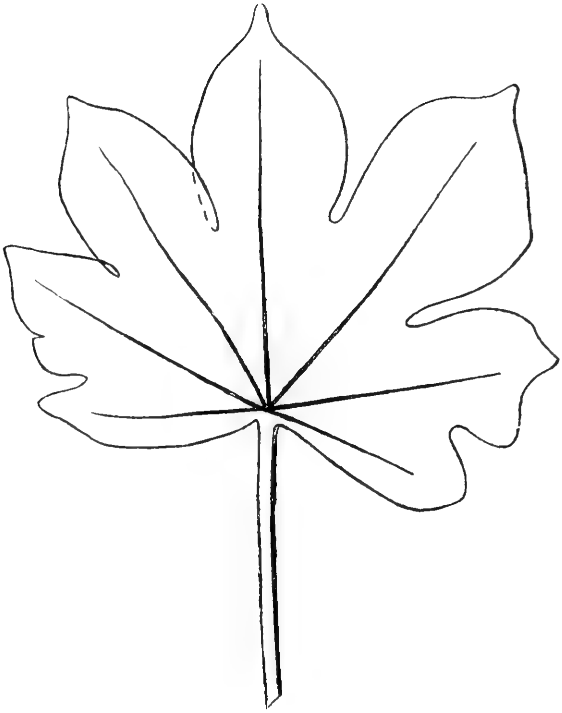
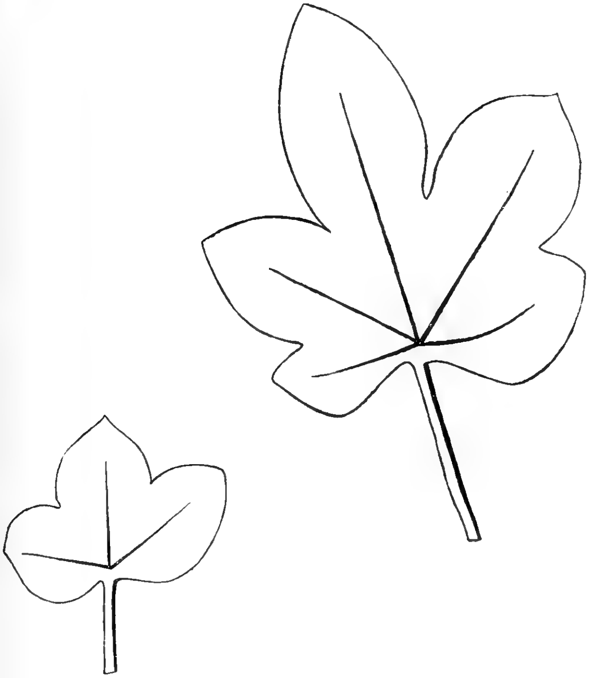


Fig. 2.



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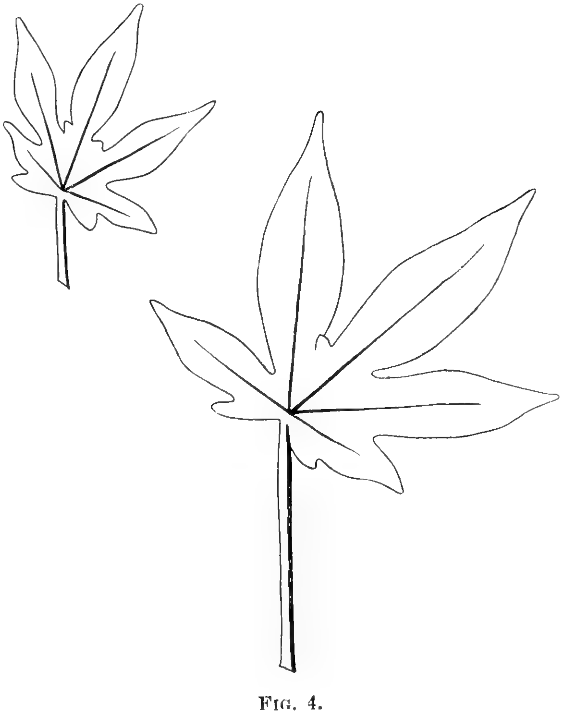

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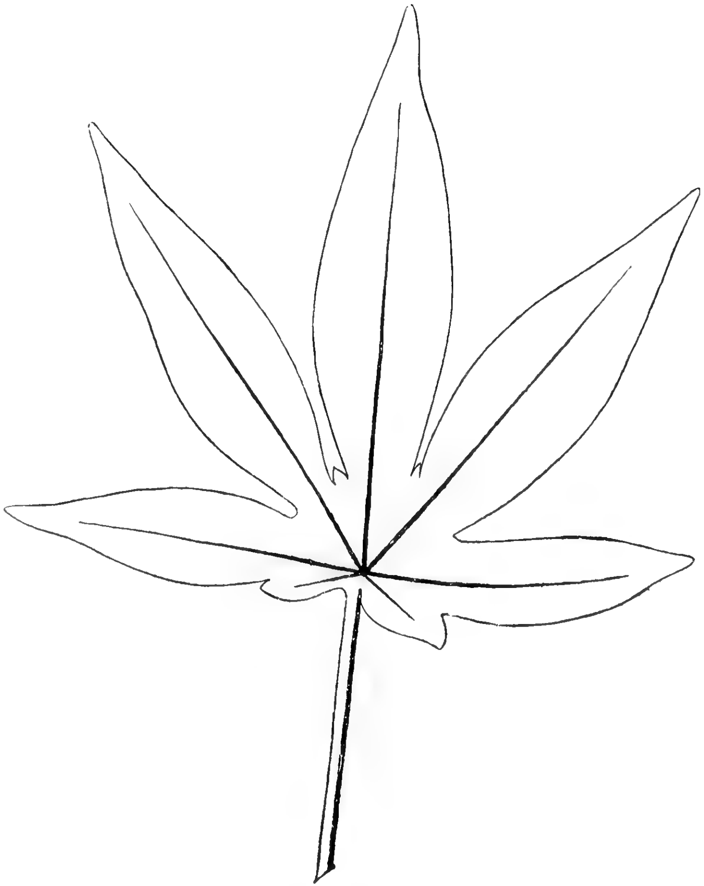
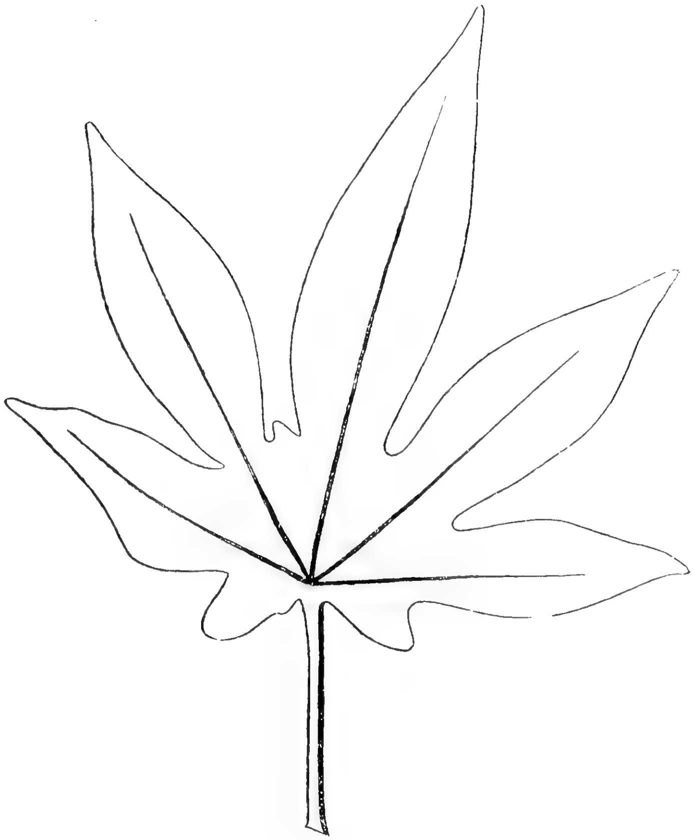


FIG. 5.



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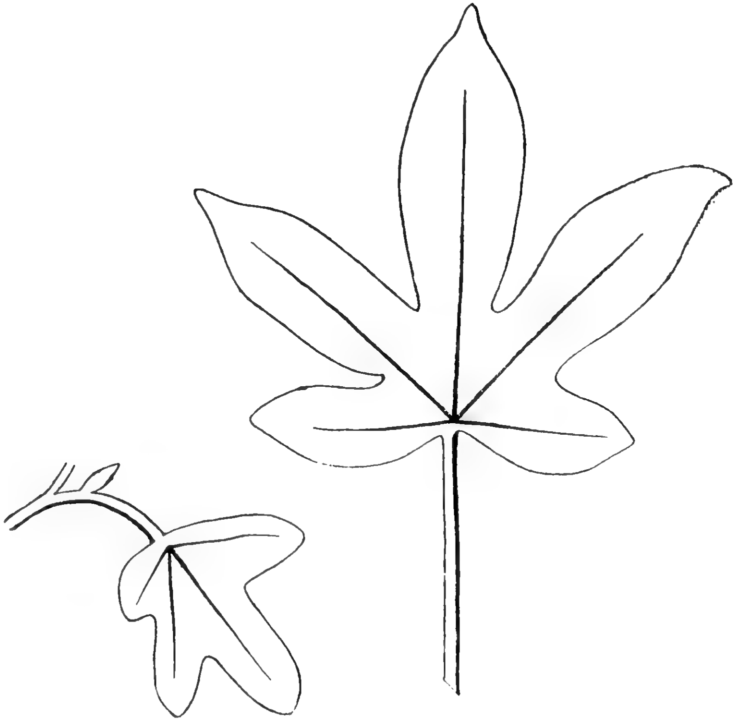

FIG. 7.

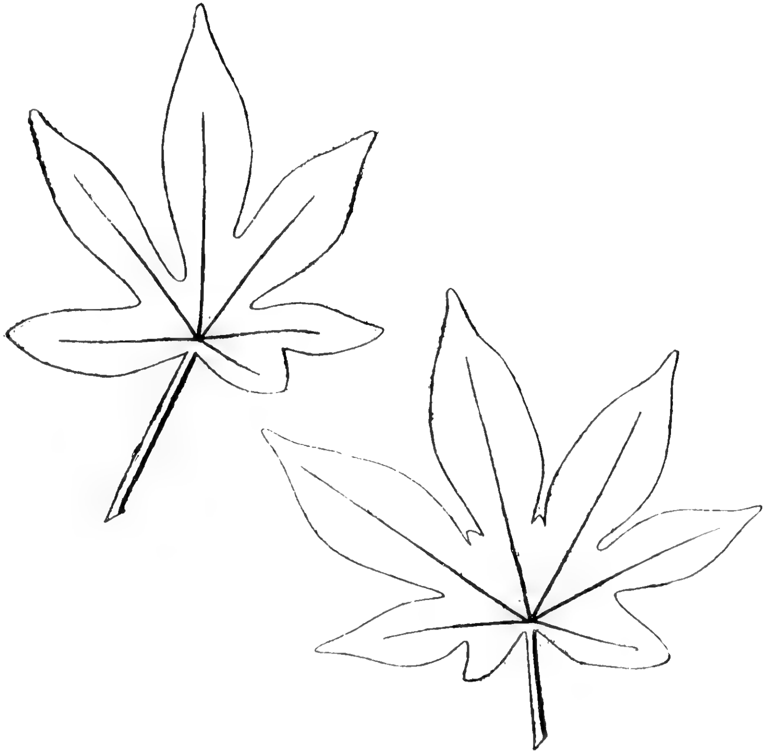

FIG. 8.

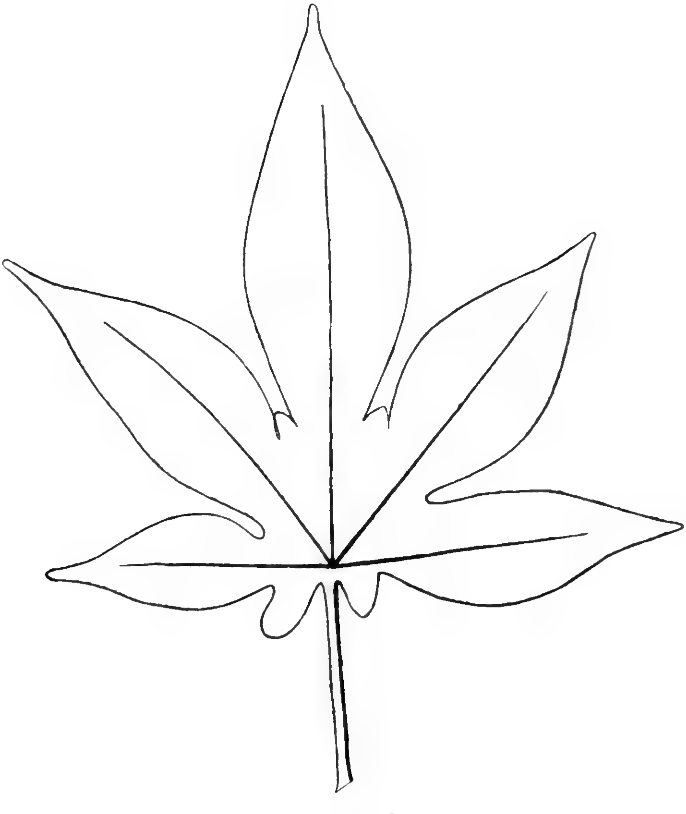

Fig. 9.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.

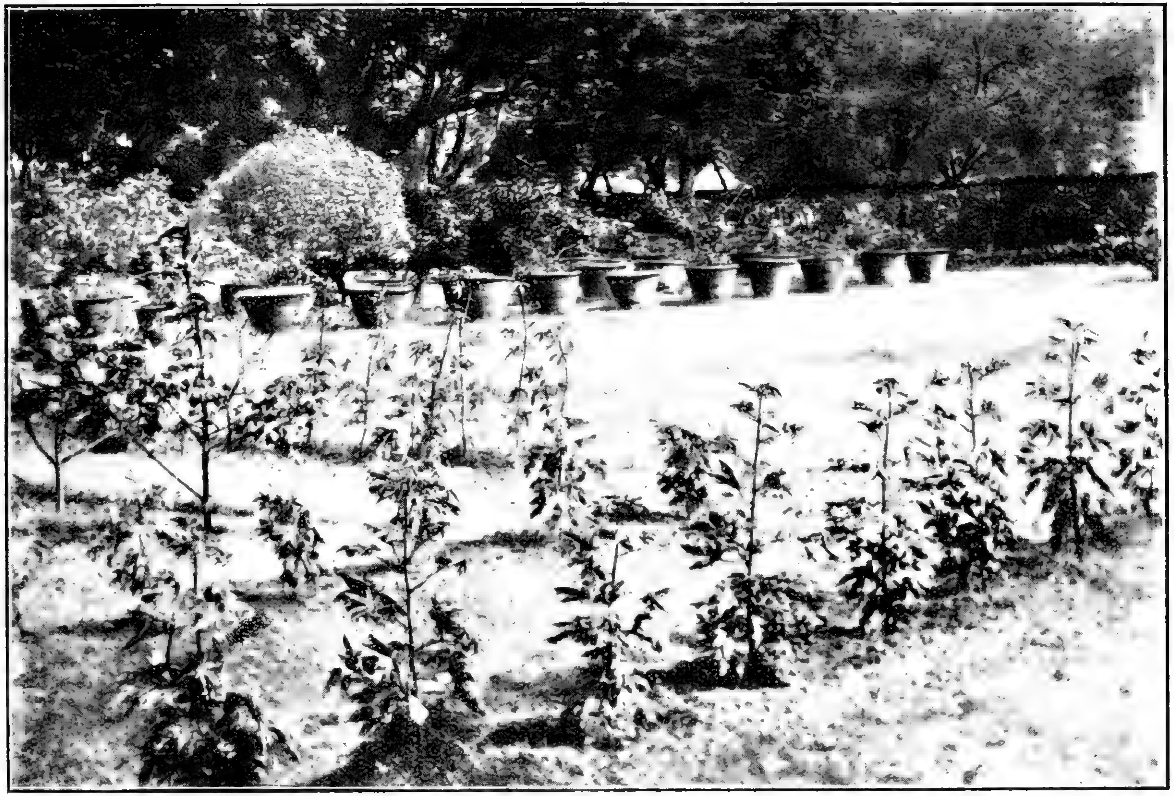

FIG. 15.

FIG. 16.

FIG. 17.

FIG. 18.

FIG. 19.

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Imperial Economic Botanist

AND

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I. INTRODUCTORY.

During the year 1905, a collection of the wheats grown on the various experimental farms in India was made at Pusa and sown in October of that year. At the same time, a very large set of samples of the wheat actually sown by the cultivators in the districts of the Central Provinces and Bengal was, thanks to the assistance of the Directors of Agriculture and the District Officers of these Provinces, placed at our disposal. An analysis of these samples and of the crops grown in the field in many parts of India during the harvest of 1906, showed that the degree of admixture of totally different types in the wheat fields of India is very great. Further, many of the wheat plots on the experimental farms considered to be pure cultures were in reality mixed, and it became evident that the first condition of wheat improvement in India was the isolation and growth in pure culture of the types already in the country. The importance of this work cannot be overestimated. Pure cultures are necessary for all wheat experiments both for breeding purposes and also for manurial, cultivation and variety trials, for seed distribution and for milling and baking tests. Everything therefore depends on this preliminary work, and until we know with precision the characters of the wheats now in the country, there is not much point in introducing into India wheats from other parts of the world.

The isolation of pure types from single plants and single ears was commenced at Pusa in 1905 and at Lyallpur in the following year, and has extended over three wheat-growing seasons at both stations. In addition to the work done at these places, we have collected a very large number of wheats from the various Provinces in India and have made extensive tours during the last three wheat seasons. The present paper sums up a large amount of the work so far done on the varietal characters of wheats and the influence of varying conditions on these characters, especially the effect of climate, soil and moisture on the composition and quality of the grain. Attention has also been paid to the milling and baking characters. Another subject of great interest has incidentally been investigated, namely, the frequent occurrence, in the Punjab, of natural cross-fertilisation in the field.

An exhaustive study of the wheats of the Punjab was made at the request of Mr. Renouf, Director of Agriculture of that Province, and the detailed classification of these wheats has been included as an example of the system of classification described in the following pages.

We desire to thank all the officers of the Indian Agricultural Department who have sent us specimens and, in particular, we wish to express our indebtedness to the following: to Mr. F. G. Sly, I.C.S., formerly Officiating Inspector-General of Agriculture in India, to Messrs. Renouf and Dobbs of the Punjab Agricultural Department, and to Messrs. W. H. Moreland, C.I.E., and H. M. Leake of the United Provinces Agricultural Department.

Dr. J. W. Leather, Imperial Agricultural Chemist, has assisted us by making a large number of analyses.

In the milling and baking aspect of the subject we have been fortunate enough to secure the invaluable assistance of Mr. A. E. Humphries, formerly President of the National Association of British and Irish Millers and a well-known authority on these questions.

II.

THE SPECIES AND VARIETIES OF CULTIVATED WHEATS.

The wheats of the world fall into three well-defined species :—

1. *Triticum sativum*, Lam. (= *Triticum vulgare* Vill. in erweitertem Sinne of Koernicke).[1]
2. *Triticum polonicum*, L. Polish wheat.
3. *Triticum monococcum*, L. Einkorn.

The wheats of the whole of the Continent of India, so far as we have been able to ascertain, belong to the first of these three species. These species are well marked and may be distinguished as follows :—

CONSPECTUS OF THE SPECIES.

I. The tooth (Seitenzahn) of the outer glumes blunt, rounded or absent. Pale undivided. Apical spikelet fertile.

1. *T. sativum*, Lam. Outer glumes shorter than the flowering glumes, parchment-like. Pale the same length as the flowering glume.
2. *T. polonicum*, L. Polish wheat. Outer glumes as long or longer than the flowering glumes, papery.

II. The tooth (Seitenzahn) of the outer glumes acute or acuminate, stiff, the ripe pale divided into two halves.

3. *T. monococcum*, L. Einkorn or one-grained wheat.

The first of these three species, *Triticum sativum*, Lam., is subdivided into six sub-species as follows :—

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[1] Koernicke, *Die Arten und Varietäten des Getreides*, Berlin, 1885.

TRITICUM SATIVUM LAM.

Ears with a fertile terminal spikelet and brittle or tough rachis. Outer glumes shorter than the flowering glumes with or without a blunt tooth (Seitenzahn). Pales as long as the flowering glumes, undivided.

I. RACHIS BRITTLE. GRAIN ENCLOSED IN THE GLUMES WHEN THRESHED.

1. *Triticum spelta*, L. Spelt. Ears bearded or beardless, long and thin, lax and somewhat square. Outer glumes very broad and truncated with a very short and blunt apex (Mittelzahn) and a somewhat undeveloped keel.

2. *Triticum dicoccum*, Schrk. Emmer. Ears nearly always bearded, dense, broader on the two-rowed side. Outer glumes sharply keeled with an acute apex.

II. RACHIS TOUGH. GRAINS SEPARATING FROM THE CHAFF WHEN THRESHED.

3. *Triticum compactum*, Host. Dwarf wheats. Ears bearded or beardless, extremely short and very compact, more or less quadrangular. Outer glumes keeled above, rounded below. Straw very short and stiff. Grains rounded.

4. *Triticum turgidum*, L. Rivet wheats. Ears bearded, large and four-sided with the spikelets closely packed on the rachis. Straw very tall, stiff, often solid. Grains large, short and thick with a blunt apex.

5. *Triticum durum*, Desf. Macaroni wheats. Ears large, dense, with long awns. Outer glumes sharply keeled to the base. Straw stiff, usually solid. Grains long, somewhat pointed, hard.

6. *Triticum vulgare*, Vill. Common wheats. Ears bearded or beardless, more or less lax (much laxer than *T. compactum*). Outer glumes keeled above, rounded below. Straw hollow, medium in length. Grains not rounded, more than twice as long as broad.

Only three of the sub-species of *Triticum sativum*, Lam., are represented in the plains, namely, *T. compactum*, Host.; *T. durum*, Desf.; and *T. vulgare*, Vill.; and the majority of the types, including all those of agricultural importance, fall into the group known as common wheats.

Up to the sub-division of *Triticum sativum*, Lam., into six sub-species, arranged in two groups, most modern botanists are in agreement and the classification of Koernicke in the *Handbuch des Getreide baues* which we have quoted above is the one now in general use. From the point of view of the study of the numerous sorts of wheat in cultivation this classification, however, does not carry us very far. There are a very large number of distinct wheats in each of the six sub-species, and it is necessary to find some means of distinguishing these numerous forms. It is at this point that divergencies are to be met with in the literature[1] on the classification of the cultivated wheats. These differences of opinion arise from the varying degree of importance assigned by investigators to the characters used in separating the types. None of the existing schemes of classification appear to us to be beyond criticism, and we accordingly decided to make a detailed study of the characters of Indian wheats with a view of evolving a method of classification which would combine the botanical and agricultural aspects of the question.

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[1] The systems of classification of wheats are dealt with by Eriksson in a paper entitled Beiträge zur Systematik des kultivierten Weizen, *Die landwirtschaftlichen Versuchs-Stationen*, Bd. 45, Heft 1 & 2, 1894.

III.

A CRITICAL STUDY OF THE VARIETAL CHARACTERS OF INDIAN WHEATS.

The influence of the environment on cultivated plants is well known and wheat is no exception to the rule. To a greater or less extent wheat is grown all over India and consequently the conditions, as regards climate, soil and moisture, under which the crop is cultivated, are very variable.

The most important conditions influencing the growth of wheat in India are :—

1. The maximum duration of the growth period in each tract.
2. The available soil moisture during that period.

The duration of the growth period is strictly limited and depends on the time when the hot weather begins in the spring. This varies with the latitude, being earlier in Bombay, the Central Provinces and Behar, a little later in the United Provinces and still later in the Punjab and North-West Frontier Province. As soon as the temperature rises above a certain point and the hot winds begin to blow, the wheat crop ripens off very quickly and dries up if not fully developed by that time. In general the crop may be said to ripen under a rapidly ascending temperature. Harvest takes place in Bombay and the Central Provinces in February, in Behar and Oudh in March and in the Punjab from the last week of April to the end of May. Only rapidly maturing wheats are of use in India either for purposes of cultivation or use in hybridisation.

Of more importance than the growth period is the variation from year to year in the available moisture. Wheat is grown on natural rainfall alone, on excessive canal irrigation as in the canal colonies of the Punjab, on inundation water from the previous summer, on limited irrigation as in the well-irrigated tracts of the United Provinces, and finally, by means of both natural rainfall and irrigation. The great variation both in the amount and manner in which the water is supplied to the soil produces well-marked differences in the wheat crop both in the external characters such as length and strength of straw and to a greater extent in those characters connected with the quality of wheat such as the consistency of the grain and the brightness of the sample.

Accidental variations in the season have a great influence on the wheat crop in India. Among these may be mentioned excessive wet and cloudy weather just before ripening begins, leading to severe rust epidemics and exceptionally early hot spells leading to loss of soil moisture and consequent loss of maturity. Frost at the period when the grain is coming into ear is not unknown. All these vicissitudes have a marked effect on chaff colour, length and density of the ear and on straw characters, and influence the wheat plant much more than the accidents of the season do in Europe. Consequently workers on wheat improvement in India have to deal with a plant which may not reach its fullest development and may not ripen under normal conditions. It appeared, therefore, that a critical study of the various characters of wheat in India was most desirable with a view of determining how far these characters are modified by circumstances and also to decide which are most useful in India in distinguishing the varieties met with in the country. For this purpose during the last three seasons many different kinds of wheat have been grown both at Lyallpur and at Pusa. These two places in geographical position and climate represent the extreme conditions of the Indian plains. At Lyallpur, the cold weather is long and (for India) intense and the wheat is entirely grown with canal irrigation, the soil being a heavy loam. At Pusa, the cold weather is short, frost is almost unknown and wheats are grown on natural rainfall, the soil being a highly calcareous loam. At Lyallpur the air is in general very dry, whereas at Pusa in January and February the atmosphere is often damp and heavy dews and mists are frequent.

1. The presence or absence of awns.

The character used by almost all botanists from Linnaeus onwards as the first in order of importance in distinguishing varieties of wheat is the presence or absence of awns. As was to be supposed (with the exception of a few cases such as those mentioned below) the amount of bearding or its absence is constant in India and the presence or absence of awns is an important botanical character.

In our pure cultures of Punjab wheats at Lyallpur, which were started from single ears in 1906 and in other similar pure cultures at Pusa we have found that the amount of bearding and also the entirely beardless condition are not absolutely constant but that some variation takes place. Occasionally, in the so-called ''beardless wheats,'' individuals with a certain amount of bearding may be found. In the Punjab wheat known as the Buggi of Leiah two types of ear were observed in the harvest of 1906 which only differed in one respect, one type being quite beardless, the other slightly bearded. These were sown from single ears at Lyallpur and Pusa in 1906 and again in 1907. The produce of both sets of ears was similar and each plot contained both beardless and slightly bearded ears. Often on single plants representatives of both could be found. The beardless and slightly bearded forms appear to be merely examples of fluctuating variability.

In bearded varieties a similar variation is to be met with. In the Punjab types 4 and 9 ears are often seen but slightly bearded. In pure cultures of macaroni wheats, *e.g.*, in the hard grey of Bengal *Gangajali* we have sometimes found beardless ears, due to the shedding of the awns. This is often brought about by rust attacks.

It is to the student of genetics that the variations in bearding are of greatest interest. In the study of the inheritance of awns in wheat breeding it has been found by Biffen,[1] Tschermak[2] and others that the beardless condition is a dominant character.

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[1] Biffen. *Journal of Agr. Science*, 1905, Vol. I, p. 93.

[2] *Die Zuchtung der landwirtschaftlichen Kulturpflanzen*, Bd. IV, 1907.

Saunders,[1] however, states that in some cases the F_1 generation is not always beardless, and that in the F_2 generation forms appeared exhibiting every variation between fully bearded and perfectly beardless types. In some of the crosses made at Lyallpur in 1907 between bearded and beardless parents, grown in pure culture from single ears, we found that the F_1 generation was not quite beardless.

As might be expected from the hot and dry climate of India,[2] the wheats of cultivation are usually bearded. These are preferred by the cultivators to beardless wheats, as they do not so readily shed their grain and can, therefore, be left standing at harvest time for some days after they are dead ripe—a practical point of some consequence where labour is scarce and dear at harvest time as in some districts of the Punjab. It is not likely that beardless wheats, will, on this account, be readily taken up by the ryots unless they possess obviously superior qualities to the bearded forms.

2. CHAFF CHARACTERS.

(*a*) *Felted and smooth chaff.*—The chaff of wheat is either felted (covered with fine velvety hairs) or smooth. In fixed types these characters are exceedingly constant even to the degree of hairiness involved. In all our crosses up to the present where one of the parents has been felted, hairy chaff has proved to be a dominant character thereby confirming the previous observations of Tschermak,[3] Biffen[4] and others.

The degree of hairiness of the Indian types varies very greatly. The Punjab macaroni wheats are very densely felted and the hairs are long, whereas the glumes in the common and dwarf wheats are generally sparsely covered with short hairs. Type 9 of the Punjab, a common wheat, resembles, however, the Punjab macaroni wheats

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[1] *Report of the third International Conference on Genetics* (1906).

[2] Koernicke, l. c. and Vilmorin, *Les meilleurs Blés*, Paris, 1880.

[3] Tschermak, l. c.

[4] Biffen, l. c.

in the length and density of the hairs on the glumes while the Behar macaroni wheats have only sparse short hairs.

Felted wheats are much commoner in the drier climate of the Punjab than in the damper wheat-growing tracts of the United Provinces, while in Bengal they are very rare. Possibly this rarity may be due to the disadvantage of hairy glumes in these moister tracts. Felted chaff holds water much more than smooth chaff, and therefore affords greater opportunities for infection by rusts. Even in the Punjab the felted wheats are often stained through the growth of mould fungi of the genus *Cladosporium* and *Alternaria*.

(*b*) *Colour of the chaff.*—The usual colour of the chaff of Indian wheats is red or white. In some cases the chaff is greyish white and varieties are met with both in the Punjab and Behar where the chaff is blackish or nearly black.

In the case of red-chaff wheats not only does the depth and tone of redness vary greatly between different types, but there is also a well-marked relation between the ripening season and the amount of redness developed in any one variety. If the weather during ripening is wet and cloudy, the red colour is not produced and real red-chaffed wheats might be then described as having white chaff. Thus, at Pusa in 1906, when the ripening period was especially unfavourable, the two Bengal macaroni wheats, which are really red-chaffed kinds, were considered by us to be white-chaffed macaronis. Even in good years, red-chaffed wheats often develop side shoots with white chaff due to premature ripening. It is only in good seasons, such as the 1906 and 1908 harvest at Lyallpur and in the present year at Pusa, that the full red colour of Indian wheats is developed. In such cases the differences in redness in the various red-chaffed types is most pronounced. While red chaff is a constant character of the variety, great care must be taken, especially in the damper wheat-growing tracts, in India in deciding this character, and it is not safe to say a wheat has white chaff unless the ears are fully and normally developed. In the Punjab one red-chaffed wheat, type 12, often shows a blackish border on the glumes. In

Bengal a form with black chaff occurs, but this black colour is only developed in good seasons.

White-chaffed wheats in India are very different from the white-chaffed varieties of Europe. Most of the Punjab white-chaffed forms have a marked reddish tinge about the glumes and awns, while the glumes have often a distinctly pink edge. A similar reddish tint is observable in the white-chaffed wheats of the United Provinces and Behar. This reddish tinge of the chaff and awns of the white-chaffed wheats combined with the poor development of colour in bad years in red-chaffed wheats makes the determination of chaff colour sometimes most difficult. One of the Punjab wheats, type 9, has greyish white chaff, but this is, no doubt, due to the thick felting on the chaff. In one case in the Punjab, the chaff is distinctly yellowish-white, but in this instance it is probable that the wheat in question was introduced into India from Australia.

Several of the wheats of India have black awns. The development of this black colour, which is seen in types 1, 2 and 9 of the Punjab, varies from year to year and only comes out well in a good year. Even in the best seasons, however, some of the ''black-awned wheats'' do not develop the black colour in all the ears. In 1906 at Lyallpur several ears belonging to type 1 were isolated which had perfectly white awns and only differed in this respect from ears in which the awns were deep black. The black and white-awned ears were sown singly in 1906 and again in 1907, and gave rise to absolutely similar plots. These observations agree with those of Koernicke[1] who grew the variety black-awned Emmer (*T. dicoccum* var. *atratum*) for eight years in East Prussia and seventeen years at Popplesdorf. It was found that the black colour of the awns was not always developed to the same extent and in one year was entirely absent, the variety simulating in that year the white-eared Emmer (*Triticum dicoccum* var. *majus*). In the following year, however, the awns were blacker than ever.

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[1] Koernicke, l. c.

3. Grain characters.

(*a*) *Colour.*—The colour of the matured grains of the Punjab and other Indian wheats we have so far examined is either red or white. The tint of colour of both classes varies a good deal. The red wheats vary from dark brownish-red to light red, while the white wheats include yellowish and amber tints. We have experienced no difficulty in determining the colour except in cases of unripe ears where the red colour is not so well marked. As a general rule, the Indian white wheats exhibit a clearer and more marked white colour than those of colder countries.

While the various red and white wheats show different and often characteristic tints, we have not used these tints to separate the kinds on account of the influence of soil and temperature during the ripening period on the tone of colour. As will be seen in the next section, the particular tone of colour depends partly on the consistency of the grain, and since consistency varies in the same variety, both from year to year in the same locality and also in different localities in the same year, it is not safe to use tone or tint of colour as a distinguishing character. As an example of the change of tone of colour, the cultures from the same sample of Muzaffarnagar white wheat at Muzaffarnagar, Lyallpur and Pusa in 1908 may be quoted. The three samples, when placed side by side, appear quite different. The Muzaffarnagar sample is clean white, the Pusa sample amber, and the Lyallpur one intermediate.

We have been at great pains to obtain reliable evidence on the question of the change of white wheats to red when introduced into fresh localities. There are a large number of loose statements both in the Indian and European literature on this subject, and many observers consider that white wheats change into red ones when grown on certain soils. Thus, Percival[1] states:—"White wheats, however, become red in warm climates or when grown on certain soils, so that this character is of little value in a scientific scheme of classification of the different varieties." Eriksson[2] believes that white wheat

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[1] Percival, *Agricultural Botany*, New Edition, 1902, p. 504.

[2] Eriksson, l.c.

becomes red and quotes Werner in support, and even goes to the length of stating that the colour of the grain is useless in distinguishing a variety. In no case, however, have we found that these supposed transformations are based on recorded scientific evidence. It is, of course, often found that when an *ordinary sample* of white wheat is tested in a new locality, the resulting grain in a few years is entirely or almost entirely red. A little consideration, however, will show that this result is no evidence of the change of a white wheat into a red one. White wheats as *ordinarily grown* in Europe and much more so in India are not pure cultures. They generally contain red wheats as impurities and, as a rule, red wheats are hardier than white sorts. Consequently, when a white wheat containing red impurities is grown in a non-white wheat locality, the struggle for existence between the red "weeds" and the white sort which at once begins, may easily result in the gradual victory of the red. In a few years, the white wheat may have disappeared entirely. The result of this alteration from a white to a red sample is of course due to the victory of the red over the white and affords no proof of a change[1] from white to red. We have so far found no evidence in the literature on wheat of a white wheat changing into a red one *when grown in pure culture from a single ear and in land where contamination of the cultures, from stray seeds left from a previous crop or from manure or irrigation water, has been guarded against.*

In seeking to obtain experimental evidence on this point in India, we were fortunate enough in 1906 to obtain a very good example. The white wheat, known as Muzaffarnagar white, has been tested in many parts of India including Oudh and Behar. In the samples grown at Pusa, Cawnpore, Lyallpur and in the Muzaffarnagar district itself, we found that the wheat was not pure but contained among other things a red wheat very similar in the ear to the true Muzaffarnagar white wheat. Pure cultures of these wheats from single ears have been grown at Lyallpur and

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[1] See de Vries, *Species and Varieties—their Origin by Mutation*, 2nd Edition, page 99, and Darwin, *The Variation of Animals and Plants under Domestication*, Vol. 1, page 334.

Pusa for the last two years. No change from white to red has yet taken place, but at both stations the red form grows more vigorously than the white, and if grown in competition, there is no doubt that the red sort would win.

In many other pure cultures of both red and white wheats at Lyallpur and Pusa during the last two years, no change of white to red grain or the reverse has been noticed except in cases of natural cross-fertilisation at Lyallpur which will be discussed later on. We accordingly believe that the colour of the grain is a constant character and one of considerable value in systematic work.

In our hybridisation experiments in India we have so far found that red grain is dominant over white, a result previously obtained by many other investigators.

(*b*) *Consistency.*—A large number of observations have been made both in Europe and America on the consistency of wheat. The subject is of great importance on account of the fact that strength is often associated with a hard and translucent endosperm. The general result so far has been to indicate that consistency depends on the soil, on the available moisture and on the nutrition of the crop. Thus, in the United States, Le Clerk[1] states in the case of Durum wheats, that in humid districts and under irrigation the grain tends to become starchy, while in drier localities the grain remains flinty with a higher nitrogen content. Eriksson[2] in Sweden concludes that consistency is of no systematic value and depends more on the season than on the kind of wheat. He found that wheats brought to Sweden from Southern Europe became more and more glassy except in good years. Koernicke[3] at Poppelsdorf found there was often a change from floury grains to flinty and also the reverse, and that these changes depended both on soil and season. Fruwirth[4] in a recent discussion of the subject concludes that consistency varies with the season, soil and nutrition of the crop, and that in Europe wheats become increasingly floury from east to

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[1] Le Clerk, *Yearbook of the U.S. Department of Agr.*, 1906.

[2] Eriksson, l. c.

[3] Koernicke, l. c.

[4] Fruwirth, l. c.

west and from south to north. Raum[1] at Munich found that the North German and exotic varieties became more and more flinty each year and tended to resemble the flinty Bavarian wheats. The consistency of the exotic kinds was also found to be influenced by season to a much greater extent than that of the local wheats. At Pusa, Leather has found in pot cultures of one of the Bengal macaroni wheats, that the addition of superphosphate and oil cake to the local soil alters the proportion of nitrogen to starch.

Our attention was drawn to this question during the harvest of 1906 in the Punjab. We found that in numerous cases, especially in the so-called soft white wheats, ears could be found which contained soft, hard and spotted grains. Similar observations were made in 1907 and 1908 both at Pusa and Lyallpur, and in the case of numerous samples of ears sent to us from other parts of India. We found in the case of pure culture wheats from single ears that both at Lyallpur and at Pusa soft wheats tend to become flinty. The reverse change from hard to soft is rarer, but is to be met with in macaroni wheats, *e.g.*, Punjab types 1 and 2, and the Bengal durum wheats at Pusa. A very large number of our Punjab white wheats at Lyallpur in 1908 showed hard, soft and spotted grains. There was no question of admixture, as the original selection from one ear in 1906 was made by us as well as all the subsequent sowings and harvestings and the samples were kept in safe custody. Our general experience has been that hard wheats do not change in consistency so easily as soft wheats. Both at Pusa and Lyallpur we have obtained samples differing in consistency from the same variety grown the same year in different fields or on slightly different soils. In 1908, with large cultures of selected Muzaffarnagar wheat, obtained the previous year from Muzaffarnagar, at both Pusa and Lyallpur the grain was more flinty than the original and also gave a higher nitrogen content on analysis. We conclude, therefore, with Eriksson, Koernicke and Fruwirth that consistency is useless as a varietal character and that it depends on the environment. We

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[1] Raum, *Zur Kenntnis der morphologischen Veränderungen der Getreidekörner unter dem Einflusse klimatischer Verhältnisse*, Munich, 1906.

further think that it is likely that soft white wheats are only naturally produced in India in certain well-defined localities such as the western districts of the United Provinces, in the Nerbudda valley and in South Behar. Other localities, such as North Behar and Oudh and the Chenab colony of the Punjab, tend to produce more glassy wheats.

(*c*) *Shape.*—The general shape of the grain in the macaroni, dwarf and common wheats of the plains varies greatly and is characteristic of the sub-species. The macaroni wheats are, long berried, Punjab type No. 3, particularly so. Humphries[1] considers that the seeds of this type are too long to be milled in the machinery in use at present in England, and that it would pass over standard sieves with the larger impurities. The dwarf wheats have small rounded grains, especially types 7 and 4. All these dwarf wheats are unsuitable for use in England on account of the fact that the machinery used in extracting the small seeds would simultaneously take out a large proportion of the sample itself. As regards the shape of the grain in the common wheats of the Punjab, no differences of systematic value have been observed.

4. STRAW CHARACTERS.

(*a*) *Strength.*—In the selection of wheat varieties for cultivation, the strength of the straw is of great importance. Weak-strawed forms, however excellent in other respects, are very apt to be laid by rust, rain and wind during the ripening period, a circumstance which greatly diminishes the yield. Among the common wheats of India there are great differences in the strength of straw. Most of the wheats of the United Provinces are particularly weak as regards the straw. In general, there seems to be a connection between the strength of straw and the erectness of the ear—the stronger-strawed forms being those with erect ears at harvest time, while ears of the weaker-strawed forms bend over when ripe. Further observations on this point are desirable.

(*b*) *Structure.*—The distinctive characters of the straw of the sub-species of wheat found in the plains is well maintained. The

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[1] See Appendix A.

macaroni wheats have tall straws solid in the upper portion, the other two sub-species have hollow stems. The dwarf wheats, however, have short, stiff and strong straws, while those of the common wheats are taller, thinner and on the whole weaker. No exceptions to the general rule, such as macaroni wheats with hollow stems and common wheats with solid straws, as mentioned by Koernicke,[1] have been noticed.

(*c*) *Length.*—The common wheats have straw intermediate in length between the tall stems of the macaroni wheats and the short straw of the dwarf wheats. There is considerable variation, however, in the length of straw between the various common wheats of the Indian plains.

(*d*) *Colour.*—The colour of the straw may be white, yellow or pink. The pink colour is especially well-developed in some of the Punjab dwarf wheats (types 5 and 7) and in type 19, a common wheat. It is also seen in the two Bengal durum wheats but only in good years. After exposure to the sun or after long storage the colour fades to a dirty greyish tint. It is best seen in the field just before the crop is ripe.

As regards the general straw characters, besides the main differences in the sub-species, the numerous varieties of each sub-species show well-marked straw characters. In some the straw is tall and strong and not liable to lodge and the colour may be pink. Such straw characters, however, are difficult to determine, for the length of the straw as well as its strength depends to a very large extent on the nature of the soil, the nutrition and the soil moisture. Fortunately, the character of the straw is not often needed as the sole means of distinguishing types, but if it has to be used, the wheats must be grown next to next in similar soil and under equal conditions in order that reliance can be placed on such characters. In studying the Punjab wheats, we have found it necessary in one case to separate two agricultural types mainly on their straw characters and also on earliness and lateness. In this case, however, the

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[1] Koernicke, l. c.

wheats were grown in pure culture next to next under uniform conditions and were sown at the same time and at the same seed rate. This was done for two years and at each harvest the wheats differed markedly in length and strength of straw and in time of maturity, and we had no doubt that we were dealing with two different agricultural types.

5. Leaf characters.

The leaves of the three sub-species are quite distinct. The macaroni wheats have very large leaves, the dwarf wheats short and erect foliage, while the common wheats are intermediate in this respect. The leaves of the various types differ both in colour and in the degree of hairiness, but these characters were not found necessary for distinguishing the types and were not studied in any great detail. There seemed to be a distinct relationship between the water requirements of some of the sorts and the extent and character of the leaf surface, but we have so far had no opportunity of following out this point. The dwarf wheats appear to be able to mature with little moisture, while the macaroni wheats and also type No. 9 require more water to reach maturity than the other Punjab common wheats. On account of the importance of irrigation in wheat-growing in the Punjab, it appears desirable to work out in detail the water requirements of the various kinds when grown under the conditions of ordinary cultivation.

6. Earliness and lateness.

The relative earliness and lateness of varieties in India is not easy to determine with precision. It is a character which is very apt to be masked by the result of differences in soil moisture. The wheat crop in India is so exceedingly sensitive to small differences in soil moisture that a small change of level in a plot is sufficient to make a considerable difference in the time of ripening. This character must therefore only be used when the varieties are grown next to next in uniform soil and under uniform conditions. In one of our plots of macaroni wheat at Lyallpur in 1908 one-half was quite green while the other half was ripening off, the level of the unripe end being a little lower and consequently damper than the other. Similarly at Pusa in the same year several sorts were sown in duplicate, one set on somewhat light loam, the other on heavy soil. The difference in the time of ripening of the two sets of plots was about 14 days, that on the lighter soil being of course the earlier. In our three years' study of the Punjab wheats we have always noticed certain broad distinctions in the time of ripening. The macaroni wheats and type 9 are distinctly later than the rest. Two agricultural types of common wheats were distinguished by paying attention to this point among others, but in general we have left the further details connected with this character to be settled when the types are grown on a larger scale. Several years' careful study will be required to decide the relative earliness and lateness of these types with precision. The wide differences in earliness and lateness inherent in the kinds such as are obvious in Europe are not to be seen in India as the shortness of the season renders the cultivation of really late kinds impossible. Even Canadian wheats like Red Fife only form shrivelled seed at Lyallpur while many of the European sorts do little more than come into ear before they are dried up by the hot winds. Some of the kinds, including Einkorn, do not even begin to shoot.

7. SUSCEPTIBILITY TO RUST.

We have observed the pure culture plots at Lyallpur and Pusa during the last two years with a view of finding rust resistant kinds for use in hybridisation. In dealing with this point it is necessary to realise that rust in India as elsewhere is only a general term and that there are several distinct wheat rusts in India. This aspect of the subject has been dealt with by Butler and Hayman.[1] The only season during the last three years at Lyallpur when the crop was damaged by rust was in 1907 when there was an epidemic of yellow rust (*Puccinia glumarum*, Eriks. and Henn.) and also a certain amount of black rust (*Puccinia graminis*, Pers.). All the 25 types of Punjab wheat were attacked by yellow rust, the only

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[1] Butler and Hayman, *Memoirs of the Dept. of Agr. in India*, Botanical series, Vol. I, No. 2, Calcutta, 1906.

Indian wheats which were resistant being Emmer[1] (*T. dicoccum* Schrk.) In 1906 and 1908 the amount of rust at Lyallpur was slight. Further detailed observations are necessary to work out the relations between the Punjab wheats and the rusts which attack them and the work is now possible as the types have been isolated and grown in pure culture. As in other characters, observations on rust resistance are of no value when the plots are mixtures of many different kinds. Some of the Punjab types have been grown at Pusa when most of them were severely attacked by brown rust (*Puccinia triticina* Eriks.). Both at Pusa and Lyallpur we observed great differences in the amount of rust on the same variety when sown on slightly different soils. At Pusa, there is as a rule much more rust when the soil moisture is liable to give out, than there is on the heavier moisture retaining soils. The degree of susceptibility of the various kinds to the three Indian rusts is of importance in plant breeding as Biffen[2] has found in England that immunity to yellow rust is a recessive character.

8. STRUCTURE OF THE EAR.

(*a*) *The form or shape of the ear.*—The shape of the ear of the common wheats of the plains of India does not exhibit the same range as in Europe, and it is not possible to utilise this character to the same extent as has been done at the Svalöf[3] Experiment Station in Sweden.

(*b*) *Density of the Ear.*—The density of the spikelets on the rachis has been used by many observers as a character for differentiating the various kinds. Wheats are often referred to as lax, medium or dense according to the distance between the spikelets. These terms, however, are not very definite, and we have followed von

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[1] Howard, A. & G. L. C., *Jour. Agr. Science*, Vol. II, 1907, p. 278.

[2] Biffen, R. H., *Jour. of Agr. Science*, Vol. II, 1907, p. 109.

[3] Fruwirth, l. c.

Neergard[1] in expressing the density of the ear by a number (D) which gives the number of spikelets per 100 mm. of the rachis.

Most of the common wheats are very much alike as regards density. From the measurements of D in the Punjab 1908 crop they fall into two groups represented by densities of 20 or 24. This fact combined with the great variation in density produced by the conditions of growth in India has led us to reject density as a means of distinguishing the kinds in India. Differences in soil moisture and nutrition affect the length of the ear considerably, while the onset of the hot weather often cuts short the development of the later shoots, the ears of which are much shorter and denser than the earlier formed ears on the same plants. We have found that greater differences in density in ears of the same plant can be obtained than exist between different kinds of common wheat. Eriksson[2] has laid great stress on density in his classification of European wheats and in fact divides up his botanical varieties by means of this character. The conditions in India are such that his classification could not be usefully adopted.

(*c*) *Character of the spikelets and glumes.*—In one instance the shape of the spikelets and glumes has been used to help to separate two kinds very similar in most other respects. The ease with which the spikelets shed their grain is also an important character and one which is very constant for any particular kind. As a general rule in India, the beardless wheats shed their grain more readily than the bearded forms and are consequently not favourites with the ryots. Thin glumes generally go with easily shed grain while the thick glumed forms hold their grain much more strongly. An extreme case of a thick glumed wheat which holds the grain is to be seen in Indian Emmer.

The character of the keel of the outer glumes is of great importance. In macaroni wheats the keel is very pronounced right down to the base of the outer glumes, while in the dwarf and common

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[1] von Neergard, Normal system för bedömande af axets morfologiska sammansättning hos vara sädesslag, *Allm. svenska Utsädesföreningens anberättelse för ar* 1887, s. 37.

[2] Eriksson, l. c. See also Fruwirth, Bd. IV, page 146.

wheats the keel is only pronounced in the upper portion and fades away or entirely disappears in the lower half. In Punjab type 9, however, the keel, although not so pronounced as in the macaroni wheats, is nevertheless distinctly represented in the lower part of the outer glume.

(*d*) *Erectness of the ear.*—The erectness of the ear is a character which we have found most useful in distinguishing in the field agricultural kinds which are very similar morphologically. In the arrangement of our Lyallpur plots all the wheats which, in the first selection in 1906, appeared to be either identical or else closely related were sown next to next. In some cases where a difference existed between two similar but not identical sorts, it was often easy to see by the position of the ears that the two kinds were different. In the one case the ears had a tendency to bend over while in the neighbouring plots the ears stood erect. Such differences in erectness were naturally accompanied by other differences in straw character and tone of colour of the chaff. It is a character which can only be used in the field and in plots which cover a certain amount of ground like that occupied by the produce of a single ear in the second season. It is not always possible to observe it in the first selection from a mixed plot.

9. SUMMARY OF BOTANICAL & FIELD CHARACTERS.

It will be convenient to deal with the above characters under two heads: (1) botanical or morphological: and (2) field or agricultural characters.

Botanical or morphological characters are those characters which remain constant with change of environment or season and which are inherited. They can be determined in the laboratory from properly developed specimens. These botanical characters are :—

1. Presence or absence of awns.
2. Felted or smooth chaff.
3. Colour of the chaff.
4. Colour of the grain.

5. Structure of the straw.
6. Character of the leaves.
7. Form or shape of the ear.
8. Character of the spikelets and glumes.

Field or agricultural characters are less conspicuous and cannot be distinguished in the laboratory or from individual plants. They can only be fully appreciated in pure cultures in the field grown side by side and under uniform conditions. The erectness of the ear, the tone of colour of the chaff and straw are field characters influenced less by season and environment than such agricultural characters as the strength and length of straw, earliness and lateness, the density of the spikelets and susceptibility to rust. All the above are characters of the greatest use and are to a very large extent inherited, but the latter group are liable to the effects of environment and season. How change of soil, moisture and locality affects them has already been dealt with and need not be repeated.

The consistency of the grain and the brightness of the sample are exceedingly variable even in the same locality, and we have not used these characters at all in separating sorts.

In considering the detailed classification of the wheats a difficulty is met with on account of the very different meanings attached to the various sub-divisions of the species. Such terms as variety, sub-variety, race, type, kind, sort are very seldom defined and where they are explained it is found that different writers use them in very different senses. The best discussion of the subject we have found is that given by Fruwirth.[1] He deals at considerable length and in detail with the development of the conception of varieties, and "Sorten" up to the present time.

We have followed Koernicke[2] as to the meaning of the term variety. By variety is understood those forms of a sub-species or

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[1] Fruwirth, *Die Zuchtung der landwirtschaftlichen Kulturpflanzen*, Bd. 1, Zweite auflage, 1905.

[2] Koernicke, l. c.

species which can be differentiated in properly developed single individuals by definite, inherited and easily distinguishable characters, such as the presence or absence of the awns, smooth or felted chaff, colour of the glumes and grains. Our varieties are therefore the botanical units of the species and sub-species and represent the lowest limit to which wheats can be divided in the laboratory with precision. Each variety, however, may comprise several agriculturally distinct types. We have divided the varieties where necessary into types by means of the field characters, such as length and strength of straw, earliness or lateness, tone of colour of chaff and straw, erectness of the ear, and susceptibility to rust. The types represent the agricultural units of a variety in a similar manner as the varieties are the botanical units of the species or sub-species. The agricultural types are just as constant as the botanical varieties, but are not so readily distinguished except in the field. To determine the types it is necessary to grow them in pure culture for several years under uniform conditions. We have in our study of the Punjab wheats carried the classification down to the type. Our types are practically synonymous with the "Sorten" of Fruwirth and Koernicke. In more than one case the same botanical variety contained valuable and almost useless types. We have found it best to distinguish the types not by one character alone but by the sum of their field characters.

As regards the system of classification in the cultivated wheats, three have been proposed—those of Koernicke,[1] Eriksson[2] and Vilmorin.[3] It has been already pointed out that the system of Eriksson depends on the density of the spikelets and is unsuitable for use in India. Vilmorin has not sufficiently distinguished between the types, while Koernicke in *Die Arten and Varietäten des Getreides*, only considers the botanical varieties. Koernicke's classification has been extended by Werner[4] in *Die Sorten und der Anbau des Getreides*, but he has only

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[1] Koernicke, l. c.

[2] Eriksson, l. c.

[3] Vilmorin, l. c.

[4] Werner. *Die Sorten und der Anbau des Getreides*, Berlin, 1885.

described the " Sorten" one after the other under Koernicke's varieties, and there is nothing to show how far the names really represent different types.

We have followed Koernicke as regards the varieties using his varietal names and have extended the classification down to the types.

In the following classification we have therefore used :—

1. As varietal characters :—
    - *a.* Presence or absence of awns.
    - *b.* Felted or smooth chaff.
    - *c.* Colour of chaff (red or white).
    - *d.* Colour of grain (red or white).
2. As agricultural type characters :—
    - *a.* Tone of colour of chaff.
    - *b.* Erectness of ears.
    - *c.* Characters of straw (length, strength and colour).
    - *d.* Earliness and lateness.
    - *e.* Susceptibility to rust.

IV.

CLASSIFICATION AND DESCRIPTION OF THE WHEATS OF THE PUNJAB.

The material from which our types were segregated consisted of 72 plots of wheat at Lyallpur (collected by the Director of Agriculture from all the districts of the province), and also a collection of the wheats grown by the cultivators of the Chenab colony. These plots were carefully searched in the field during the harvest of 1906, and all the constituents of each plot collected. These were then examined in the laboratory at Pusa and separated into botanical varieties. The same botanical variety was thus often found to occur in many plots.

The botanical varieties were sown at Lyallpur in 1906 as follows: the constituents of each variety found in the various plots were sown separately from single plants, and in 1907 these cultures were carefully examined both for vegetative characters at flowering time and also for further agricultural or field characters at harvest time. In this way it was found that in many cases the variety was made up of several types, in others there was only one type. The types were then described and the cultures repeated in 1907. In 1908, the types were finally determined in the field from a study of the comparatively large plots then available. Twenty-five different types were distinguished, the classification and description of which are given below. In many cases it was found that the types occur all over the province either in partly pure or very mixed culture under different names, and that many of the wheats cultivated in the new Chenab colonies were brought by the settlers from other parts of the province. Many of the wheats commonly grown are without doubt of a poor character and not very valuable for export purposes. Others, on the other hand, including some of the rarities, are likely to be of considerable value:—

CLASSIFICATION OF THE PUNJAB WHEATS.

TRITICUM DURUM DESF. MACARONI WHEATS.

I. Glumes felted.
    A. Glumes white, awns often black.
        a. Grain white.
            var. *melanopus* Al.
                Type 1.

        b. Grain red.
            var. *africanum* Kcke.
                Type 2.

II. Glumes smooth.
    A. Glumes white, awns always white.
        a. Grain white.
            var. *leucurum* Al.
                Type 3.

TRITICUM COMPACTUM HOST. DWARF WHEATS.

I. Ears bearded.
    1. Glumes smooth.
        A. Glumes red.
            a. Grain red.
                var. *erinaceum* Kcke.
                    Type 4.

II. Ears beardless.
    1. Glumes felted.
        A. Glumes white.
            a. Grain white.
                var. *linaza* Kcke.
                    Type 5.

2. Glumes smooth.
  A. Glumes white.
    a. Grain white.
      var. *Humboldti* Kcke.
        Type 7.
    b. Grain red.
      var. *Wernerianum* Kcke.
        Type 6.

TRITICUM VULGARE VILL. COMMON WHEATS.

I. Ears bearded.
1. Glumes felted.
  A. Glumes red.
    a. Grain red.
      var. *barbarossa* Al.
        Type 8.
  B. Glumes greyish white, awns black.
    a. Grain red.
      var. *fuliginosum* Al.
        Type 9.
2. Glumes smooth.
  A. Glumes red.
    a. Grain white.
      var. *erythroleucon* Kcke.

Type 10—Chaff dull light red, heads bend over when ripe, early, straw short and weak. D = 21.

Type 11—Chaff bright red, heads erect when ripe, late, straw tall and strong. D = 25.

Type 12—Chaff dull light red, with a somewhat bluish tone and with occasional blackening of the awns, chaff sometimes blackish also, heads bend over when ripe, grain easily shed, straw pink turning black on ripening, tall, of medium strength. D = 21.

    b. Grain red.

var. *ferrugineum* Al.

Type 13.

B. Glumes white.

a. Grain white.

var. *graecum* Kcke.

Type 16.

b. Grain red.

var. *erythrospermum* Kcke.

Type 14—Ears bend over when ripe, grain shed rather easily, early, straw weak, short, somewhat resistant to yellow rust. D = 23.

Type 15—Ears erect, less readily threshed than type 14, late, straw strong, tall, liable to yellow rust. D = 25.

II. Ears beardless.

1. Glumes felted.

A. Glumes red.

a. Grain white.

var. *Delfii* Kcke.

Type 17—Chaff with a bluish tinge, straw medium. D = 19.

Type 18—Chaff yellowish red, ears erect when ripe, straw stronger than 17, later in ripening. D = 26.

B. Glumes white.

a. Grain white.

var. *leucospermum* Kcke.

Type 19.

2. Glumes smooth.

A. Glumes red.

a. Grain white.

var. *alborubrum* Kcke.

Type 20—Chaff light yellowish red, ears more erect and later than in type 21, straw taller and stronger. D = 24.

Type 21—Chaff brownish red, dull, ears bend over when ripe, earlier than type 20, straw medium. D = 20.

b. Grain red.

var. *milturum* Al

Type 22—Sometimes slight bearding, chaff dark brownish red, shiny, grain dark red. D = 19.

Type 23—chaff dull yellowish red, grain easily shed, light red. D = 23.

B. Glumes white.

a. Grain white.

var. *albidum* Al.

Type 24—Spikelets blunt, outer glumes short and rounded, chaff white with a reddish border, ears bend over slightly, straw strong. D = 20.

Type 25—Spikelets pointed, outer glumes long and pointed, chaff yellowish white, shiny, ears erect, straw very strong. D = 20.

DESCRIPTION OF THE TYPES OF PUNJAB WHEAT.

TRITICUM DURUM DESF. MACARONI WHEATS.

Ears flat, flowering glumes with long awns, outer glumes sharply keeled to the base, straw stiff and solid.

There are three varieties of Macaroni wheats found in the Punjab, var. *melanopus* Al. (type 1), var. *africanum* (type 2), var. *leucurum* Al. (type 3). Of these, the first is the most common and represents the so-called "Vadanak" wheat of the province. The other two were only found in very small quantities, especially type 3. Macaroni wheats on account of their large water requirements are generally only grown round wells and their cultivation is very limited. The flour is used mostly for confectionery. These wheats ripen late and are more attacked by birds than the ordinary wheats. This may be due to the stiff straw and ears on which it is possible even for heavy birds to perch and also to the fact that on account of their tall straw they range above all the other wheats. These wheats have broad long leaves smooth on the upper surface with hairs on the claws. Even when thinly sown they do not tiller much.

var. *melanopus* Al.

Type 1. Awns long, black but the black colour is lost very easily; chaff densely felted, white with a pinkish tinge, often spotted with mould fungi; grains long, amber, generally hard and flinty although occasionally mottled ones are found;[1] density varies with the rankness of growth;[2] straw tall, slender but stiff; somewhat liable to rust; ripens late.

This is the common macaroni of the Punjab and was found in the Wadanak of Zira, Wadanak of Sialkot, Wadanak of Batala, Wadanak Kalchingari of Montgomery, Wadanak of Amritsar, Dagar of P. D. Khan, Dagar of Wazirabad, Dagar of Shahpur, Pamman of Ferozepore, Dagar of Muzaffargarh, Dagar of Multan, Dagar of Montgomery and in the Wadanaks of Lyallpur, Ferozepore and Amritsar and the Palestine of Lahore.

var. *africanum* Kcke.

Type 2. Similar in most respects to type 1 but the ears taper to a point and are slightly longer; grain very dark red, hard on the whole, with a very few mottled grains; length of ear 84 mm.;[3] D = 28. This type is more liable to rust than type 1.

Type 2 was only met with as an impurity in Wadanak Kalchingari of Montgomery.

var. *leucurum* Al.

Type 3. Awns long, white with a reddish tinge; chaff smooth, shiny, white with a pinkish tinge due to the veins on the glumes being red; grain very long and thin, white, much lighter in colour than type 1, generally very hard and translucent, hardly a mottled

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[1] The descriptions of the consistency refer to the samples obtained in the harvest of 1908 when the types were grown in small plots next to each other.

[2] Both the length of ear and the density vary very much in type 1. At first it seemed possible that there might be two types differing only in density but from the single ear culture we were unable to isolate two strains constant as regards density.

[3] Length of ear & D were both measured in specimens from the harvest of 1908 and are the average of 20 typical ears. As explained in the earlier pages no great stress can be laid on these measurements. They are merely given as an indication of the value of these quantities.

grain to be found; length of ear 75 mm.; D = 22; straw good; ripens late; not so liable to rust as type 1.

Type 3 was only found as an impurity in the Wadanak of Lyallpur in very small quantity. The grains of this wheat are so long that in cleaning prior to grinding they would pass over standard sieves with the large impurities.

TRITICUM COMPACTUM HOST.—DWARF WHEATS.

Ears exceedingly dense and short, rarely over 5 cms. long, outer glumes keeled in the upper half and rounded in the lower half, straw very short and stiff, grains rounded.

There are four varieties of dwarf wheats grown in the Punjab. These wheats are drought-resisting and are generally grown on inundation moisture with little rain. They are also said to be good yielders and type 7 has a good reputation for bread making. Owing to the smallness of their grain they can however only be used for indigenous consumption and they are therefore being gradually replaced by common wheats. They agree with the common wheats in time of ripening and showed themselves exceedingly susceptible to early rust, *P. triticina* Eriks, when grown at Pusa, in fact they were almost destroyed by it. They are, however, fairly resistant to yellow rust. The ears are short and erect, the straw stiff, short (generally about 3′ 6″ or 4′), hollow throughout as in common wheats but much stouter.

Humphries[1] remarks that "types 4 and 7 are extraordinarily small in the berry, so small that millers would hesitate to buy them if they contained any small seeds because the machinery used for extracting the small seeds would take out simultaneously a very large proportion of the wheat berries themselves."

var. *erinaceum* Kcke.

Type 4. Ears bearded with short bristly spreading awns very irregular in length, awns red; chaff smooth and dark red; grain very small, round, rather a light dirty red in colour, very difficult to distinguish from a dark amber, hard on the whole with a few soft

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[1] See Appendix A.

grains; ear length 50 mm.; D = 38; straw shows no pink colour.

To this type belongs the Makkhi of Chiniot.

var. *linaza* Kcke.

Type 5. Ears beardless; chaff felted with short hairs, white with a pinkish tinge due to the pink colour of the edges and veins of the glumes; grain round, small but larger than in type 4, amber coloured, hard on the whole with a few soft and mottled grains; ear length 49 mm.; D = 38; straw pinkish, turning black or greyish pink on ripening.

This type was only met with in small quantity in the Makkawali of Dera Ghazi Khan.

var. *Wernerianum* Kcke.

Type 6. Ears beardless, but with occasional very slight bearding; chaff smooth, white with a pinkish tinge; grain round, about the same size as in type 5, a clean light red, all soft; ear length 44 mm; D = 39; straw has no pink colour.

This type was only found in small quantity in the Makini of Multan.

var. *Humboldti* Kcke.

Type 7. Ears beardless; chaff smooth, white with a pinkish tinge; grain round, about the same size as in type 5 but possibly a little smaller, amber coloured, consistency very variable, hard, soft and mottled grains found in about equal proportions; ear length 45 mm.; D = 41; straw pinkish, turning black on ripening.

This is the common dwarf wheat of the Punjab and was found in the Rodi of Shahpur, Rangrih or Ghiali of Kangra, Makini of Multan, Daudi of Muzaffargarh, Daudan of Multan, Makkawali of D. G. Khan and in Daudi of Multan.

Mr. A. C. Dobbs, of Lyallpur, found that this wheat was grown at Rawalpindi and that it was considered in that district as the best for bread-making.

TRITICUM VULGARE VILL.—COMMON WHEATS.

Eighteen of the 25 types of wheat found in the Punjab belong to this species and among them are found the wheats most commonly grown. These 18 types belong to 11 botanical varieties and are equally divided into bearded and beardless, there being 9 types belonging to each class. Among the 18 varieties only 5 are felted but among these felted types are to be found some of the best wheats of the Punjab. The range in quality is very various, type 9, one of best being a good wheat fit for export, whereas some have a most inferior grain hardly worth growing for local consumption.

var. *barbarossa* Al.

Type 8. Ears bearded; awns red; chaff felted with short, rather sparse hairs, yellowish red; grain dark red, consistency variable, hard, soft and mottled grains found in about equal proportions; ear length 78 mm.; D = 24; straw good; ears erect and rather slender.

This type was found in the Lal Kasar-wali of Lyallpur in very small quantity.

var. *fuliginosum* Al.

Type 9. Ears bearded; awns stiff, stout, rather short, black but lose their colour very easily; glumes sharply keeled to the base: chaff densely felted with long hairs, the felting resembles very closely that found on the macaronis, chaff greyish white or yellowish white, pink at the edges, generally with black spots of *Cladosporium;* grain very dark red, on the whole hard with a few mottled grains, the shape resembling that of a common wheat: ear quadratic in section, somewhat club-shaped at the top, somewhat compact; ear length variable about 70 mm. on the average; D = 25; straw stiff, stout, hollow throughout; ears very erect.

This type was found in the Lal of Batala, Ratti of Montgomery and in the Lal Kale Kasar-wali of Lyallpur, it was also found in small quantity in the Lal Desi of Jhelum, Lal of Delhi, Pamman of Ferozepore, Dagar of Multan, Kunjhari of Muzaffargarh.

This wheat is one of the most interesting types found in the Punjab for although it must be classed as a common wheat, it appears to possess many of the characters of the macaronis. The felting resembles very closely that of the macaroni wheats and is quite different to that found on the other felted common wheats or on the felted dwarf wheat. The shape of the glumes with the keeling continued sharply to the base resembles that of macaronis. The hollow straw and the shape of the grain are, however, those of a common wheat. The shape of the ear with its compact sometimes club-shaped top, the stoutness of the straw and the stiff awns remind one of the dwarf wheats and it seems quite possible that this wheat, which is unique in India, may have arisen from a natural cross between a dwarf and macaroni wheat. This supposition is supported by the fact that we have found a dwarf wheat to be the female parent in some of the natural crosses found by us and described in the last part of this paper. At flowering time this wheat (type 9) appears to shed a vast amount of pollen and probably gives rise in this way to further natural crosses (see p. 61). It is interesting to note that this wheat is marked by Humphries as being the best of the 25 Punjab types submitted to him.

var. *erythroleucon* Kcke.

Type 10. Ears bearded; awns red; chaff smooth, dull light red; grain amber coloured, liable to sprout in the ear, consistency variable, hard, soft and mottled grains found in equal proportions; length of ear 82 mm.; D = 21; straw short and weak, ears bend over when ripe; early.

This type was found in the Safed of Moga, Mundi of Ludhiana, Jogia of Karnal.

Type 11. Ears bearded; awns red; chaff smooth, a more intense and brighter red than in type 10; grain amber coloured, liable to sprout in the ear, consistency variable but with a majority of soft grains; ears squarer and denser than in type 10, ear length 76 mm.; D = 25; straw tall and strong, ears stand erect; later than type 10.

This type was found in the Safed of Amritsar, Sohan of Chiniot, Kunjhari of D. G. Khan, Daudi of Lyallpur, and in the Jogia of Karnal.

Type 12.[1] Ears bearded: awns red with occasional blackening: chaff smooth, dull light red with a somewhat bluish tone, occasional blackening on the chaff; grain amber coloured, hard on the whole; ear length 86 mm.; D = 21; straw intermediate in strength between that of types 10 & 11, pink, turning black on ripening, tall; ears bend over when ripe; early; grain easily shed.

This type was found in the Rangrih of Palampur.

var. *ferrugineum* Al.

Type 13. Ears bearded; awns red; chaff smooth, shiny, yellowish or brownish red; grain red, intermediate in colour between the dark and light red grained types, rather small, consistency variable, about two-thirds being hard; ear length 96 mm.; D = 18; straw medium; ears fairly erect; rather late.

This type was found in the Lal Kasar-wali of Lyallpur. The hard red of Gujar Khan also belongs to this type, but ripened a little later than the Lal Kasar-wali. This difference may easily disappear after the hard red of Gujar Khan is acclimatised at Lyallpur.

var. *erythrospermum* Kcke.

Type 14. Ears bearded; awns pinkish yellow; chaff smooth, white with a reddish tinge when ripe; grain light red, hard and soft grains in about equal proportions; ear length 80 mm. D = 23; straw weak and short; ears bend over when ripe; early fairly rust-resistant; sheds its grain more easily than type 15.

This type was found in the Lal of Karnal, Lal of Sialkot, Lal of Attock, Lal Safed of Sirsa, Lal of Zira, Kasalu or Surkh of Ferozepore, Ratti or Lal of P. D. Khan, Lal of Ludhiana, Desi Surkh of Jullunder, Lal Desi of Jhelum, Lal of Rawalpindi, La of Delhi, Kunjhari of Muzaffargarh.

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[1] We have found some difficulty in describing the differences between these three types (10, 11 and 12): they are best seen in the field.

Type 15. Ears bearded; awns pinkish yellow; chaff smooth, white with a reddish tinge when ripe; grain light red, consistency variable but the majority are soft grains; ear length 80 mm.; D = 25; straw tall and strong; ears erect when ripe; late; susceptible to rust; grains less easily shed than in type 14.

This type was found in the Ratti or Lal of P. D. Khan, Watni of Shahpur, Kunjhari of Multan.

Types 14 and 15 form the common red wheat of the Punjab. A glance at the names of the varieties will show that they are cultivated all over the province. They are very similar to, if not identical with, the common red wheats cultivated in the United Provinces. These two types are absolutely identical in the laboratory but quite different in the field.

var. *graecum* Kcke.

Type 16. Ears bearded; awns rather pinkish yellow; chaff smooth, white with pink edges and veins; grain white, rather small, on the whole soft but with some hard and mottled grains; ear length 78 mm.; D = 23; straw fairly strong.

This type was found in the Ghoni of Lahore, Safed of Ludhiana, Safed of Rohtak, Safed of Batala, Daudkhani of Dāsuya, Daudkhani of Delhi, Pori of Montgomery and in the Safed Kasar-wali of Lyallpur.

var. *Delfii* Kcke.

Type 17. Ear beardless; chaff felted with short, rather sparse hairs, red with a bluish tinge; grain amber coloured, consistency variable, hard, soft and mottled grains present in equal proportions; ear length 94 mm.; D = 19; straw medium.

This type was found in the Rodi of Attock, Ghoni of Gujrat, Ghoni of Sialkot, Khoni of Jhelum, Ghoni of Chiniot, Ghoni of Amritsar, Khoni of Batala, Mundli of Karnal, Mundli of Ludhiana, Safed of Lahore, Kanku of Palampur, Jhakrehun of Palampur, Safed Brij Sondha of Rohtak and in small quantity in the Rodi of Muzaffargarh, Ghoni Lal, Ratti of Muzaffargarh, Desi of D. G. Khan, Suthra of Multan.

This is a very common wheat in the Punjab.

Type 18. Ears beardless; chaff felted with short, rather sparse hairs, yellowish red; grain amber coloured, consistency variable, but the majority of the grains are soft; ear length 72 mm.; D = 26; ears squarer and denser than in type 17; straw stronger than in type 17; later in ripening.

This type was found in the Rodi of Muzaffargarh, Ghoni Lal, Ratti of Muzaffargarh, Desi of D. G. Khan, Suthra of Multan and in small quantity in the Ghoni of Chiniot, Ghoni of Amritsar, Jhakrehun of Palampur.

var. *leucospermum* Kcke.

Type 19. Ears beardless but occasional slight bearding met with; chaff felted with some short somewhat sparse hairs, white with pink veins or edges to the glumes; grain whiter than in 17, 18 and 21 but darker than 16; consistency variable but about three-quarters of the grains soft; ear length 74 mm.; D = 24; straw strong, pinkish, turning black on ripening.

This type was found only in very small quantity in the Buggi of Leiah at Lyallpur.

var. *alborubrum* Kcke.

Type 20. Ears beardless with occasional very slight bearding; chaff smooth, light yellowish red; grain amber coloured, rather large, consistency variable but about two-thirds of the grains soft; ear length 78 mm.; D = 24; straw taller and stronger, ears more erect and later in ripening than type 21; grain very easily shed.

This type was only found in the Ghoni of Amritsar.

Type 21. Ears beardless, with occasional very slight bearding; chaff smooth, brownish red, dull; grain amber coloured but somewhat whiter than 17, 18 and 20, consistency variable, about an equal amount of hard, soft and mottled grains; ear length 90 mm.;

D = 20; straw medium; ears bend over when ripe; earlier than type 20; grain very easily shed.

This type was found in the Kanku of Palampur and in small quantity in the Rodi of Attock, Ghoni of Gujrat, Ghoni of Sialkot, Khoni of Jhelum, Khoni of Batala, Mundli of Karnal, Mundli of Jullunder, Mundli of Ludhiana, Jhakrehun of Palampur, Ratti of Muzaffargarh, Kunjhari of Muzaffargarh, Kunjhari of Multan, Safed Ghoni and Ghoni Lal.

var. *milturum* Al.

Type 22. Ears beardless sometimes slightly bearded; chaff smooth, shining, dark brownish red; grain very dark red, consistency variable but on the whole the sample is hard; ear length 94 mm.; D = 19; straw medium but rather better than in type 23.

This type was found in small quantity in the Ghoni of Sialkot and in Safed Ghoni.

Type 23. Ears beardless; chaff smooth, dull, yellowish red; grain very light red, somewhat small, entirely soft; ear length 81 mm.; D = 23; straw medium.

This type was only found in the Ratti of Muzaffargarh.

var. *albidum* Al.

Type 24. Ears beardless; spikelets blunt; outer glumes short and rounded, chaff smooth, white with a reddish border; grain yellowish white, resembles 19, rather large, consistency variable but on the whole the sample is soft; ear length 93 mm.; D = 20; straw strong; ears bend over slightly.

This type was found in the Koni of Chakwal, Kunj of Muzaffargarh, Buggi of Leiah and Safed Ghoni.

Type 25. Ears beardless, often slightly bearded; spikelets pointed, outer glumes long and pointed; chaff smooth, yellowish white, shiny, with very slight reddish border; grain larger than in any other of the types of common wheat in the Punjab, greyish white of a different tone of colour to any of the other white wheats, on the whole soft: ear length 100 mm.; D = 20; straw very strong; ears erect.

This type was found in Buggi of Leiah and Safed Ghoni.

These two types, 24 and 25, differ in appearance so much from all the other wheats of the Punjab and bear such a strong resemblance to the Australian wheats introduced into the province that we cannot help suspecting that they originally came from Australia.

V.

THE QUALITY OF INDIAN WHEAT.

There are two points to be taken into account when considering the quality of the wheats produced in a country like India. In order of importance they are, firstly, the needs of the local market and, secondly, the requirements of the export trade. It is commonly supposed that the classes of wheat best suited to the Indian and European markets are quite distinct. We shall endeavour to show in this section that such an idea is erroneous and that the wheats in greatest demand for local consumption and those preferred by the English millers are of the same general class, namely, hard and flinty wheats. We propose to put forward evidence, to show that the present cultivation of weak soft wheats like Muzaffarnagar white for export is a mistake and has been the means of lowering the status of Indian wheat in the English market and consequently has entailed the loss of large sums of money to the Indian producer.

The quality of a wheat for bread-making purposes depends chiefly on the consistency, colour, composition and milling characters of the grain and on the colour and baking value of the resulting flour. These matters will be dealt with in order.

1. CONSISTENCY.

In a previous section (p. 14) the subject of the consistency of the wheat grain from the systematic point of view has been considered and it has been shown that for purposes of classification this character varies to too great an extent with the environment to be of any value. From the milling point of view the consistency of the wheat grain is of the greatest importance and to some extent determines the market value of a wheat. Millers like wheats of uniform consistency and on this account definite grades are maintained in the United States and Canada, and an inspection system has been built up for the purpose of maintaining these grades. As far as possible, hard and soft wheats are kept distinct and fall into the various hard or soft grades. It is in the conditioning or in the adjustment of moisture prior to grinding that the miller finds it an advantage to handle hard and soft wheats separately and where a mixture of hard and soft leads to trouble and loss. Consequently it is an advantage to export wheats uniform in consistency. Unfortunately, however, in India, wheats do not always come true to texture and we have found in the Chenab Colony of the Punjab, where wheat is grown under excessive Canal irrigation, there is a tendency towards the production of mottled grains—hard and soft in places—and to an unevenness in consistency. As has been pointed out above (p. 14), new wheats introduced into a district tend to develop the same consistency as that of the country wheats. Thus at Pusa, wheats tend to become hard and flinty. In some parts of the United Provinces, for example the Muzaffarnagar district, uniform soft grades appear to be developed.

To bring out this point a pure sample of Muzaffarnagar white was grown in 1908 in three localities—at Lyallpur in the Punjab, at Muzaffarnagar in the United Provinces and at Pusa in North Behar. In consistency, the resulting harvest was quite distinct. At Muzaffarnagar, the sample was uniformly soft white, at Lyallpur there was a fair proportion of flinty and semi-flinty grains, while the general tint was a duller white. At Pusa, the colour was amber and the majority of the grains were hard or semi-hard. As will be seen below, both the composition and baking values of these three samples were notably different, and the Pusa grown specimen was considerably the best. It is one of the future problems in Indian wheat investigations to see how far consistency can be regulated by cultivation and irrigation and in what tracts wheats uniform in consistency can be produced.

2. COLOUR.

The change, now almost complete in Great Britain, from the old system of grinding wheat under mill-stones to that of the modern roller mill has led to quite different views on the part of millers as to the importance of the colour of the grain. Under mill-stones more of the skin of the grain found its way into the flour and consequently red wheats did not yield flour of such good colour as white wheats.[1] With roller mills, however, the separation of the skin is almost complete and the disadvantages of red wheats no longer exist to any appreciable extent. That this is so is evident when it is remembered that Canadian Fife wheat which is one of the strongest wheats exported to England is a hard red wheat but realises prices about the highest in the market.

While it is not possible to judge the milling value of a wheat from the colour, yet it is safe to state that, as a rule, the hard wheats with a somewhat dark tint have the highest nitrogen content and give the best results in the bakehouse. Very light red and white wheats often give weak flours.

3. COMPOSITION.

Although a great deal of work has been done on the chemical composition of wheat and of wheat flour, yet no accurate relation has hitherto been found between the chemical composition and the breadmaking value of wheat. The only determination of any value is the nitrogen content which is usually determined by Kjeldahl's method and which, when multiplied by the factor 5·7, gives the percentage of proteids. Hall[2] found that *as a rule* the higher the nitrogen content the stronger the flour, but there are exceptions as some wheats high in nitrogen give very weak flours.

The range in total nitrogen and proteid content in wheat is very great. Thus Soule and Vanatter[3] in America give 8·1 & 13·6 as the limits of the proteid percentage in the American wheats

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[1] Maurizio, *Getreide. Mehl und Brot*, Berlin, 1903, p. 112.

[2] Hall, A. D., *Journal of the Board of Agriculture* (England), Vol. XI, No. 6.

[3] Soule and Vanatter, *Bull. IV, Agr. Expt. Sta. Tennessee*, 1903.

investigated by them. Far higher values, however, can be obtained, some of the stronger wheats of Hungary, Roumania and South Russia often containing 20 per cent. or more of gluten.

According to Fruwirth,[1] climate in Europe has a considerable effect on the composition of wheat. "Dryness and poverty of soil clearly increase the gluten content. Besides this it must be remembered that according to Wollny high summer temperature and low rainfall in Hungary, Roumania and South Russia favour nitrogen content and flintiness: cooler damper climates, on the other hand, favour starch production and flouriness. In agreement with this the nitrogen content of wheat in Europe in general diminishes from South to North and from East to West. Thus the gluten content in South Russia, Roumania and Turkey is 20 per cent. or over, in Germany and France 10 to 15 per cent., and in England seldom more than 10 per cent."

Tschermak[2] quotes several cases of change of composition when European wheats were removed from one country to another.

During the season 1907-08 in India we obtained results with Muzaffarnagar white similar to those discussed by Tschermak. Samples of this wheat grown at Lyallpur, Muzaffarnagar and Pusa gave very different results on analysis and also differed considerably in bread-making value.

Composition and baking value of Muzaffarnagar wheat grown at three stations in 1908.—

	% Nitrogen. (Leather).	Order in Baking value (Humphries).
1. Grown at Pusa	1·86	Fifth.
2. Grown at Lyallpur	1·50	Eighth.
3 Grown at Muzaffarnagar	1·38	Ninth.

The nitrogen content of the 25 Punjab types has been determined on the 1908 crop by Leather as follows :—

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[1] Fruwirth, l. c.

[2] Tschermak, l. c.

Nitrogen content of Punjab wheats.

Type No.	1	2	3	4	5	6	7	8	9
Percentage of Nitrogen ...	1·75	2·61	2· 2	2·14	1·78	1·62	1·71	1·52	2·01

Type No.	10	11	12	13	14	15	16	17	18
Percentage of Nitrogen ...	1·40	1·31	1·50	1·57	1·37	1·43	1·39	1·42	1·39

Type No.	19	20	21	22	23	24	25
Percentage of Nitrogen ...	1·35	1·43	1·45	1·38	1·35	1·37	1·62

It will be seen that with one exception the common wheats, Types 8 to 25, all give nitrogen values below 2 per cent. and are therefore low in gluten. The macaroni wheats, types 1 to 3, and the dwarf wheats, types 4 to 7, on the whole, are distinctly higher in nitrogen than the common wheats.

4. MILLING AND BAKING TESTS.

A considerable amount of information as to the probable usefulness of a wheat can be given by an expert miller who is accustomed to buy wheats on hand samples and to grind them into flour. Accordingly, the types of Punjab wheat were submitted to Mr. Humphries of Weybridge and his report is given in Appendix A. From this it will be seen that types 8 and 9, both red wheats, were considered to be the best. A still more reliable opinion, however, can be obtained from an actual milling and baking test, if conducted by an expert provided with a suitable mill and baking facilities. This was done for us this year by Mr. Humphries with ten samples, each about 60 lbs. in weight, from various parts of the Indo-Gangetic plain.

Six of these wheats were obtained from Lyallpur, one from Gujar Khan, one from Muzaffarnagar, and two from Pusa :—

Description and composition of ten samples of Indian wheat tested in England in 1908.

No.	Name.	Grown at	Character of grain.	Percentage of Nitrogen (Leather).
1	Pusa No. 6	Pusa ...	Hard white	2·52
2	Lal Kasarwala.	Lyallpur ...	Hard white	Not determined.
3	Punjab type 9	Lyallpur	Hard red	2·01
4	Gujar Khan	Gujar Khan ...	Hard red ...	1·76
5	Muzaffarnagar white.	Pusa	Semi-soft white	1·86
6	Punjab type 16.	Lyallpur	Soft white ...	1·39
7	Punjab type 14.	Lyallpur ...	Soft red ...	1·37
8	Muzaffarnagar white.	Lyallpur	Soft white	1·45
9	Muzaffarnagar white.	Mazaffarnagar	Soft white ..	1·34
10	Australian 27...	Lyallpur ...	Soft white ...	Not determined.

Numbers 1, 3, 5, 6, 7 and 8 were pure cultures grown by us at Pusa and Lyallpur. Nos. 2, 4, 9 and 10 were obtained in ear from cultivators' fields, all ears not true to type being picked out before threshing.

The report on the milling and baking qualities of these wheats is given below :—

REPORT BY A. E. HUMPHRIES, ESQ., PAST PRESIDENT OF THE INCORPORATED NATIONAL ASSOCIATION OF BRITISH AND IRISH MILLERS AND CHAIRMAN OF THE HOME-GROWN WHEAT COMMITTEE OF THE INCORPORATED NATIONAL ASSOCIATION OF BRITISH AND IRISH MILLERS ON THE TEN SAMPLES OF INDIAN WHEAT SENT FROM PUSA IN 1908.

I duly received, *viâ* Calcutta or Kurrachee, the ten sample lots of various wheats grown in India, upon which the Agricultural Department of the Indian Government wished me to report, and in accordance with the arrangement arrived at with you, I have cleaned, conditioned, milled and baked each lot separately and have done each operation in duplicate.

I have regarded the whole matter from the standpoint of a British miller and am accustomed to buy Indian wheats on a commercial basis for the manufacture of flour to be used in England.

The methods of milling and baking followed are those which I have used in making a great number of similar tests for the Home-grown Wheat Committee of the National Association of British and Irish Millers.

The ten samples were designated as follows :—

Red wheats.—Gujar Khan.
Punjab Type 9.
Punjab Type 14.
White wheats.—Pusa 6 grown at Pusa.
Lal Kasar Wala.
Muzaffarnagar grown at Lyallpur.
,, ,, ,, Muzaffarnagar.
,, ,, ,, Pusa.
Australian 27 Lyallpur.
Punjab Type 16.

I do not think that the colour of the husk need be or is likely to be of great importance. British millers are guided in their preferences principally by the quality and quantity of flour which Indian wheats would yield, but if on other points a red wheat and a white wheat were equal, the preference would be given to the white wheat.

Each of the ten samples was noteworthily free from dirt and extraneous matter. The arrangements arrived at by the joint action of shippers, the leading British Corn Trade Association and the Association of British and Irish Millers have brought about a great improvement on this point in the recent shipments of Indian wheat, and if it be possible to ship wheat as ''clean'' as the ten samples I have received, the relative value of Indian wheats would be still further enhanced.

As part of the process of cleaning wheat by washing, and to prevent as far as possible the pulverizing of the husk in grinding and so secure a better separation of husk from kernel, it is the custom of British Millers to ''condition'' their wheats.

The most important point in the conditioning is the adjustment of the moistures immediately prior to grinding, so that wheats with high moistures would be dried and wheats with low natural moistures would be damped. Of course, this means that practically all Indian wheats would be damped and that the driest would be worth more to the miller than those with higher moistures. Incidentally, I should like to mention the belief entertained here that some parcels of Indian wheat are artificially damped before shipment. Any such action is unwise from the Indian point of view. It is risky as regards the effect on quality, it seems silly to pay railway and ocean freight on water, and any gain so obtained on the first few transactions would be much more than lost in the long run, because all British Millers of good standing know quite well the moistures of the wheats they receive, that point enters into their calculations as to the relative values of wheats, and they are likely to base their calculations to the detriment of sellers on the highest percentage of water the wheats they buy will contain.

The ten samples were all in the best of condition on arrival.

When water is added in the process of cleaning and conditioning, it affects the kernel as well as the husk, and all varieties of wheat are not affected alike. Some remain "free grinding," that is to say, the kernel, when pulverized, makes lively granular flour which can be separated from husk with a minimum of trouble to the miller; others become "woolly" in texture, the flour is less granular and the separations in the mill are made with difficulty.

The ten samples show a striking difference in this respect. For free grinding Pusa 6 is very good indeed, Australian 27 poor. The Muzaffarnagars are also poor in this respect, and of the three the one grown at Lyallpur is the worst. The five sorts not specifically mentioned in this connection are good as regards this characteristic.

There are very great differences in the hue of the flours from the ten samples. The three Muzaffarnagars all yield flour very white in hue. Of the three, that grown at Muzaffarnagar is the whitest, that grown at Pusa is substantially the same, whilst the Lyallpur lot of this variety has a comparatively dingy hue. I think this is associated with the "woolliness" I have mentioned, because to get a commercially complete separation of husk from kernel more force in grinding has to be used and more of the husk accordingly gets pulverised in the grinding. The Australian 27 yields also a white flour. Punjab Type 9 yields a bright but very yellow flour. Gujar Khan one that is yellow in slightly lesser degree. Pusa 6 is as regards colour in a class by itself, for its very lively granular flour is neither white of chalky hue nor yellow, but a greyish white, which I associate with Canadian Fife wheat. Of the other three sorts not specifically mentioned in this paragraph, Punjab Type 16 yields flour of very good appearance as regards hue, medium between the chalky white of the Muzaffarnagar and the yellows of the Punjab Type 9 and Gujar Khan. A large number of British millers use artificial bleaching. In their hands the two last named would give good results as to colour. In some parts of England and in Ireland flour of chalky white hue is required, and for those purposes the sorts yielding such flour might be preferred, but my own preference as to colour would be Pusa 6 or Lal Kasar Wala, and this, I think, would be the verdict of most English millers.

There are great differences between the ten as regards strength, by which I mean the capacity for making large shapely loaves. On this point Pusa 6 is pre-eminent. The loaves are not only larger, but whereas those from all the other flours have the appearance typical of Indian varieties, those from Pusa 6 have a quite different and a superior crust and general appearance. Gujar Khan, Punjab Type 9 and Lal Kasar Wala are not far behind so far as size of loaf is concerned. Of the three Muzaffarnagars, the Pusa lot is distinctly the best, the Muzaffarnagar distinctly the worst, the Lyallpur lot occupies the middle position. The Punjab Types 14 and 16 and Australian 27, are only poor on this point.

As regards the stability of dough, in baking all are good. Pusa 6 is the nearest approach to the toughness which is associated with Canadian or American Spring Wheats, but that is not to be compared with those sorts, nor should I expect to find any wheats behaving in that way unless with great summer heat a high summer rainfall be associated.

In summarizing the foregoing, I unhesitatingly express the opinion that Pusa 6 is the best, and I can quite as unhesitatingly say, I do not like Australian 27 or Muzaffarnagar grown at Muzaffarnagar. There is a growing inclination amongst grain merchants to mix their wheats so as to reduce the number of grades in which they deal. No particular harm would be done if they mixed as follows :—

A. Muzaffarnagar grown at Muzaffarnagar.
,, ,, ,, Lyallpur.
,, ,, ,, Pusa.
27 Australian.
B. Lal Kasar Wala.
Punjab Type 16.
C. Punjab Type 9.
Gujar Khan.

Punjab Type 14 might be grouped with C, but would be better handled separately. Pusa 6 might be grouped with B, but would make most money if sold by itself, on its own sample or reputation. Group A should not be mixed with either B or C, nor should any individual of the group A be mixed with any member of the group B or C. If group B were mixed with group C, no particular harm would be done, but they are better apart.

Different millers may have different opinions about the same wheat, and as indicated herein some sorts may have special values in different localities, but as a miller trading in the London district, I should put the ten in the following order having regard to all the points mentioned—

1. Pusa 6.
2. Lal Kasar Wala.
3. Punjab Type 9.
4. Gujar Khan.
5. Muzaffarnagar grown at Pusa.
6. Punjab Type 16.
7. ,, ,, 14.
8. Muzaffarnagar grown at Lyallpur.

9. {Muzaffarnagar grown at Muzaffarnagar.
10. {Australian 27.

I find great difficulty in answering your question as to the relative money values of these ten Indian wheats and Canadian and American grades. Canada and the U. S. A. grow some poor weak wheats, and I would certainly pay as high or even a higher price for any of the ten as I would for Canadian Winters, or for the wheats grown on the Pacific slope of the U. S. A., or for most of the U. S. A. winter wheat shipped as they are with all their uncertainties as to grading, but these Indians are quite different to Canadian or U. S. A. Spring wheats, and are not comparable with them. So long as the world grows so much more weak wheat than strong wheat, and so long as millers are compelled to supply flours of good or great strength, wheats capable of yielding flour from which tough, stable doughs and big loaves can be made will command a large premium.

Some authorities measure strength by the number of loaves a given quantity of flour will produce, but a reliable opinion cannot be formed on this point on small lots such as you sent me. It is, however, quite safe to say that the better of your ten would rank high on this point. The relative value of Indian wheats has already gone up a great deal as a result of improved cleaning and greater reliability in quality, and if wheats as good in intrinsic quality, as well grown, as clean and as dry as say the first six on my last list are shipped here from India, the growers can rely on a still further increase in their relative value in competition with the wheats of the world.

ALBERT E. HUMPHRIES.

It will be seen from this report that the four best wheats from a milling and baking point of view are hard wheats. Further, these varieties are also hardy wheats, good yielders and with good straw and in two cases at least with considerable resistance to rust. The soft wheats such as Muzaffarnagar white are, comparatively speaking, inferior wheats.

The extension of the cultivation of soft white wheats in India for export to Europe dates from the year 1883, when a report by Messrs. MacDougall Bros. of London, on the milling and baking tests of four parcels of Indian wheat was published.[1] These wheats were as follows:—

(1) Soft white from the Meerut and Muzaffarnagar districts.

(2) Soft red from the Meerut district.

(3) Hard red from the Banda district of Bundelkhand.

(4) Hard white from Khandesh in Bombay.

These wheats were milled in London by the then ordinary process of grinding under mill stones and also by the Hungarian or roller system which was at that time a novelty in Great Britain. Comparisons were made with English, American, Australian, Russian and Egyptian sorts both in the mill and subsequently in the bakehouse.

It is clear from the report that the hard red and hard white wheats were macaroni wheats and not bread wheats and are not usually exported to England for baking purposes. The soft white wheat from Muzaffarnagar was considered to be the best of the four, and, from that time, its cultivation and that of similar weak soft white sorts has been considerably advocated for export purposes. That this has been a great mistake will be clear when it is remembered that at the time these tests were made, most of the wheats used in England were ground under mill stones for which hard wheats and especially hard red wheats were not very suitable. Since that time, however, the modern roller mills have entirely replaced the old mill stones in England. In these mills the hard flinty strong wheats of Russia and North America can be handled with ease, and red wheats are almost as good as white sorts. The use of these flinty wheats in turn set up a new standard of flour strength and they were used almost entirely to mix with the weak soft wheats which make up the larger portion of the world's production. Strong

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[1] This report is published in *The Wheat Production and Trade of India*, Calcutta, 1883.

wheats are at a premium in England. In the last 25 years, therefore, the conditions of the wheat trade in England have been revolutionised both as regards method and material. No corresponding change has been made in the wheats exported from India, only weak wheats are exported and therefore it is not surprising to find that there is a belief in England that India can only produce weak wheats. Thus Humphries and Biffen[1] in a recent paper state "the fact that India, Australia and California export wheats no stronger than our own makes it clear that abundance of sunshine does not necessarily result in the production of strong wheat." This is no doubt true of the soft Indian wheats now exported, but we do not think it is by any means true of all Indian wheats.

That strong wheats are grown in India seems to have been first discovered by Farrer[2] in 1899, who, in a letter to the Revenue Secretary to the Government of India, dated August 9th of that year, stated:—"On account of the high strength of the flour they produce, I take the liberty of recommending to you for extensive propagation the first two varieties of the three mentioned above, for I regard them as the best of all the Indian varieties which thus far have come under my notice. Your Indian varieties appear to vary greatly in the quality of flour strength."

Many enquiries in the villages in the Indo-Gangetic plain have elicited the information that for his own use the cultivator prefers hard wheats, often hard reds. These he considers to be greatly superior in food value to the soft wheats grown largely for export. The people fully understand the value of the chewing test and for their own consumption prefer those varieties which yield a sticky mass in the mouth after mastication. It will be seen from the letter from Messrs. Ralli Brothers (Appendix B) that if hard wheats were put on the market, there would be little difficulty in obtaining a premium for them.

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[1] Humphries and Biffen, *Journal of Agricultural Science*, Vol. II, 1907.

[2] Farrer in the Proceedings of the Government of India (Revenue and Agricultural Department, Nos. 1—4, October 1899). These wheats came from Etawah and Muzaffarnagar in the United Provinces. The Muzaffarnagar wheat was not Muzaffarnagar white, but a beardless variety.

It will be evident from the above that the demands of the local and export trade are the same and both prefer hard strong wheats. The growth of weak soft white sorts for export is therefore a mistake. When the English millers realise that India can produce much stronger wheats than those at present exported, the growth of weak soft wheats will be given up and the hardier, more easily cultivated flinty wheats will take their place.[1]

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[1] Yielding power will naturally have to be taken into account as well as grain quality and hardiness. In recommending new wheats to the cultivators it will be necessary to select those which combine hardiness and high grain quality with good yielding power.

VI.

NATURAL CROSS-FERTILISATION IN INDIA.

In general, the flowers of all the species and varieties of wheat are self-fertilised, pollination taking place before the extrusion of the stamens. The details of the wheat flower are well illustrated by Hays,[1] while there are good detailed accounts of the opening of the glumes and of the extension of the anthers both by Fruwirth[2] and by Hays. Koernicke[3] observes that the stigmas themselves sometimes protrude their fine points, when the glumes open at the top for the liberation of the stamens, and remain in the open even after the closing of the glumes.

Instances of natural cross-fertilisation in the field are not common. Some observers even go to the length of stating that natural crossing does not take place. Thus De Vries[4] states "wheat, barley and oats are self-fertile and do not mix in the field through cross-pollination." Garton[5] from his experiments in England comes to a similar conclusion. He states :—

" The first step was to ascertain whether natural cross-fertilisation actually existed in the cereals. At the time it was an accepted doctrine that all agricultural plants were open to artificial cross-fertilisation, but there were no definite or reliable records to prove that such was the case. On the settling of this question depended the possibility of the work attempted. The method adopted was as follows :—

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[1] Hays, *Bull.* 29, *U. S. Dept. of Agriculture, Div. of Veg. Phy. & Path.*, 1901.

[2] Fruwirth, l. c., Bd. 4, 1907.

[3] Koernicke, l. c.

[4] De Vries, *Species and Varieties, their Origin by Mutation.* 2nd Ed., 1906, p. 98.

[5] Garton, *Journal of the Farmers Club,* 1900, p. 47.

A suitable number of heads of wheat were selected in a field crop, and the immature anthers were carefully removed from about half a dozen florets on each head, the remaining florets being left intact. The ovules in the florets from which the anthers had been removed had thus every opportunity to become fertilised by pollen either from the surrounding florets left intact upon the same heads or by pollen from outside sources. Not one single embryo was developed in the florets thus treated. This was considered sufficient evidence to justify the belief that natural cross-fertilisation did not exist.''

Biffen[1] who grew over 200 varieties of wheat at Cambridge in England, says they are autogamous with rare exceptions, and he states "I have never met with a case of natural cross-fertilisation.''

Darwin in *Animals and Plants under Domestication* states: "With respect to the natural crossing of distinct varieties, the evidence is conflicting, but preponderates against its frequent occurrence.''

These observations, it will be observed, refer to comparatively damp climates, and it is no doubt true that in England natural crossing in wheats is exceedingly rare. We have so far only found three cases in the records, the first of which is quoted in the *Journal of the Board of Agriculture* of November 1905:—" It is an extremely rare thing to find a single case of natural cross-fertilisation. The possibility of such an operation being caused by bees is so extremely remote that it can be said to have no existence. Because of its rarity it may be well to put on record that in the course of the Committee's work one case or perhaps two have been met with.[2] A farmer, Mr. R. Cook, of Box near Bath, planted in 1902 a field with a mixture of Square-head's Master and Essex rough chaff—two sorts of wheat which from the breeder's point of view possess marked differences. When the crop matured, he came across a plant with nine ears of particularly robust growth. He propagated their contents (560 grains) and has supplied the

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[1] Biffen, l. c.

[2] The Committee referred to is the Home-grown Wheat Committee in England who for some years past have been working to improve the milling qualities of English wheats.

Committee with an ear of the progeny which certainly seems to indicate that a natural cross did take place. Extremely rare though such cases of natural cross-fertilisation may be, it is not at all difficult to cross-breed wheat artificially.''

Two more cases of natural crossing in England in which Red Fife was the female parent have been observed at Chertsey in 1906.[1]

Although natural crosses are very rare in the damp climate of England, it by no means follows that such occurrences are equally rare in other wheat-growing countries. In drier and more sunny climates, such as that of the continent of Europe and some of the wheat-growing districts of North America, it is quite possible that natural crossing is much more common. A perusal of the literature shows that this supposition is amply confirmed. Thus in Jersey, LeCouteur[2] found that a red-felted wheat gave rise to felted red, smooth red, felted white, and smooth white plants. Another case of natural crossing was noticed by this observer in a Kentish felted wheat which gave rise to both smooth and felted progeny. Koernicke at Popplesdorf records several cases of natural crossing in *Die Arten und Varietäten des Getreides* published in 1885. Thus on page 31 he states :—'' It will be seen that wheat is arranged for self-fertilisation, but that cross-fertilisation is not impossible. That the latter occurs in the field was proved by me by undoubted crosses which I obtained in the garden and from which I grew some peculiar forms.'' On page 49, in describing the varieties of *T. compactum*, Host., Koernicke states that this group more than any other is disposed to cross in the field. Thus his varieties 25, *rufulum*, Kcke.; 26, *creticum* Mazzucato ; 29, *crassiceps* Kcke.; 30, *rubrum* Kcke.; 37, *sericeum*, Al.; 38, *albiceps* Kcke.; 39, *rubriceps* Kcke.; 40, *echinodes* Kcke. ; were obtained from natural crosses. Further, on page 62, when discussing the varieties of *T. durum* Desf., he states that one of the difficulties in

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[1] Report of the Home-grown Wheat Committee for the cereal year 1907.

[2] LeCouteur, *The Varieties, Properties and Classification of Wheat*, 2nd Ed., Jersey, 1872, p. 132.

dividing the varieties lies in the fact that in the south there are many more intermediate forms to be found than is the case with the German wheats. He considers this is probably due to the fact that in certain countries the sowings are extraordinarily mixed—wheats from Valencia gave on sowing a large number of varieties. In such cases Koernicke considered that it is easier for crosses to occur and the limits of the groups to be lost.

Fruwirth[1] brings together most of the recorded examples of natural crossing in wheat. The possibility of cross-fertilisation is supposed to have been proved for *T. sativum*, Vill., by an experiment of Rimpau in which 59 per cent. of castrated flowers freely growing in a wheat field set seed and by a similar experiment of von Liebenberg's in which 20 per cent. of flowers in the same manner set seed. As mentioned above, Garton in a similar experiment in England obtained no setting. Rimpau observed the occurrence of spontaneous bastards when different kinds were grown next to next. He cultivated 60 kinds of *T. vulgare* for 15 years and found 17 cases in which one could assume spontaneous crossing. Hansen at Lyngby and Nilsson at Svalöf are of opinion that in warm good weather forms cross with each other which are generally considered only to be self-fertilised, and that crossing between common wheats and spelts occurs under such circum stances. Fruwirth states that at Hohenheim he also noticed similar results and also crossing between forms of *T. sativum* and *spelta*.

In the United States, Carleton[2] considers that natural crossing sometimes occurs, and states "In a majority of the instances above described the circumstances too are such that one cannot escape the thought that the abnormal heads found in the fields were the results of natural crosses." In Canada, Saunders[3] has described a case of spontaneous crossing in the field between Red Fife (female) and Rio Grande (male).

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[1] Fruwirth, l. c.

[2] Carleton, *Bull.* 24, *U. S. Department of Agriculture, Div. of Veg. Phy. & Path.*. 1900

[3] Saunders, *Bull*, 57. *Canadian Dept. of Agr.*, Oct. 1907.

As it appeared probable that natural crossing occasionally takes place in warm countries, we have paid considerable attention to this point in India. In the pure culture plots at Pusa, many hundreds in number, during the last three years no cases of natural crossing have so far been discovered.

At Lyallpur, however, the results were quite different. Of the single-ear cultures, sown in 1906, four proved to be natural crosses. Three of these ears were collected on the Lyallpur Farm in May 1906, one was found in the collection of U. P. wheats from Saharanpur sent to us by Mr. H. M. Leake. We had no suspicion of any of these wheats being natural hybrids when they were sown, but considered they were rare types of wheat in cultivation.

In the plot of Safed Ghoni (a smooth white beardless wheat) at Lyallpur in 1906, two white felted, slightly bearded, red grained plants were noticed. These were sown from single ears in 1906, and in 1907 both gave rise to mixed offspring. The first, labelled P 145 A, gave rise to felted white chaff plants with red grains. Five plants were bearded, five were slightly bearded and two were beardless. In 1908 they split up still further.

P 145 A.

FELTED WHITE CHAFF, SLIGHTLY BEARDED.
(PARENT EAR) 1906.

5 felted white chaff bearded 1907.
5 felted white chaff slightly bearded 1907.
2 felted white chaff beardless 1907.

The other plant, P 146 A, also split up into bearded and beardless smooth and felted in 1907 and still further in 1908 :—

P 146 A.

WHITE CHAFF, FELTED, SLIGHTLY BEARDED, (PARENT EAR), 1906.

Smooth white chaff.
Felted white chaff.

2 bearded 1907.
3 slightly bearded. 1907.
1 beardless. 1907.
5 bearded. 1907.
17 slightly bearded. 1907.
6 beardless. 1907.

The beardless ear obtained from Saharunpur in 1906 (U. P. 158) gave rise to bearded and beardless in 1907 and split up still further in 1908. As the seed from which this ear was raised was sent from Cawnpore to Saharunpur, the crossing must have taken place at Cawnpore.

U. P. 158. Smooth white chaff beardless (parent ear) 1906.	16 bearded smooth white chaff 1907.
	14 slightly bearded smooth white 1907.

The fourth case of a natural cross found at Lyallpur in 1906 was in the plots of *T. compactum.* In Type 5 one of the felted beardless ears gave rise in 1907 to red-felted plants differing very much in density.

P5 Felted beardless 1906.	5 red felted beardless lax	..	white chaff felted	...	lax
					dense
			red chaff felted	...	lax
					dense
	5 red felted beardless dense	...	white chaff felted	...	lax
					dense
			red chaff felted	...	lax
					dense
	1 red felted beardless very dense ... (compactum type) 1907.		all dense felted	...	red chaff
					white chaff 1908.

In the harvest of 1907 at Lyallpur a slightly bearded smooth red chaff lax plant, not at all like a compactum, was observed in one of the dwarf wheat plots. This was sown separately in 1907, and in 1908 gave rise to 12 bearded and 11 beardless plants. They could also be divided up into lax and dense and into red and white chaff. In the present year (1908) in 42 of the 108 plots grown from the produce of single ears sown in 1906, we observed stray plants, often more than one in a plot. In many cases these were red or white chaff, felted, bearded, red grained plants, and most of them appear to be first generation of a cross between type 9 (Lal Kale Kasarwala) and the type in which they were found. These must have arisen either from natural crossing in 1907 or from stray seeds (either left in the soil from a previous crop or brought accidentally by ants, birds or in the irrigation water). As they are different in appearance from any known wheat at Lyallpur, and as natural crossing has already been proved by us to occur in the Punjab, we consider it exceedingly probable that these stray plants are natural crosses in the F_1 generation. Upwards of 100 of these supposed natural crosses will be sown this year and the results will be published in a subsequent paper. We are inclined to believe that in the Punjab in good years natural crossing is exceedingly frequent, especially when one of the kinds sown is type 9. In 1907 it was observed that the glumes of this sort open to a very wide extent when the anthers are ripe and liberate a vast amount of pollen into the air. As our plots were surrounded by a belt of this wheat on all sides, there were abundant opportunities for its pollen distribution. The season at flowering time was very dry and sunshine was abundant. Our artificial crosses made at this period at Lyallpur gave nearly 100 per cent. of fertilised grains. There is no doubt, therefore, that the season was a favourable one for natural crossing to take place. In conclusion, our opinion so far is that in the Punjab natural crossing is possible to such an extent that great care will have to be taken to keep the sorts pure and that plots grown next to each other must be very carefully rogued every year. At Pusa where, as a rule, the air is much damper at flowering time, natural crossing in the field seems to be very rare.

APPENDIX A.

From A. E. Humphries, Esq., Weybridge, to the Imperial Economic Botanist, dated Weybridge, July 13th, 1908.

I duly received your letters of May 21st and 28th, and the 25 small samples of wheat have since come to hand. None of the ten large sample lots for milling and baking tests has yet arrived, but, in accordance with your request, I have examined the 25 small samples without waiting for the larger ones, and send you herewith my opinion as a British miller upon them.

When I speak of strength, I mean "a flour capacity for making big shapely loaves." Its capacity for making a large number of loaves from a given quantity of flour is in my view another matter upon which nobody can safely express an opinion by merely looking at samples. Of the many points upon which a miller bases his estimate of value in buying wheats, strength is the one to which pre-eminent importance is attached on almost all our United Kingdom markets. The very strong wheats of the world appear to be grown in countries where great heat is accompanied by a substantial or large summer rainfall, and as yet I have not come across any Indian wheat, which, on its own merits, in other words, when it is used for bread-making by itself, would come into our category of very strong wheat. I shall watch with very great interest any attempts you make to produce such wheats, especially if you experiment with Fife, but, in the meantime and particularly for my immediate purpose, I shall base my estimate of the commercial value of your wheats principally on their relative strength and the whiteness of the flour which they would yield under our modern conditions of milling. In this connection, I should like to point out that there is no invariable connection between the quality of the flour produced from the kernel of the wheat berry and the colour of the skin. A red skin does not necessarily indicate strength, nor does a white one necessarily indicate weakness, and sometimes the flour from red wheat is much whiter than the flour from white wheat. I have also to take into account how the wheats you have sent me would suit the methods of cleaning and milling in common use here. For instance, among your dwarf wheats are two (Nos. 7 & 4) which are extraordinarily small in the berry, so small that millers would hesitate to buy them if they contained any small seeds, because the machinery used for extracting the small seeds would take out simultaneously a very large proportion of the wheat berries themselves. For that reason and having regard to the practical certainty of getting some small seeds into the bulks grown under commercial conditions, I would not recommend the growth of wheats 7 & 4, nor even of Nos. 5 & 6 unless there is some other characteristic, of which I know nothing, to strongly recommend them.

In recent years, a considerably increased quantity of Durum (Macaroni) wheats have been sold on British markets for ultimate use in bread-making, although as the alternative name implies their original or better use is for the manufacture of macaroni. Their great and inherent hardness is very different to the apparent hardness of your ordinary wheats, in which the hardness is due to mere absence of moisture, and in the estimation of millers making flour for bread-making purposes, Durum wheats are now, and are likely to be, at any rate for many years to come, worth much less money than your ordinary wheats. In all wheats, and especially in Durums, uniformity of texture is a most important desideratum. Millers in preparing their wheats for milling (the separation of husk from kernel) seek to get all wheats in their mixture into one uniform condition and with that object prepare some wheats very differently to others, before the blending of the various sorts is made. From this it would be obvious that growers or dealers in grain should, so far as possible, aim at exporting grain as uniform in texture as possible. This remark applies to your ordinary wheats as well, and affects my judgment on your samples. The principle of a remark I made concerning your dwarf wheats applies also to your Durums, but in another way. Our mills are fitted with elaborate systems of sifting machines in which the wheats pass through perforations in the sifting medium and large impurities pass over them. Of course, if millers found any additional commercial value for other reasons in very long berried wheats and could get a sufficiently large and regular supply, they would make the necessary changes in machinery, but such wheat as your No. 3 would pass over standard sieves into or with the large impurities, and in this case also, I would not recommend the export to the United Kingdom of such wheats for flour milling purposes, unless there be some strong recommendation, the existence of which I do not now suspect.

I note with much interest the cleanness of your samples, that is to say, their freedom from dirt, barley, seeds, and other extraneous matter. When I was President of the National Association of British and Irish Millers, I attended conferences of shippers, merchants and millers called to deal with the grave abuses which had been introduced into the Indian wheat trade, whereby, so we learned, such impurities were deliberately added to wheat with the object of obtaining for the sellers a greater monetary return. As a result of the arrangements arising out of those conferences, a great improvement has been brought about, but I would like to take this opportunity of remarking that if Indian wheats could be bought here regularly as clean and good as your samples, British millers would pay better prices than they do for them. Manitoban wheats fetch higher prices on our markets than the corresponding grades of United States wheat because buyers believe they are more likely to get good deliveries of the former than of the latter, and Indian growers and dealers should realise that any action of theirs whereby confidence in the regularity of good deliveries is injured or destroyed, must in the long run do them much more harm than any temporary gain they may get.

Complying with your request to arrange the 25 samples in their order of merit, I set them out as follows :—

"Common wheats" : Red :

9.
8.
22.
13.
14.
15.
23.

"Common" white wheats ·

⎧ 12.
⎨ 10.
⎩ 21.
17.
18.
20.
⎧ 24.
⎪ 19.
⎨ 25.
⎩ 16.
11.

In my opinion there is no difference in money value between those I have bracketed together. In case you would like me to put all the "Common wheats" in order of merit without making the distinction as to their colour, I set them out as follows :—

9 Red.
8 Red.
⎧ 12 White.
⎨ 10 White.
⎩ 21 White.
17 White.
22 Red.
13 Red.
18 White.
20 White.
⎧ 24 White.
⎪ 19 White.
⎨ 25 White.
⎩ 16 White.
14 Red.
15 Red.
11 White.
23 Red.

Durums :—1, 3, 2. As we do not make macaroni in the United Kingdom, I think either of these would realise less money than any of the Common Wheats.

APPENDIX B.

From A. E. Anastasiades, Esq., Manager of Messrs. Ralli Brothers' Agency, Lyallpur, to the Imperial Economic Botanist, Pusa, dated Lyallpur, 12th May, 1906.

Wheat.—With reference to the conversation you had with the undersigned, our Karachi Principals write to us as follows :—

" The reason why we pay a better price for soft white wheat is that Great Britain and the North Continent, which take the bulk of Karachi wheat, generally prefer soft wheats.

" However, if purely hard wheat were produced in the Punjab in sufficiently large quantities to make it a merchantable description, and if the quality kept its characteristics from year to year and could be relied on to be matched at any time, an outlet for it could readily be found and possibly such wheat would command a premium.

" At present, purely hard wheat without an admixture of soft grain, reaches the Punjab markets in such small quantities that we are precluded from buying it on its own merits, and it has to be mixed in the so-called soft descriptions."

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APRIL 1909 **Botanical Series** **Vol. II, No. 8**

Memoirs of the Department of Agriculture in India

THE MULBERRY DISEASE CAUSED BY CORYNEUM MORI NOM. IN KASHMIR, WITH NOTES ON OTHER MULBERRY DISEASES

BY

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AGRICULTURAL RESEARCH INSTITUTE, PUSA

PUBLISHED FOR
THE IMPERIAL DEPARTMENT OF AGRICULTURE IN INDIA
BY
THACKER, SPINK & CO., CALCUTTA
W. THACKER & CO., 2, CREED LANE, LONDON

Price Re. 1-8

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The Twig Disease of Mulberry.

(*Coryneum Mori* Nomura.)

The disease caused by this parasite is probably of long standing in Kashmir. It definitely attracted notice for the first time in 1906, when there was a severe outbreak in the State mulberry nurseries, near Srinagar. Previously there is no record of losses in the mulberries from disease, but it is quite possible that earlier outbreaks would have escaped attention, and there is nothing to indicate that the disease is a new one. In the two years since 1906, the damage has been slight in the nurseries; probably the climatic conditions which favoured attack on the young trees have not since been repeated. Outside India the disease is only known in Japan, whence it was described for the first time, and the fungus named by Nomura* in 1904.

Nursery stock is not alone affected. It is fairly prevalent on full grown trees of all ages in different parts of the Valley, and must be responsible for a considerable reduction in the output of leaves.

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* Nomura, H. Intorno alla ruggine del Rengeso (Astragalus sinicus L.) e a due micromiceti patogeni del Gelso (Atti Istit. Bot. Univ. Pavia, n. ser., Vol. IX, 1904, pp. 13-14).

The parasite attacks the smaller branches, usually near the base. It is rare on those over an inch in diameter and is localized, extending only from one to three inches along the branch. At first it is usually confined to one side, but it always eventually affects the whole circumference of the attacked portion. Externally it is visible by the bursting out of a number of hard black cushions of fungus tissue, through angular cracks in the bark (Plate I, fig. 1). The whole of the affected area is slightly depressed and darker than healthy portions of the branch. The branch is killed above the attack, but internal spread backwards to healthy parts of the tree does not occur. The disease is thus truly local, attacking and killing individual branches only ; where the attacks are multiplied, the whole tree naturally suffers through insufficient nourishment. Some old trees were seen, much stunted, covered with dead branches, and bearing leaf only on feeble shoots arising directly from the trunk or older wood ; it is possible that these may be eventually killed, but no case where death resulted was seen. In the young nursery stock the attack may occur on the main stem near the ground level. In the outbreak of 1906, seedlings of the second and subsequent years were attacked and had to be cut back right to the ground in many cases. They then for the most part threw up healthy shoots from below. The young tree in the foreground of the photograph, reproduced in Plate I, fig. 2, was affected at the base of the leading shoot, just above a large pruned-off branch. This position near a cut branch or above a fork is very common and a possible explanation will be given below. Old trees are usually attacked in the young shoots of the current year's growth, which arise immediately below branches broken off during the silk-worm rearing season in April.

The fungus is not confined to living mulberry trees, but is also found on dead prunings and broken off branches on the ground. On these it may cover the whole of the branch, instead of a small part, as on living trees. It would thus appear to grow more freely within dead than within living tissues. Many parasites have this character, but are none the less destructive to living plants when they come into contact with them.

It has already been mentioned that the seat of attack is usually near the ground or above a fork in seedlings, and near the scars left in breaking off branches in older trees. The outbreak in 1906 followed a heavy fall of snow in the early spring; this partly thawed and was succeeded by frost. The result was, as pointed out by Monsieur Peychaud, Director of Horticulture, Kashmir, that the seedlings were nipped near the ground and above the larger forks where snow had collected, and the bark was injured. The attacks in the older trees are always near a wound. The branch shown in Plate I, fig. 3, which is one of many such seen, shows a patch of infection around every scar left by removing the leaf-bearing side twigs during the plucking season. These facts all point unmistakably to the fungus being one of the large class known as "wound parasites" common in woody plants. Such parasites, as the name implies, attack their victims only through wounds, not through the unbroken surface of the plant. Anything which injures the surface—not only pieces broken or cut off but the holes made by insects and the bruises caused by hail or ice—may be sufficient to allow of penetration.

The wound parasitic fungi are found most commonly on dead wood. Ordinarily they are unable to grow through the cork which forms the protective bark of living trees. If this be cut away and the wood below exposed, many of them can then penetrate and exist by consuming the living tissues of the tree. Even in these cases, however, entry is much facilitated by the wound having been made in such a manner as to kill a portion of the wood as well as removing the bark. The fungus grows for a time on the dead wood around the wound, and having accumulated a store of nourishment, gains vigour enough to enable it to attack the living tissues beyond. Hence, while all wounds that are sufficiently deep may admit a parasite of this nature, wounds which are not clean-cut, but are jagged and leave splinters of dead wood attached to the tree, do so much more freely.

A careful search for *Coryneum Mori* on other plants led to its discovery on a rough-leaved jungle tree, *Celtis caucasica* (Kash. *Brimij*). It produces an exactly similar disease to that on mulberry. The tree is not uncommon in the cultivated parts of the Valley, but is not likely to play much part in disseminating the disease.

DESCRIPTION OF THE PARASITE.

THE body of the parasite, as of fungi generally, is composed of numerous branching threads. These penetrate throughout the tissues of the attacked portion of the branch, where they are naturally hidden from view ; they can only be seen on examining microscopically very thin sections of the wood, such as that, a portion of which is shown in Plate II, fig. 2. The examination of such sections shows that every part of the branch-tissues becomes infected, pith, wood, bast and bark. Towards the centre of the branch the threads are mostly colourless, while nearer the surface they are deep brown. They vary greatly in size, from large thick-walled brown threads, such as those in the large vessel of the wood to the left in fig. 2, to fine colourless ones in the small cells of the inner part of the wood and in the pith. They grow from cell to cell with the greatest ease, boring through even the thick walls of the large vessels. Towards the surface of the wood they begin to accumulate into twisted, brown masses. These increase in the inner layers of the bark, and it may be noticed that whereas the walls of the wood-cells are not materially altered, those of the bast and inner bark are largely destroyed by the dense fungus growth. Immediately under the cork cells of the bark, numerous solid cushions of fungus tissue are formed by the continued branching and intertwining of masses of threads. These become divided by cross walls into rounded or angular cells, whose appearance in section under the microscope is shown in the central part of fig. 1, plate II. Along the margin of these cushions, spores are produced in large numbers as shown in the figure, and, by the continued growth of cushions and spores, the bark is ruptured. Hence each of the ruptured areas on the bark visible in the photograph in Plate I, fig 1, is lined by a black cushion of the fungus similar to that shown in vertical section in the figure, from the surface of which quantities of spores are set free into the air. The mode of formation of the spores is shown in fig. 3, and the different shapes assumed by them in fig. 4. *

The spores germinate readily in water, putting out colourless threads from several of the cells into which each spore is divided (fig. 5). These threads branch freely and become divided up into short lengths by cross walls. Infection of the wounds on mulberry branches no doubt takes place as the result of such spores (which are very minute, measuring only from 25 to 40 by from 10 to 18 thousands of a millimetre in diameter) being blown about from the branches of previously attacked trees or from prunings on the ground. The threads penetrate into the wood and there take the appearance shown in fig. 2. Fig. 4, plate IV, shows the microscopic appearance of the threads produced from spores germinated on dead mulberry wood in a moist still atmosphere ; under these conditions the fungus forms a fine white or grey mould-like growth on the surface of the wood. It will be noticed that the side branches show a tendency to fuse by their tips with other branches.

Treatment.—In considering the best methods of checking this disease, the two cardinal points to be borne in mind are that the parasite can be found on dead branches and twigs of the mulberry, whether prunings or broken off from any other cause, and that all its characters go to show that it is a wound parasite, attacking healthy trees only through unhealed scars left when branches are removed.

It is a fortunate circumstance that in Kashmir, as in most other parts of India, dead wood of any sort is not left long on the ground, but is promptly gathered for firewood. In the nurseries, however, this is not the case, and here care should be taken that the prunings and all broken twigs are regularly removed and burnt. Excepting for this matter the treatment of the trees in the

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* The spores are often divided by vertical as well as by cross-walls, as the figures show. In the genus *Coryneum* the walls are usually transverse only. A few species are, however, already known that have occasional vertical walls (e. g., *Coryneum Notarisianum* Sacc. on oak and birch twigs), and it seems better to refer the mulberry fungus to this genus than to form a new one to receive it.

nurseries leaves nothing to be desired. The young trees are exceptionally strong, and the pruning is such as to secure well-shaped trees, capable of bearing the maximum quantity of leaf if properly treated afterwards. The superfluous wood is removed by clean cuts, which are rapidly healed by the formation of protective wound tissue. Except in the event of unavoidable injury such as that caused by frost in 1906, there appears to be no reason to anticipate a recurrence of the disease in a severe form in the nurseries.

The condition of the trees from which leaf is actually gathered in the silk-producing villages is very different to that of those in the nurseries. They are of all ages and sizes, up to very large old trees preserved, no doubt, by the rule prohibiting the felling of mulberry trees in the Valley. Contrary to what should be the case, the young trees are not, at least in those villages that I visited, giving as much leaf proportionately to their size as the old ones, and neither are giving nearly as much as they should under proper treatment. This is entirely due to the neglect of pruning and to the manner in which the leaf is gathered.

It would be impossible to exaggerate the damage which is caused at present by the clumsy and ruthless treatment of the bearing trees. I should say that it is quite out of the question for the industry to maintain its present extent, much less to increase, unless this matter is more carefully attended to and the care of the trees secured by instruction and stringent regulations.

The pruning of the mulberry tree is little, if at all, less essential than that of the tea bush, where it is considered by many to be the most important individual operation in the tea gardens during the whole season. The objects aimed at are in both cases the same :—to induce the plant to assume a convenient shape, to increase or keep at a high average the yield of leaf, to retain or improve the quality of the leaf, and finally, to maintain these conditions for the longest possible time. In the silk-producing parts of France and Italy pruning is a highly scientific process and is almost universal in one form or another. A full account of the different methods adopted may be found in the "Traité sur le Ver à Soie du Mûrier et sur le Mûrier" by Maillot and

Lambert, published by Masson & Cie., Paris, in 1906. Even where regular pruning is not practised, care is taken to remove all dead wood, withered twigs and such as are useless for good leaf-production.

While there can be no question of the value of pruning, it is necessary to point out that bad pruning is often worse than none at all. The best results will be obtained if the plants are regularly pruned on a definite system from the nursery onwards. This could be quite easily secured in the young trees which have been distributed from the State nurseries, by periodical inspections. The treatment of the older trees is more difficult as they have been allowed to get into a condition from which it would usually be hopeless to expect to secure well-shaped trees. The most that can be done is to attempt to restore their vigour by judicious removal of all weakly shoots and of the less productive wood. What can be done in bad cases is shown in the photographs reproduced in Plate III, which were taken in the nursery under M. Peychaud's charge at Harwan. But the greatest care should be taken to secure clean-cut wounds, and where the axe is used at all, it should be followed by trimming with a sharp knife. The methods followed at Harwan may be taken as a safe guide.

As already mentioned, *Coryneum Mori* can grow on dead mulberry wood on the ground. It is not less common on dead twigs found on the trees, and every such twig left may serve to increase the production of spores and the consequent danger of infection to healthy parts.

The systematic pruning of the trees is called for not only on account of the necessity of removing all dead and weakly twigs and useless wood in view of the manner in which the injurious action of the twig fungus is favoured by their presence, but also because of the improvement in the quality and amount of leaf which it causes. The two photographs reproduced in Plate III show the result of pruning. They were taken from trees of the same variety growing near together and about the same age. The pruned tree is thickly covered with strong leaf-bearing shoots and the leaves are large. It was entirely free from disease. In the unpruned trees a number of the branches (of which some are visible on the extreme left) have been killed by *Coryneum Mori*; the remainder are scantily furnished with small, ill-nourished leaves. Though the branch system is larger, the total leaf is much less. It is well known that the quality of the leaf has a marked effect on the health of the worms and on the amount and quality of the silk produced. There can be no doubt from a comparison of the photographs that the pruned tree is superior in quality of leaf as in every other respect to the unpruned.

In Europe it is usual to gather the leaves only, whereas in Kashmir branches are taken; it is apparently contended by some that this, in large trees, serves the purpose of pruning. This would probably be the case to a certain extent if the branches were cut with any system and if the cutting were done with reasonable care. As it is, the trees are being directly injured instead of improved in power of leaf-production and in quality of leaf, by the hacking to which they are subjected. Branches thicker than a man's finger are not supposed to be taken, but little attention is paid to this regulation, and it is probably not a useful one if applied indiscriminately. On young trees it does not prevent over-plucking; on old, it leaves much of the useless wood behind. Trees can be seen in most villages in which so much young wood has been removed that the leaf-bearing twigs of the current year's growth spring largely from the trunk or main branches. Such shoots are usually of short growth, bear often small leaves, and never form the basis for a new system of leaf-bearing shoots in the following year. In many comparatively young trees seen, the leaf-bearing shoots were for the most part dead at the tips and for a variable distance back from the tips. This condition, which is known as "dying back," is a common result of defoliation of plants from any cause, such as the attacks of insects or fungi or from frost. Excessive plucking of leaves in tea and mulberry is known to lead to dying back, and an examination of the trees left no doubt that this was the cause here. The very rapid growth of the industry in the last few years is responsible for this state of affairs. The smaller trees, being easily reached, are stripped of the greater part of their young leaf-bearing woo during the rearing season. The sudden loss of a large proportio of leaf so affects the upward current of water and food materia from the soil that the younger tissues of the twigs dry up and di of inanition.

This over-plucking affects chiefly the younger trees, as th older are not so easily denuded. Trees of all ages are, however injuriously affected by the manner in which the branches ar gathered. If the cutting were done with a proper implement s as to secure a clean-cut surface on the part attached to the tree the wounds would be rapidly occluded and strong young shoot would be thrown out below the point cut. As a matter of fact clean cuts are the exception rather than the rule, and much of th crop is apparently obtained by the simple method of breaking th twig in the hand, leaving naturally jagged splinters and wound behind. The parts immediately around and below these wound rot and die as with any other tree, and the buds just below th portion removed, whence the next season's leaf should come, ar often killed outright or injured. Numbers of twigs of the curren year's growth may be seen springing from the margins of ol ragged wounds, and these bear, as might be expected, small feebl leaves and show a tendency to die back from the tip.

Unoccluded, jagged wounds with dead splinters attached, o just the sort that will most readily allow of infection by a woun parasite, the presence of the latter on dead twigs attached to th trees, numbers of weakly shoots arising from the injured branches these are the conditions which are common in the mulberries of th silk-worm rearing villages, and which constitute a real danger t the industry. That under favourable conditions the twig fungus i capable of causing great damage, is evident from the experienc in the nurseries in 1906. The two years that have intervened ma be taken to be years when conditions were against the parasite ; th nurseries have practically escaped, though the losses in the villages are appreciable. Heavy injury to older trees was not reporte in 1906, but would not be so likely to attract notice as in th nurseries ; there is no reason to believe, however, that the forme are less liable to injury from this cause than the latter. The reverse is likely to be the case. The great increase in the demand for food for the worms in the past few years has greatly improved the prospects of the parasite finding wounds through which it may gain an entry into the trees. Hence there is a decided possibility that the disease is on the increase, and it would seem advisable to attempt to diminish the annual moderate loss and the risk of periodical heavy losses.

The first requirement is an improvement in the manner of obtaining the crop. As already mentioned, branches, not individual leaves, are gathered. I could not discover any real reason why this is done except that the worms are fed on the floors of the houses instead of on frames, and the presence of branches ensures a certain amount of ventilation from below and enables the worms to mount when about to form cocoons. From the point of view of diminishing risk of infection by *Coryneum Mori* leaf-plucking would be preferable. Frames would not be expensive and the capacity of the rooms would be increased. The relative advantages of the two systems under the conditions prevailing in Kashmir might be more fully inquired into and the change gradually introduced if found suitable.

A good cheap knife for cutting the branches is much needed. Several patterns of pruning implements are used in France and Italy, each with its own advantages. Some are described and figured in Maillot and Lambert's book referred to above. There would be no difficulty in making the simpler forms in Srinagar, probably very cheaply. The cutting implements used in Kashmir in gathering the branches are primitive to a degree and incapable of producing a clean cut.

Every opportunity should be taken of instructing the silk-worm rearers regarding the necessity of removing the branches in as clean a manner as possible, and of trimming the wound where necessary so as to avoid leaving splinters attached to the tree. Clean wounds will heal naturally and rapidly and the danger of infection will be reduced. At the same time the injurious results of over-plucking should be explained.

During the pruning operations special attention should be paid to removing all dead twigs and unproductive or feeble wood. This is a point which is liable to be overlooked, but its importance is great, not alone directly because of the danger from twig disease, but also because such wood is merely a drain on the tree and diminishes the quality of the leaf. The prunings should, of course, be burnt, but this will probably not require any special precautions being taken as they will be removed for fuel as soon as permission is given. In the nurseries this point requires to be attended to.

Once pruning is adopted as a regular practice and the methods of gathering the crop are improved in the manner indicated above, I feel confident that all real danger to the industry from an increase in this disease will disappear.

Mulberry Leaf-spot.

(*Septoglœum Mori* (Lév.) Briosi & Cavara.)

This disease is extremely common in Europe where it is sometimes called mulberry leaf-rust though caused by a fungus not belonging to the true rusts. It occurs throughout Kashmir, but does not appear to cause much damage except in the moister parts.

It affects chiefly the younger leaves, which become covered with angular spots, pale brown in the centre and surrounded by a dark reddish-brown band (Plate IV, fig. 1). On the upper surface of these spots, and sometimes also on the lower, little raised pustules appear. In moist weather these swell up into rounded blisters of a pale colour from the development of numerous colourless spores. Affected leaves drop off prematurely and are avoided by the worms. In bad cases the reduction in leaf is said to amount to ten per cent. in individual trees, but this is only likely to occur in seasons of exceptional moisture, and even then is not likely to be general.

The spots are caused by a fungus whose filaments penetrate the tissues of the leaf but are limited in growth and affect an area usually not exceeding a quarter of an inch in diameter. After sufficient food has been accumulated from the living cells of the leaf (which are killed and turn brown) the parasite comes to the surface to form spores. Cushions of dark fungus hyphæ are formed beneath the leaf epidermis, where they are early visible as small raised black dots. On the surface of these the spores appear and burst through the epidermis to be shed into the air (fig. 2, plate IV). The spores (fig. 3) are elongated, colourless, rounded at the ends, divided into segments by three to five cross-walls, and usually curved. They germinate readily in water and new spots are caused by the penetration of threads from germinating spores into the tissues of the leaf.

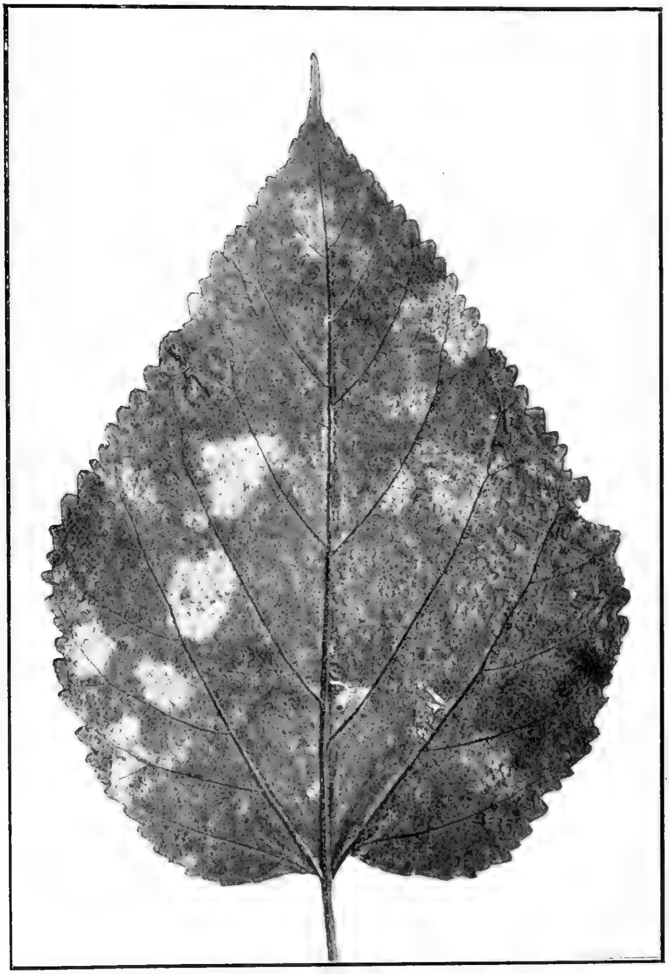
Treatment would not repay expenses in ordinary mild cases. In the nurseries it might become necessary in the event of a bad attack, when spraying with Bordeaux mixture would probably be effective. Pulling off and burning spotted leaves early in the season would much reduce the spore formation and consequently the spread of the disease from leaf to leaf.

Mulberry Mildew.

Phyllactinia Corylea (Pers.) Karst.

The mulberry mildew is fairly common in India and occurs also in Japan and Madagascar, but not, it would seem, in Europe. It has hence not been the subject of detailed researches, especially in the direction of treatment, as have the allied vine mildew and other common European mildews. Fortunately the disease does not appear to be ordinarily a serious one in Kashmir. In Madagascar it is said to attack, above all, mulberry trees planted near paddy fields or exposed to winds that have blown across marshy land. The losses are heavy in these cases, and would, no doubt, be equally heavy in India under similar conditions.

The fungus attacks only the leaves. These are covered with a fine white powdery layer over the whole or a part of the undersurface, and are sometimes deformed or stunted, especially if attacked when young. They are not liked by the worms and eventually turn brown and dry up. The parasite differs from the leaf-spot fungus in developing chiefly on the surface of the leaf and only sends short sucker-branches into the air-pores and the air-cavities lying below (fig. 5, plate IV). From these, fine suckers penetrate into the leaf cells and kill their contents which are absorbed as food Instead of being limited in growth as in *Septoglœum Mori*, the threads ramify over the leaf surface for considerable distances and may eventually cover the greater part with their web.



MULBERRY MILDEW.

From the superficial web short branches stand up vertically into the air. On the top of each of these a single large spore is formed (fig. 5). The spread of the fungus from leaf to leaf is due to these spores breaking off from their stalks and being blown on to the under surfaces of healthy leaves where they germinate and give rise to a fungus web which sends sucker-branches into the leaf.

A second spore-form is known but has only been found on a small number of leaves. It is produced in little hard reddish black receptacles visible to the naked eye as small, round, shining grains lying on the surface of the old webs (fig. 6). Inside each is a number of thin-walled sacks within which two or three spores are ultimately developed. It is probable that the latter ripen slowly, as mature spores were not found in any of those examined. This spore-form is concerned with the transmission of the fungus from season to season and through periods when food in the shape of living leaves is not available.

Though, as already said, treatment has not been tried, experience with allied diseases enables one to say with fair confidence that sulphur dusting, as practised in the vineyards against vine mildew (*Oidium*), is likely to prove successful. Or the leaves may be sprayed with potassium sulphide (liver of sulphur) solution, made by dissolving half an ounce of the sulphide in a pint of hot water and making up to one gallon with cold water. This is not likely to be required except in the nurseries, and from what I saw in 1908, is not at present required there.

The mildew is more destructive to young plants than to full-grown trees. Its attacks are likely to be worst in low-lying places and like most mildews damp hanging ground-fogs greatly favour its spread. Hence, in opening new nurseries, the site should be selected so as to avoid these conditions as far as possible. Similarly in planting out the nursery trees in the villages, high ground should be selected in preference to low, particularly in the lower parts of the valley, adjoining the Wular and Dal Lakes.

MULBERRY TRUNK-ROT.

Polyporus hispidus (Bull.) Fr.

THIS fungus belongs to the class of the large bracket-fungi which are familiar objects on the trunks of trees and on old logs. It is extremely common on mulberries and was found also attacking apple, plum and apricot trees in Kashmir. In Europe it is known on these as well as on several other broad-leaved trees.

It is found usually on the trunk but also attacks the larger branches. Being a "wound parasite" the infection takes place by means of spores lodging on the scars which are so common on Kashmir mulberries owing to the manner in which the leaf is obtained for silk-worm food. In the scars left by removing large branches a portion of the heart-wood is exposed, and it is here that infection occurs. Scars left by breaking off small twigs which have no heart-wood, are not liable to attack, though, as already mentioned, they are the usual place of entry for the twig-disease fungus.

When the spores germinate, the young threads penetrate into the branch heart-wood and from that to the heart-wood of the trunk, attacking first the central portion and then the outer, younger layers. The tissues are little by little destroyed from within out, becoming soft, spongy and yellowish white. Separating the outer healthy layers of young wood from the rotten central portion, is a hard brown zone, consisting of cells filled with a brown, gummy matter ; in this the parasite takes its main development. It is nourished in the brown zone mainly by the cell-contents while the walls are at first left unaltered. Only at a later period, when the cell contents are exhausted, is the wall corroded and the wood itself softened.

Branches attacked by this heart-rot dry up and die. The trunk may be almost completely hollowed, but often a ring of still living wood is left, which is sufficient to keep the crown green. In most cases it is probable that rotted trees are blown down before the parasite can directly cause their death, for while partially rotted and hollow trees are fairly common, few that are obviously near death can be found.

The fungus is perennial within the tree, and about August each year grows out to the surface to form spore-bearing organs. These appear externally on the trunk or main branches, and can be artificially induced to form, by exposing the heart-wood of a part where the threads are numerous, and keeping the wound moist.

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surface becomes strongly convex, the lower less or almost flat. Soon the colour deepens into a characteristic chestnut shade on the top, while the upper surface becomes clothed with thick soft hairs formed of agglutinated threads. At the same time hundreds of small pores are formed on the under surface, and these develop into long yellowish brown tubes, which often exude water in drops while forming, even in dry weather. The body remains soft until quite old when it becomes hard, black, shrunken and cracked. The inner flesh always retains a deep yellowish or almost chestnut brown.

Within the tube, spores are formed in large numbers on special cells which line their walls. Each such cell bears four spores on short stalks. The spores are smooth, single-celled, egg-shaped and brown. They are shed through the tubes into the air. Infection only takes place by means of spores blown from the spore-bodies on the surface of diseased trees.

The remedy consists in cutting out the affected part, when this is a branch, and can be recognised by the presence of the spore-bearing bodies ; in taking care to remove and destroy the latter as soon as they are noticed on the surface ; above all, in endeavouring to reduce chances of infection by removing the branches during pruning or when feeding the worms, in such a manner as to promote rapid healing of the scars. It is noticeable that the fungus is much commoner on mulberries than on apples or plums, and this is undoubtedly due to the abundance of unhealed wounds on the former.

It is probable that the regulation prohibiting the felling of mulberry trees in the Valley is too strictly enforced. There are many old trees hollowed by the action of trunk-rot, which would be better out of the way. They yield leaf of poor quality and bear annual crops of *Polyporus hispidus* which must lead to the infection of neighbouring trees. It would be a comparatively simple matter for the mulberry inspectors to mark such trees, whose removal could then be permitted on condition that they are replaced by a certain number of seedlings.

DESCRIPTION OF THE PLATES.

PLATE I.

Fig. 1. Base of leading shoot of young tree of *Morus alba*, showing external characters of attack by *Coryneum Mori*. From a photograph.

,, 2. State mulberry nursery, Harwan, Kashmir, with young tree attacked by *Coryneum Mori* in foreground. From a photograph.

,, 3. Branch from a bearing mulberry tree, showing a patch of twig-disease at each scar left by removing side twigs.

PLATE II.

,, 1. Vertical section through a cushion of *Coryneum Mori* in the bark of *Morus alba*. Magnified 125.

,, 2. Portion of a transverse section through the wood of a twig of *Morus alba* attacked by *Coryneum Mori*, showing the fungus threads in the cells and vessels of the wood. Magnified 500.

,, 3. Cells at the surface of a cushion of *Coryneum Mori* bearing spores. Magnified 500.

,, 4. Spores of *Coryneum Mori*. Magnified 500.

,, 5. Germination of the spores of *Coryneum Mori* when sown in water.

PLATE III.

,, 1. Pruned tree of *Morus alba* at Harwan. From a photograph.

,, 2. Unpruned trees of same variety and growing near by. Many of the terminal twigs, especially of the tree to the left, have been killed by *Coryneum Mori*. From a photograph.

PLATE IV.

,, 1. Mulberry leaf-spot (*Septoglœum Mori*) on leaf of *Morus alba*. Natural size.

, 2. Section through a pustule of *Septoglœum Mori* on mulberry leaf. Magnified 333.

,, 3. Spores of *Septoglœum Mori*. Magnified 666.

,, 4. Portion of the aerial growth resulting from the germination of spores of *Coryneum Mori* on the surface of a block of mulberry wood.

,, 5. Section through a mulberry leaf attacked by mildew (*Phyllactinia Corylea*) showing external web sucker-branches penetrating the air-pores, and spore-bearing branches projecting downwards into the air. Magnified 333.

6. Durable spore-receptacle of mulberry mildew. Magnified 70.

PLATE I.

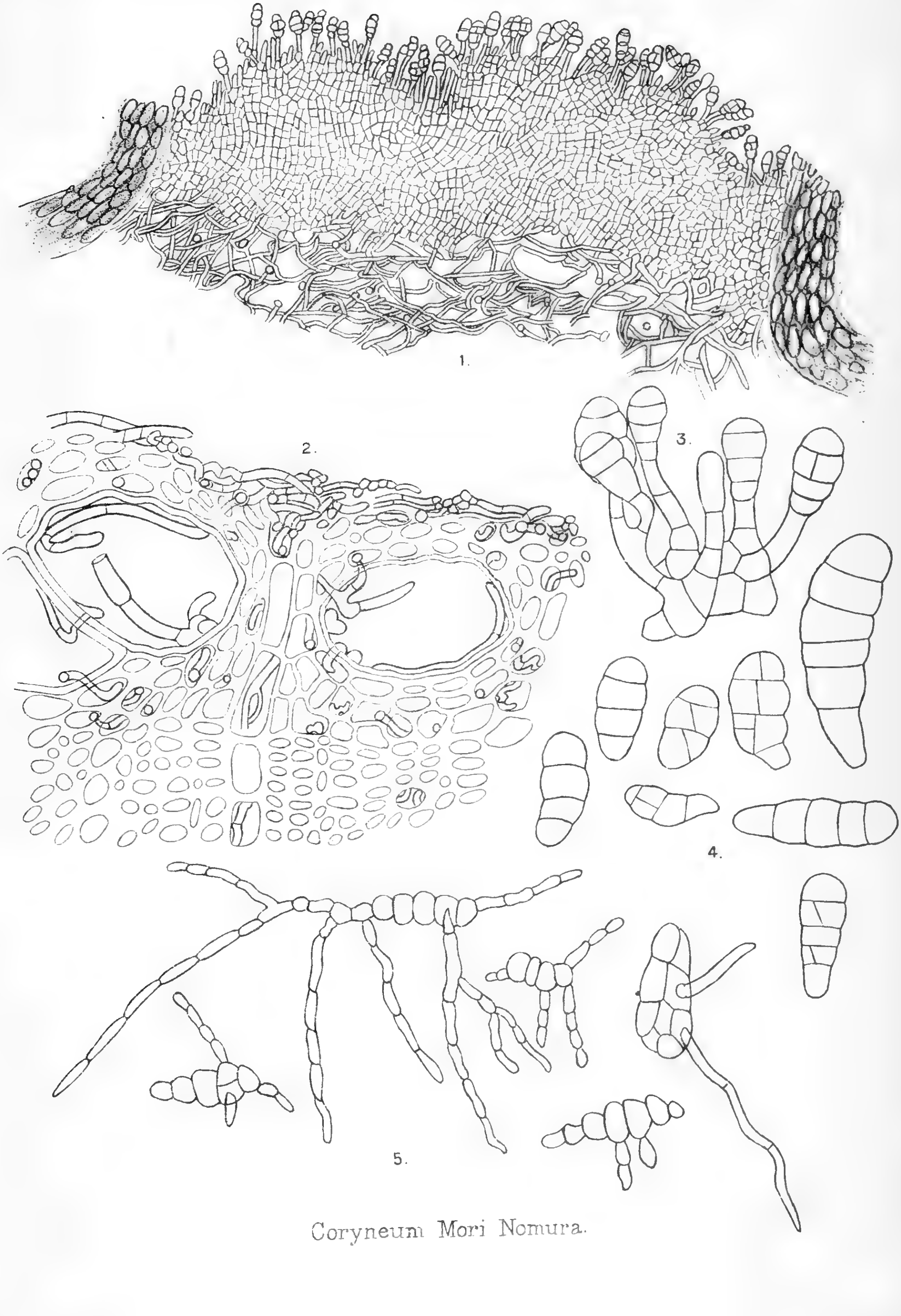
FIG. 1.

FIG. 2.

CORYNEUM MORI ON MORUS ALBA.

FIG. 3.

PLATE II.



Coryneum Mori Nomura.

PLATE III.

FIG. 1. PRUNED.

FIG. 2. UNPRUNED.

EFFECT OF PRUNING MULBERRY TREES.

ERRATUM.

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VOL. II, No. 8.

THE MULBERRY DISEASE CAUSED BY CORYNEUM MORI NOM. IN KASHMIR, WITH NOTES ON OTHER MULBERRY DISEASES.

BY

E. J. BUTLER, M.B., F.L.S.

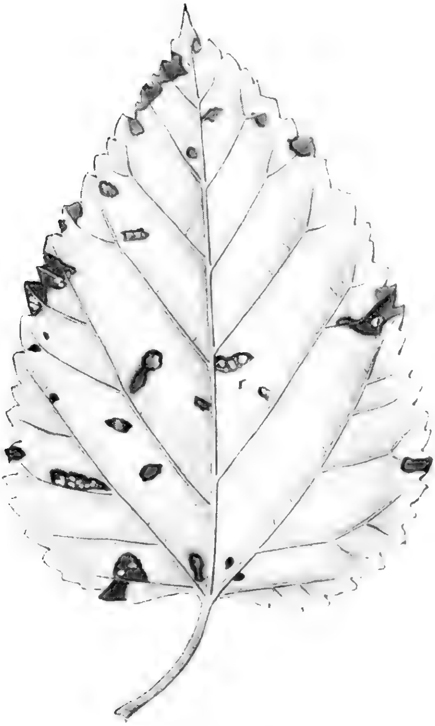
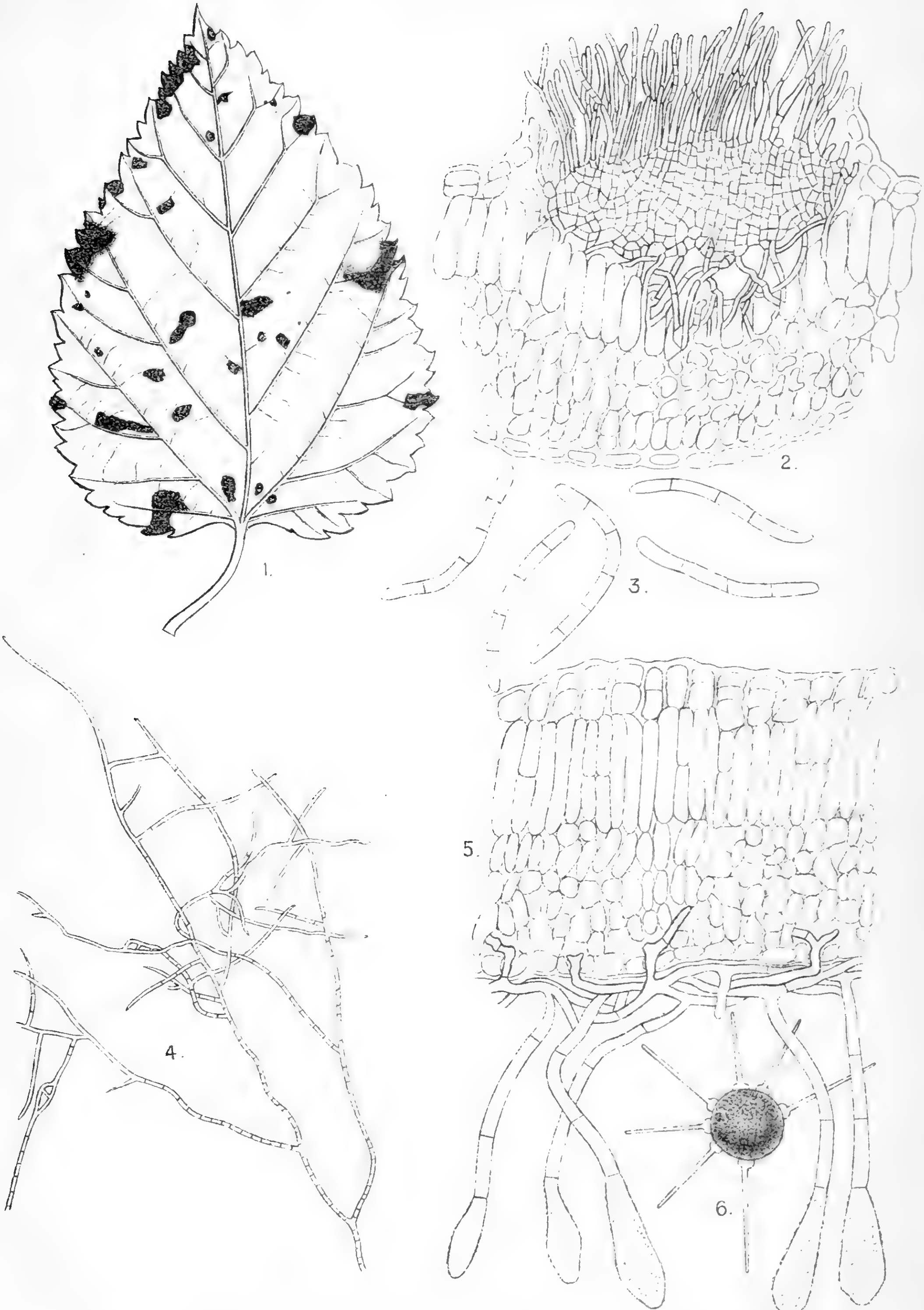


PLATE IV, FIG. 1.

(Substitute this for existing figure.)

PLATE IV.



Septogloeum Mori (Lév.) Briosi & Cavara (figs. 1-3.) Coryneum Mori Nomura (fig. 4.) and Phyllactinia Corylea (Pers.) Karst. (figs. 5-6.)

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THE WILT DISEASE OF PIGEON-PEA

AND

THE PARASITISM OF NEOCOSMOSPORA VASINFECTA SMITH

BY

E. J. BUTLER, M.B., F.L.S.,
Imperial Mycologist

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January, 1910.] BOTANICAL SERIES. [VOL II, No. 9

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CHAPTER I.

THE PIGEON-PEA NECTRIA.

IN 1906 the writer (1) [1] described diseases of pigeon-pea (Cajanus indicus) and black pepper in India, with all the characters of the large group of wilt diseases induced by parasites of the genus Fusarium, which have recently attracted the attention of mycologists in many parts of the world.

The symptoms on pigeon-pea were such as would arise from a total or partial stoppage of the water-supply from the roots to the aerial parts of the plant. The result was a "wilting" or withering, more or less sudden according to the degree to which the root system was involved, and the intensity of transpiration at the time. The xylem vessels of the root were in all cases found to be plugged by masses of hyphæ, offshoots from which extended into the parenchyma of the central cylinder and into the cortex. On short simple branches within the larger vessels small elliptical spores were found budded off apically; pure cultures obtained from these proved them to belong to the form-genus Cephalosporium. Within the vessels were also sometimes found special durable thick-walled cells (chlamydospores) attached to the hyphæ in various ways and capable of germinating on being sown in water.

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[1] These numbers refer to the bibliography at the end of the present paper.

Besides these two spore-forms found attached to the hyphæ within the plant tissues, two others were found on the surface of the bark over blackened areas which occur on diseased plants at the base of the stem. One of these was a Nectria, characterised by bright red perithecia within which were numerous cylindrical asci, each with eight colourless, bicellular spores. The other, which was always present in great quantity on the bark, was a Fusarium, a genus the members of which are in several cases known to be merely the lower stages of species of Nectria and allied fungi.

Pure cultures made from the Nectria ascospores gave rise in turn to Cephalosporium, Fusarium and chlamydospores indistinguishable from those found as described above on the diseased plant. The Nectria form itself was not again obtained in these cultures, though some of them were maintained for more than two years on a large variety of media. It was, however, once obtained in culture from the similar fungus found on black pepper.

Infection experiments with pure cultures of the fungus were carried out. As mentioned on page 28 of the previous paper, the results were irregular, the inoculated plants taking the disease in some of the experiments and not in others.

As the details of these were not given, the results of a few may be summarised here.

Experiments with Nectria and Cephalosporium from wilted Pigeon-pea.

A preliminary experiment showed that infective material occurred on the surface of diseased roots and of the base of the stem, a washing from these parts after they had lain for two days in a moist chamber, proving fatal to healthy plants.

SERIES I.

The culture used was a nutrient gelatine subculture from a plating from the surface of the bark of a wilted plant, overlying a blackened area in the wood where the tissues were full of hyphæ, and chiefly consisting of Fusarium spores. The subculture was salmon-pink in colour, as the Fusarium beds on the bark of the wilted plants are. It was determined microscopically to contain both unicellular conidia formed at the tip of short lateral branches and elongated curved several-celled spores, and to agree entirely with the Cephalosporium and Fusarium stages of the Nectria. It bore no perithecia either then or in subsequent subcultures.

The plants were grown in 24 flower pots, seeds, soil, and pots being unsterilised.

The inoculation was made by sprinkling the culture, broken up in distilled water, over the seeds and soil, after sowing but before covering with soil, 12 pots being thus treated, while 12 were left uninoculated to serve as controls.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
32 plants in 12 pots.	Inoculated with Fusarium and Cephalosporium spores.	Sown and inoculated. 22-11-04.	1 plant wilted on 23-1-05. 3 plants wilted on 25-1-05. 2 plants wilted on 29-1-05. 1 plant wilted on 30-1-05.	All the remaining plants were killed by frost on the night of 30-1-05.
27 plants in 12 pots.	Not inoculated (control).	Sown 22-11-04.	No deaths up to 30-1 05.	

This experiment showed that pure cultures of a fungus present on the bark of wilted pigeon-pea plants and agreeing with the Cephalosporium and Fusarium stages of the Nectria found in the same locality are capable of producing wilt. Examination of the roots of three of the wilted seedlings showed them to be infested with hyphæ in the manner above described, and copious *Cephalosporium* spores were developed on the surface of the roots when they were placed in a moist chamber for a few days.

On February 25th the twelve pots that had been inoculated were resown with pigeon-pea. On April 19th two of this second batch of seedlings wilted in one pot. The roots of these were examined and showed clear signs of fungus-attack. Many of the lateral roots were marked by shrunken blackened patches, in some cases near the tap root, in others some distance away. Most of the fine rootlets arising from these had been killed, and the appearances suggested that the disease had originated in the latter and extended backwards to the larger roots. The tap root itself was unaffected. The parasite, therefore, remains in the soil and is capable of infecting successive crops of pigeon-pea, a fact which is besides only too evident from field experience of the disease. Observation of the remaining seedlings ceased soon after April 19th owing to my absence from head-quarters.

SERIES II.

The culture used was the 5th successive subculture (on pigeon-pea slab) from an ascospore of the Nectria already mentioned. It contained Cephalosporium and Fusarium spores, but neither it nor the four previous subcultures had given rise to perithecia.

The plants were grown in two pots in the same way as in Series I and sowing was done with germinated seeds.

The inoculation was made after the seedlings were up by scraping away the soil down to a lateral root and applying the culture to this.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
4 plants in 1 pot.	Inoculated with a subculture from Nectria.	Sown 25-2-05. Inoculated 8-3-05.	No deaths up to July 05.	On April 10th made the number of plants up to 6 with germinated seedlings.
6 plants in 1 pot.	Not inoculated (control).	Sown 25-2-05.	,, ,, ,,	

Pure cultures originating from Nectria ascospores, therefore, failed to produce the disease.

SERIES III.

The culture used was the same as that in Series II.

The plants were grown in 8 pots in the same way as in the previous experiment, The inoculation was made by sprinkling the soil with the culture broken up in distilled water.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
7 plants in 4 pots.	Inoculated with a sub-culture from Nectria.	Sown 2-3-05. Inoculated 8-3-05.	No deaths up to July 05.	On April 10th made the number of plants up to 6 in each pot with germinated seedlings.
10 plants in 4 pots.	Not inoculated (control).	Sown 2-3-05.	,, ,, ,,	,, ,, ,, ,,

As in the previous experiment cultures from Nectria ascospores failed to produce the disease.

SERIES IV.

The culture was obtained as in Series I, the colony taken from the plate being one of a large number bearing Cephalosporium spores.

The plants formed part of two long rows growing in a field plot and about a month old.

The inoculation was made as in Series II above.

No. of plants.	Treatment.	Date of inoculation.	Result.
100	Inoculated with Cephalosporium originating from the surface of a wilted pigeon-pea root.	Last week of August 03.	8 plants had wilted by 6-10-03 when observations ceased.
Remainder of the rows (several hundred).	Not inoculated (control).		No deaths.

This experiment, so far as it goes, agrees with the results obtained in Series I.

CHAPTER II.

NEOCOSMOSPORA VASINFECTA SMITH.

The above experiments, except Series IV, were carried out at Dehra Dun where the Mycological Laboratory of the Indian Department of Agriculture was then situated, and the material used was all obtained in that locality. Series IV was carried out at Poona. As they were evidently unsatisfactory, work was continued at Pusa in 1907-08. The pigeon-pea wilt is common in the vicinity and provided abundant material for investigation.

Early in 1907 perithecia of the well-known fungus *Neocosmospora vasinfecta* were discovered on the roots of wilted plants. As a large proportion of the wilt diseases of plants hitherto investigated has been attributed to forms of this fungus, the discovery was significant, and further search showed that most of the dead roots examined either already bore these perithecia or could be induced to produce them by incubation in a moist atmosphere. The most careful search carried on for two years at Pusa and other localities in the plains of India has been unsuccessful in finding the Nectria met with at Dehra Dun on this host.[1] On the other hand, Neocosmospora vasinfecta has been found on pigeon-pea roots from Dehra Dun and has proved to be widely distributed throughout Northern India.

This fungus was first described by E. F. Smith (2) in the United States, in connection with wilt diseases of cotton, water-melon and cow-pea. The symptoms in all three diseases were

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[1] This is not proof that it does not occur in its lower (Cephalosporium and Fusarium) stages. The Erysiphaceæ of the plains are common enough in the conidial stage, but perithecia are rare and in some species are apparently not formed. In the more temperate parts (as in Kashmir) perithecial forms of Erysiphaceæ are common. It is quite possible that the temperate climate of Dehra Dun favours the production of perithecia in the pigeon-pea Nectria, whereas the heat of the plains checks this stage and forces the fungus to reproduce by means of conidia alone.

similar and quite agree with those described above for pigeon-pea wilt. Within the tissues were found small unicellular conidia (microconidial or Cephalosporium stage), and on the surface larger falcate spores with several septa (macroconidial or Fusarium stage). Further, bright red perithecia occurred frequently on the roots of wilted plants and were proved by single-spore culture to give rise to micro-and macroconidia indistinguishable from those found in nature on diseased roots, and finally, in old cultures, to chlamydospores similar to those found accompanying the microconidia on the bark. The perithecia differ from those of Nectria in being found usually on the roots (whereas the pigeon-pea Nectria occurs on the stem, never on the roots) and in containing characteristic unicellular spores with a thick wrinkled brown wall. For this hitherto undescribed fungus Smith established the genus Neocosmospora, with one species N. vasinfecta (Syn. Fusarium vasinfectum, Atk.) on cotton and varieties tracheiphila and nivea on cow-pea and water-melon respectively.

The biology of the fungus was very fully investigated by Smith, particularly its behaviour as a pigment-producer, in which it shows certain definite characters. His experiments regarding its powers as a parasite led to less definite results, or rather showed that there were points in its life as a parasite that required elucidation. The chief of these were the following.

Though the fungus on cotton and cow-pea resembled that on melons in cultural characters and anatomical details and the diseases on all three were similar, he entirely failed to produce wilt in the first two cases by inoculating healthy plants with cultures of the fungus associated with the disease. In the water-melon on the other hand disease was easily induced by pure cultures of the fungus obtained from melon roots. All attempts at cross inoculations, using the fungus obtained from one host to inoculate the other two, failed. Hence, as stated on p. 46 of his paper, the parasitism of the variety on water-melon was fully established, while that of those on cotton and cow-pea was "not proved."

The virulent strain of the water-melon fungus was isolated from an internal microconidium and maintained its virulence as long as the work extended, through several years. No perithecia ever appeared in these cultures or in any made from external or internal conidia taken from cotton or water-melon. The genetic connection of the conidial forms on water-melon was proved, but not their connection to the perithecia. No inoculations were made with cultures derived from ascospores from the perithecia of the water-melon fungus. Hence, while it was proved that the water-melon wilt is due to a fungus possessing microconidial (Cephalosporium) and macroconidial (Fusarium) stages, it was not proved that this fungus is Neocosmospora vasinfecta ; the only evidence being that Neocosmospora possesses exactly similar stages.

Orton (3) in a paper published the year following Smith's, mentions that the cotton wilt had been subsequently produced in healthy cotton plants by inoculating the soil in which they grew with pure cultures of conidial stages of Neocosmospora vasinfecta. It is not, however, stated that these cultures were derived from ascospores; in other words, it is not proved (so far as the published observations go) that the fungus used really belonged to Neocosmospora vasinfecta.

More recently Reed (4) has endeavoured to throw doubt on the parasitism of Neocosmospora, in the case of a wilt disease of ginseng (Aralia quinquefolia). The disease agrees with that described by Smith and the fungus present resembles the conidial stages of Neocosmospora, to which Reed refers it while holding that it always follows in the path of other fungi, and is, therefore, only a weak parasite. As, however, perithecia were not observed, there is no evidence at all that Reed's work was done with Neocosmospora. When this was pointed out by Smith, Reed subsequently admitted that the two fungi may not prove to be identical.[1]

Outside of the United States wilt diseases of various plants have been attributed to Neocosmospora vasinfecta in several

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[1] See discussion in Science, New Series, Vol. XXVI, 1907, under heading, "The parasitism of Neocosmospora—inference versus fact" by E. F. Smith, p. 347, and "The parasitism of Neocosmospora" by H. S. Reed, p. 441.

instances. Delacroix (5) referred to it the Egyptian cotton wilt, and in the same paper suggested that the cause of a disease of carnations, previously investigated by him (17), was identical: Jaczewski (6) that of sesamum in Turkestan where he has also recorded it on cotton and Hibiscus (7) : Malkoff that of cotton in Sadovo (8) : Zimmermann that of cotton in German East Africa (9) : and van Hall that of the same host in the Dutch West Indies (10). In these cases, except Zimmerman's, perithecia were not found and the identification was made from conidial stages alone.

The absence of perithecia has led several observers to exercise greater caution in the identification of the parasites. Thus the "St. Johannis" disease of peas in Holland was attributed by van Hall (11) to "Fusarium vasinfectum Atk. var. Pisi," a terminology which while implying specific identity with the conidial stages of Smith's fungus, leaves the genetic connection with Neocosmospora open. Similarly Farneti (12) and Montmartini (13) used the terms Fusarium niveum Sm. and Fusarium vasinfectum Atk. for wilt diseases of cucurbitaceous plants and of Capsicum respectively in Italy.

In the important paper published by Schikorra (14) the name Fusarium vasinfectum Atk. var. Pisi van Hall is retained for the parasite of the "St. Johannis" diseases of peas, but the author is careful to point out (p. 173), that further investigation is necessary to decide how far the various Fusaria found within the vascular bundles of cultivated plants belong to one or to several different species.

So far as I have been able to ascertain, Neocosmospora vasinfecta Sm. has only been found in its perithecial stage, outside of the United States, by Zimmermann in German East Africa until its discovery in India in 1907.

The resemblance between its conidial stages and those of the Nectria found on wilted pigeon-pea in Dehra Dun was at once evident. Figs. 3, 4 and 5, plate II, of the writer's previous paper may be compared with fig. 6, plate V, fig. 9, plate III, and fig. 7, plate II. of Smith's paper on this point. Microscopical preparations taken from cultures on nutrient agar, showed no definite character by which the conidial stages of the two fungi could be differentiated.

As the successful infection experiments carried out at Dehra Dun were made with conidia obtained from the roots of pigeon-pea and not directly from Nectria ascospores, it at once became evident that these conidia might have belonged to either of two distinct fungi, Nectria or Neocosmospora, and that in this might lie the explanation of the irregular results obtained. It appeared possible that the successful experiments might have been made with conidia belonging to Neocosmospora, but erroneously taken for those of Nectria. This became the more probable when it was found that Neocosmospora occurs not only at Dehra Dun, but throughout a large area of Northern India, where pigeon-pea wilt is common, and also that on almost every diseased root examined, Neocosmospora perithecia should be induced to form by appropriate treatment. Work was therefore continued with the latter fungus.

Experiments with Neocosmospora vasinfecta Smith on Pigeon-pea.

To test the parasitism of Neocosmospora a series of infection experiments was carried out with pure cultures of the fungus. Only ascosporal cultures or those known to have originated from perithecia were used, since it was evidently useless to work with conidial forms, which there was no means of referring to their proper genera.

SERIES V.

The cultures used were obtained as follows :—

Some young perithecia of Neocosmospora were washed carefully in several changes of distilled water, and were sown separately in decoction of pigeon-pea. They sprouted freely from the perithecial cells (as most Hypocreaceous fungi will) and produced quantities of Cephalosporium spores.

A plating from one of these sprouting perithecia was made on April 7th, 1907, and several of the resulting colonies bore perithecia in turn. From one of these perithecial colonies, well isolated, a trace of aerial mycelium bearing Cephalosporium spores was again plated and good isolated colonies originating from a single spore were obtained. Subcultures were made from one of these colonies which was marked and showed perithecia a few days after the subcultures were obtained. The media were boiled pigeon-pea slabs, carrot, onion, boiled rice and plantain.

The plants were grown in pots, the earth in which was sterilised by intermittent steaming on three days in the Koch. The soil was damped and packed loosely into perforated kerosine oil tins. Under these conditions the interior of the mass reached about 87° C. after two hours' steaming, and was kept at this temperature for about three hours each day. Higher temperatures were not obtained with the ordinary Koch steriliser, but the above may be taken as sufficient to kill all life, but the most heat resisting bacteria in soil. Subsequently (in 1908) a Hearson's thermostatic dry steam steriliser was used and a temperature of 100° C. throughout was easily reached with this. The soil was loaded into twelve unsterilised pots, in each of which about twenty-five unsterilised seeds were sown. Germination was good.

The inoculation was made by sprinkling the soil with the culture broken up in distilled water just after the plants were up.

No. of pot.	Treatment.	Date of inoculation.	Result.	Remarks.
I	Inoculated with culture on pigeon-pea slab.	11-5-07.	No deaths.	
II	,, ,, ,, ,,	,,	,, ,,	
III	,, ,, ,, carrot	,,	,, ,,	
IV	,, ,, ,, onion	,,		
V	,, ,, ,, rice	,,	Wilt appeared.	Two plants wilted on July 3rd. All were dead but one on August 14th.
VI	,, ,, plantain	20-5-07.	No deaths.	
VII	Not inoculated (control)	...	,, ,,	
VIII	,,	...	,, ,,	
IX	,,	...	,, ,,	
X	,,	...	,, ,,	
XI	,,	...	,, ,,	
XII	,,	...	,, ,,	

Wilt appeared in pot No. V only. The subsequent history of the contents of this pot will be given below under Series XIV (p. 36). The plants from the remaining eleven pots were transplanted into my garden on August 14th, having become too large for their pots. On September 8th those from pots II and III were attacked at the collar by a swarm of small red ants, and several were killed. One of these was pulled out on October 9th, and bore numerous perithecia of Neocosmospora on the roots. The rest remained healthy up to July 1908, and will be referred to again under Series XVII.

SERIES VI.

The cultures used were sub-cultures on nutrient agar, rice and onion from the rice tube used in the successful inoculation in Series V (pot V).

The plants were those growing in pots I, III, IV and VI of Series V. They were transplanted into my garden soon after inoculating.

The inoculation was made in the case of pot I by scraping away the soil from the base of the stem until lateral roots were exposed, scraping off the bark from these and placing a piece of the culture watered with distilled water on the wound, and in the case of the other three by simply watering the soil with the culture broken up in distilled water.

No. of pot.	Treatment.	Date of inoculation.	Result.
I	Inoculated at a wound with culture on rice.	27-7-07.	No deaths up to July 1908.
III	Inoculated by watering with rice, onion and agar cultures.	12-8-07.	On September 8th several plants killed by ants, rest remained healthy up to July 1908.
IV	,, ,, ,,	,,	No deaths up to July 1908.
VI	,, ,, ,,	,,	,, ,, ,,

Though the plants in pot V of Series V, inoculated from a rice culture of Neocosmospora, contracted wilt, subcultures from the same culture failed in the inoculations of this series. Hence the infection could not have come from the culture but from another source, probably either from the unsterilised seed or pot-walls or from the air.

SERIES VII.

The cultures were subcultures on nutrient agar, rice and onion from the rice tube used in the successful inoculation in Series V (pot V).

The plants were fitty consecutive plants in a row in the centre of a field plot on the Pusa Farm, and were about 18 inches high.

The inoculations were made as in Pot I of Series VI.

No. of plants.	Treatment.	Date of inoculation.	Result.	Remarks.
50	Inoculated at a wound with mixed agar, rice, and onion cultures.	11-8-07.	4 deaths.	Perithecia of Neocosmospora found on 2 dead plants.
Remainder of a plot of about $\frac{1}{10}$ acre.	Not inoculated (control).	...	7 deaths.	Perithecia of Neocosmospora found on one dead plant.

The proportion of deaths in the inoculated row was not sufficient, when compared with the deaths in the remainder of the plot, to afford proof that the former had died as a result of inoculation.

SERIES VIII.

The culture used was obtained by plating ascospores from a perithecium on pigeon-pea root, the ascospores being tested and found to germinate freely in water. In one plate ten well-isolated colonies of Cephalosporium appeared, and all bore perithecia on the 8th day. From one a subculture was taken on the 5th day, and this subculture bore perithecia after four days. From it, when two days old, three subcultures were made on glucose agar. These were used for the inoculation when eleven days old and with numerous perithecia.

The plants were grown in a small plot 8 by 4 feet, in my garden, a similar plot being sown as control. The plots were separated by a trench about a foot in depth. The seeds were sterilised by steeping in ·1 per cent. formaldehyde for two hours.

The inoculations were made by sprinkling the seeds and soil after sowing, but before covering, with the cultures broken up in distilled water.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.
Contents of a plot, 8 by 4 feet.	Inoculated by sprinkling with glucose agar cultures.	Sown and inoculated 18-7-08.	Seven plants died between the 10th and 25th August 1908. No more of the several hundred plants died up to the end of the year.
,, ,, ,,	Not inoculated (control).	Sown 1-7-08.	No deaths up to October 26th, 1908.

I am unable to explain the seven deaths in the inoculated plot. Not a single death occurred subsequently to August 25th, and this is almost conclusive evidence that the deaths were not due to true wilt. I have never seen a case of the latter where sooner or later neighbouring plants have not taken the disease. In a neighbouring plot affected by true wilt (that described under Series XVI below), deaths were numerous and spread was continuously going on up to early in the following year.

Series IX.

The culture used was a subculture originating from the first subculture from the plating in Series VIII.

Subcultures were taken once a month and all gave very numerous perithecia during the four months which elapsed between Series VIII and IX.

The plants were grown in pots which were immersed in ·001 per cent. corrosive sublimate solution for about five minutes before filling with soil. The soil was sterilised by intermittent steaming for three days, the internal mass being maintained at 100° C. for about two hours each day. The seeds were sterilised by steeping in ·1 per cent. formaldehyde for two hours.

The inoculations were made by sprinkling the seeds after sowing, but before covering, with the culture broken up in distilled water.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.
26 plants in 4 pots.	Inoculated with a culture on glucose agar.	Sown and inoculated 1-11-08.	No deaths up to 5-3-09.
17 plants in 2 pots.	Not inoculated (control).	Sown ,, ,, ,,	,, ,, ,,

No difference in growth could be detected between the inoculated and control pots. All the plants appeared equally healthy.

SERIES X.

Attempts were made to infect pigeon-pea with pure cultures derived from the ascospores of Neocosmospora obtained from the roots of other host plants.[1] Cotton, indigo, and gram were selected.

The culture used in the case of the cotton Neocosmospora originated from a plating of ascospores from a perithecium on the root of a wilted cotton plant from Sind. The subcultures were taken from an isolated Cephalosporium colony and bore perithecia in about a week. The series was maintained by regular subculturing every few weeks, and was fourteen months removed from the parent plating at the time of the inoculations below. Every subculture of the series bore quantities of perithecia. That used in the inoculation was about a fortnight old.

In the case of the indigo Neocosmospora some perithecia from a wilted indigo (Indigofera sumatrana) plant were well washed

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[1] See below, p. 18 *et seq.*

in distilled water and crushed to obtain ascospores. These were plated. A good growth occurred in the trace of agar left on the walls of one of the tubes used for plating and was seen under the microscope to arise from a group of three or four ascospores. From this an agar tube was inoculated and the subculture thus obtained showed perithecia on the fifth day. Seven days later three subcultures were made from the first and gave microscopically pure growths, which bore numerous perithecia when examined after twelve days. Two of these tubes were used for the inoculations, the cultures being twelve days old.

In the case of the gram Neocosmospora a plating was made of mature ascospores from a root of a wilted gram plant obtained from Bannu, North-West Frontier Province, and preserved in the laboratory for a year. Several good isolated Cephalosporium colonies resulted and a subculture from one, grown on agar, proved microscopically pure and bore numerous perithecia after five days. Subcultures were maintained regularly, all of which bore perithecia in large quantity. That used in the inoculations was five months removed from the plating and was about a week old.

The plants were grown in pots, the sterilisation of pots, soil and seeds being the same as in Series IX, except in the case of the indigo fungus where the pots were not sterilised.

The inoculations were made as in Series IX, except in the case of the indigo fungus where the seeds were sown in pots after pulling out indigo plants which had been previously watered with the cultures broken up in distilled water. In this and in subsequent tables the control experiment, when one was employed, is always given immediately below the experiment to which it relates.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
16 plants in 2 pots.	Inoculated with cotton Neocosmospora.	Sown and inoculated on 1-11-08.	No deaths up to 5-3-09.	

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
17 plants in 2 pots.	Not inoculated (control).	Sown on 1-11-08.	No deaths up to 5-3-09.	
About 50 plants in 3 pots.	Sown in soil previously inoculated with indigo Neocosmospora.	Sown on 28-3-08.	No deaths up to 26-10-08.	Transplanted to garden soil on 1-7-08, the plants having become too big for the pots.
8 plants in 2 pots.	Inoculated with gram Neocosmospora.	Sown and inoculated 1-11-08.	No deaths up to 5-3-09.	In another experiment pigeon-pea was sown in 4 pots previously inoculated with gram Neocosmospora. 45 plants grew and no deaths occurred in 4½ months.
17 plants in 2 pots.	Not inoculated (control).	Sown on 1-11-08.	,, ,, ,,	

Attempts to produce pigeon-pea wilt by inoculating with ascosporal cultures of Neocosmospora obtained from the roots of wilted cotton, indigo and gram failed.

Summary of experiments with Neocosmospora vasinfecta Smith on Pigeon-pea.

The above experiments (Series V to X), in which attempts were made to induce pigeon-pea wilt by inoculating with Neocosmospora, may now be considered as a whole. Apparently successful results were obtained in Series V (one pot out of six inoculated), Series VII (four plants out of fifty inoculated), and Series VIII (seven plants out of several hundred inoculated).

In each of these cases the experiment was not carried out under conditions which precluded the entry of foreign spores. In Series V the pots and seed were not sterilised, and it is proved by Series VI that the infective material did not arise from the tube with which the inoculation was made. Further work, the details of which will be found under Series XIV on p. 36 below, showed that the soil of this pot contained eventually another fungus which there is abundant evidence to prove is the real cause of pigeon-pea wilt. Series VII and VIII were field experiments, in which, of course, the soil was not sterilised. The four deaths out of the fifty inoculated plants in the former were accompanied by seven deaths in the non-inoculated portion of the plot. No significance therefore attaches to them, except as showing that the infective material is not uncommon in local soils. In Series VIII there is good reason to suppose that the deaths were not due to wilt.

On the other hand, in Series IX, where all the material used was rigidly sterilised, no deaths occurred, nor did any in Series VI (if we exclude the few plants killed by ants), though the seeds and pots were not sterilised and the plants were transplanted into open garden soil soon after inoculation. In five out of the six pots inoculated in Series V, no death occurred, nor did any deaths occur in Series X, in which pigeon-pea was inoculated with Neocosmospora from cotton, indigo and gram.

Even though taken as negative evidence, the results so far given are sufficient to justify the conclusion that the Neocosmospora found on the roots of wilted pigeon-pea, cotton, indigo and gram plants in India is not the cause of the disease in the first of these crops; the positive results obtained with another fungus detailed in Series XIV to XVII below leave no room for doubt on this point.

Experiments with Neocosmospora vasinfecta Smith on Cotton, Indigo and Gram.

The experiments with Neocosmospora on pigeon-pea must give rise to doubts regarding the generally believed parasitism of this fungus. The disease of this crop in India is a typical wilt, closely resembling those of cotton and other plants in the United States, where the cause is definitely stated to be this fungus, and of peas in Europe, where the same is suggested by the use of a name (Fusarium vasinfectum) given by Smith as a synonym for Neocosmospora vasinfecta. It is unlikely that what is a virulent parasite on widely different hosts in other countries should be a harmless saprophyte on another host suffering from a similar disease in India. The fact that, so far as published statements show, all successful inoculations obtained in other countries have been made with the

Fusarium and Cephalosporium stages of the parasite strengthens this doubt. It has already been shown above that exactly similar stages are possessed by a fungus of another genus, the Nectria found on wilted pigeon-pea plants at Dehra Dun. It is indeed well known that it is scarcely possible to distinguish by the microscope alone, many of the members of the form-genus Fusarium from one another, and the same applies to an even greater degree to the form-genus Cephalosporium.[1]

Both these form-genera are known to be in many cases lower stages of various genera of the Hypocreaceæ, and there are few groups amongst the fungi where it is more difficult to determine the genus by observation of conidial stages alone. In the present state of our knowledge it is not possible to refer a Fusarium or a Cephalosporium to its ascomycetal genus without actually deriving it in culture from the perithecial stage. This does not appear to have been done in the cultures with which successful inoculations of wilts have been carried out, and on this account the question of the parasitism of Neocosmospora cannot be regarded as settled.

Wilt diseases, associated with the presence of Neocosmospora on the roots, have been found in the following crops in India :—Pigeon-pea, cotton, indigo, gram (Cicer arietinum), sunn-hemp (Crotalaria juncea) and cow-pea (Vigna Catiang). Of these, cotton, indigo, and gram were selected for a further test of the parasitism of the fungus. In planning the experiments it was decided to try inoculations with the fungus from each of the three crops, and to add that from pigeon-pea in each series.

Cotton Wilt.

Cotton wilt has been reported from Sind, Gujarat, the Central Provinces and the Punjab in India. In the two latter areas it has caused considerable loss in the past few years. Perithecia of

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[1] *c. f.* for Fusarium the synonyms given on page 50 of Smith and Swingle's paper on the "Dry rot" of Potatoes (Bibliography (15)), and the remarks by Schikorra ((14), p. 176) and for Cephalosporium Brefeld's Untersuchungen, Vol. X. Plates IV and V amongst others.

Neocosmospora were found on the roots of wilted plants from the Central Provinces and Sind.

In the Central Provinces the disease is said to have been known for the past 50 years. It appears to have become more severe recently, possibly as suggested by Evans (16) because, owing to the recent cotton boom, the crop has been grown without proper attention to rotation. In parts of the Saoner tract it was estimated that 5 per cent. of the crop was killed in places in 1907. In Akola the percentage of deaths was 30 on an area of 80 acres severely affected in 1908. It was noticed that varieties of Gossypium neglectum and G. indicum are chiefly attacked, G. hirsutum, as represented by the kind known as *buri*, an upland Georgian type, being immune.

In Akola the wilting began soon after germination and went on progressing from the originally attacked plants all through the season. Details of the attack on the Nagpur Experimental Farm in 1907 are given in Evans' note just mentioned.

The examination of the specimens sent in from these two localities disclosed a condition entirely agreeing with the published descriptions of the disease in the United States. The Akola specimens were young plants, and externally appeared sound except for a discolouration of the bark at the base of the stem and on the tap root. On removing this the tissues below were found blackened just as in pigeon-pea wilt, and sections showed that many of the xylem vessels were quite choked with hyphæ. On these microconidia, quite agreeing with those figured by Smith, were found. Chlamydospores similar to those formed by many Fusaria were also formed within the vessels and Fusarium beds were common on the bark. There is practically no doubt that the disease is a Fusarium wilt, and it cannot be distinguished from that of the United States and Egypt.

SERIES XI.

(*a*) *Cotton inoculated with Neocosmospora vasinfecta from cotton.* The culture used was one of the earliest of the series mentioned under Series X.

The plants were grown in pots sterilised by immersion in ·001 per cent. corrosive sublimate for five minutes before loading with soil. The soil was sterilised by intermittent steaming for three days as in Series V. The seeds were steeped in ·1 per cent. formaldehyde for two hours. The plants in this and the following experiments were of the variety known as *bani*, a variety of Gossypium indicum which is susceptible to wilt ; and part of the same lot of seed sown on the Nagpur Farm was badly attacked by the disease.

The inoculations were made by sprinkling the culture, broken up in distilled water, over the seeds and soil after sowing but before covering.

(*b*) *Cotton inoculated with Neocosmospora vasinfecta from gram.*

The cultures were part of the regular series mentioned under Series X above.

The plants were mature plants of *bani* cotton seven months old, pots and soil being unsterilised but the seeds steeped in formaldehyde as above.

The inoculations were made by scraping away the soil down to the roots and placing the culture on these.

(*c*) *Cotton inoculated with Neocosmospora vasinfecta from indigo.*

The cultures were the same as those used in Series X above.

The plants were grown in pots containing soil to which the cultures had been added about six months previously and which had in the interval grown a crop of indigo, being in fact the same pots as those mentioned below in the 3rd column of Series XII.

The seeds were steeped in formaldehyde before sowing as before.

(*d*) *Cotton inoculated with Neocosmospora vasinfecta from pigeon-pea.*

The culture was that used to inoculate pot V of Series V above.

The plants were grown in pots containing soil to which the culture had been added ten months previously and which had borne pigeon-pea in the interval. The soil was mixed with enough fresh soil to fill five pots.

The seeds were steeped in formaldehyde before sowing as before.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
About 50 plants in 6 pots.	Inoculated with cotton Neocosmospora.	Sown and inoculated 3-4-08.	No deaths up to March, '09.	Transplanted to my garden on 1-7-08.
Do. do.	Not inoculated (control)	Sown ,,	,, ,,	,, ,,
17 plants in 2 pots.	Inoculated with gram Neocosmospora.	Sown 28-3-08. Inoculated 1-11-08.	,, ,,	
About 30 plants in pots.	Sown in soil previously inoculated with indigo Neocosmospora.	Sown 28-3-08.	No deaths up to November, '08.	Transplanted to my garden on 18-6-08.
About 50 plants in 5 pots.	Sown in soil previously inoculated with pigeon-pea Neocosmospora.	,, ,,	,, ,,	

Though the variety of cotton used in the experiments was one which is highly susceptible to wilt, inoculation with cultures derived from ascospores of Neocosmospora vasinfecta, whether from cotton, gram, indigo, or pigeon-pea, failed to produce the disease in a single instance.

Indigo Wilt.

About the middle of 1907 a serious disease of indigo appeared in Behar, the centre of the indigo industry of India. A few years previously the species of indigo known as "Java" (Indigofera arrecta Hochst.) was introduced experimentally into cultivation. Its superiority to the species previously grown, "Sumatra" (Indigofera sumatrana), was so marked that a rapid extension of its cultivation occurred. The coincidence of the introduction of a new species and the appearance of a disease not previously known in the crop, was such as to lead to a strong suspicion that the disease had been introduced with the seed. Enquiry from Java, whence the seed originated, showed, however, that the disease was not known there. Its field characters were similar in many respects to those of the wilts described above, and perithecia of Neocosmospora vasinfecta were found to be common on the roots of diseased plants. What connection, if any, exists between the introduction of the new species of plant and the outbreak of disease is not clear, but it appears possible that a parasite already present on some other crop found the new species susceptible to attack and through it passed to the species common in the district. The interesting conception of "bridging species" already established for the host plants of the Erysiphaceæ and rusts may be called into account for the appearance of wilt in indigo. Both the species of indigo, Indigofera sumatrana and I. arrecta, were attacked, but the disease was most severe in the latter.

Inoculation experiments were undertaken with Neocosmospora vasinfecta from indigo, cotton, gram and pigeon-pea.

SERIES XII.

(*a*) *Indigo inoculated with Neocosmospora vasinfecta from indigo.*

The culture used was obtained as described under Series X from the root of a wilted plant of Indigofera sumatrana, and bore numerous perithecia.

The plants were grown in pots, the pots and soil being unsterilised. The seed of the Sumatra variety was untreated in any way, while that of the Java variety was steeped for 20 minutes in strong sulphuric acid to promote germination, since it belongs to the category of "hard seeds" requiring treatment to rupture or soften the seed coat before sowing.

The inoculations were made by sprinkling the seed and soil after sowing but before covering, with the culture broken up in distilled water.

A second series was made, using a culture derived from a wilted plant of Indigofera arrecta.

The culture was obtained by planting ripe ascospores obtained from the root of a plant in a badly diseased field. On the fourteenth day a colony, bearing perithecia, was selected and an agar tube inoculated with a trace of the aerial mycelium. This gave a pure growth which produced perithecia after five days. Subcultures from this were made and used for the inoculations when three days old.

The plants were grown in pots, pots and soil being sterilised as in Series XI (*a*). Half the number of pots were sown with seed derived from plant imported from Java and grown for two generations in India; the seed used having been carefully gathered from plants of the same field as that from which the fungus was obtained, and showing the earliest signs of disease. It was therefore of a susceptible strain. The other half were sown with Indigofera arrecta seed originating from Natal, and which had also shown itself to be susceptible. All the seed was treated with strong sulphuric acid for 20 minutes.

The inoculations were made as before.

(*b*) *Indigo inoculated with Neocosmospora vasinfecta from cotton.*

The culture used was one of the regular series mentioned above, under Series X. It bore numerous perithecia.

The plants were those in one of the control pots of (*a*) above, being Java seed two generations in India, and were nearly three months old.

The inoculations were made by scraping away the soil down to the roots and applying the culture broken up in distilled water.

(*c*) *Indigo inoculated with Neocosmospora vasinfecta from gram.*

The culture used was one of the regular series mentioned above, under Series X, and bore numerous perithecia.

The plants were those in two of the control pots of (*a*) above, being Java seed two generations in India, and were nearly seven months old.

The inoculations were made as in (*b*) above.

(*d*) *Indigo inoculated with Neocosmospora vasinfecta from pigeon-pea.*

The culture used was that used to inoculate pot V of Series V above.

The plants were grown in pots containing soil to which the culture had been added several months previously and which had grown pigeon-pea in the interval. The soil was mixed with enough fresh soil to fill four pots. Two were sown with untreated Sumatra seed and two with Java seed, treated for 15 minutes in strong sulphuric acid.

No. of plants and variety.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
About 50 plants of I. arrecta from Java seed in 4 pots.	Inoculated with Neocosmospora from I. sumatrana.	Sown and inoculated 21-8-07.	No deaths up to July, '08.	All the plants in 1 pot were wounded by cutting down to the cambium below the ground level, 8 weeks after sowing.
Ditto.	Not inoculated (control).	Sown 21-8-07.	Ditto.	Ditto.
About 100 plants of I. sumatrana in 6 pots.	Inoculated with Neocosmospora from I. sumatrana.	Sown and inoculated 2-9-07.	No deaths up to March 28th, '08.	Ditto in 2 pots.
Ditto.	Not inoculated (control).	Sown 2-9-07.	Ditto.	Ditto.
60 plants of I. arrecta from Java seed in 4 pots.	Inoculated with Neocosmospora from I. arrecta.	Sown and inoculated 17-4-08.	No deaths up to March, '09.	
50 ditto.	Not inoculated (control).	Sown 17-4-08.	Ditto.	
58 plants of I. arrecta from Natal seed in 4 pots.	Inoculated with Neocosmospora from I. arrecta.	Sown and inoculated 17-4-08.	Ditto. Ditto.	
About 100 ditto.	Not inoculated (control).	Sown 17-4-08.	Ditto.	
11 plants of I. arrecta in one of the control pots of the third experiment above.	Inoculated with Neocosmospora from cotton.	Sown 17-4-08. Inoculated 9-7-08.	Ditto.	

No. of plants and variety.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
25 plants of I. arrecta in 2 of the control pots of the third experiment above.	Inoculated with Neocosmospora from gram.	Sown 17-4-08. Inoculated 3-11-08.	No deatns up to March, '09.	
About 20 plants of I. sumatrana in 1 pot and about 25 plants of I. arrecta from Java seed in 2 pots.	Sown in soil previously inoculated with pigeon-pea Neocosmospora.	Sown 15-11-08.	No deaths up to July, '08.	
About 20 plants of I. sumatrana in pot.	Ditto.	Sown 21-8-07.	No deaths up to November 25th, '07.	

This series appears to give conclusive evidence that Neocosmospora vasinfecta, though common on the roots of wilted indigo plants, is a pure saprophyte on them.

Gram Wilt.

The wilt of this crop (Cicer arietinum) occurs in Bengal, the United Provinces and the North-West Frontier Province. It is a typical wilt, having all the characters of the Fusarium wilts previously described. A severe outbreak was reported from Bannu on the North-West Frontier, and the specimens received in June, 1907, bore numerous perithecia of Neocosmospora on the roots. The wood of the coller and main roots was blackened and on section was found permeated by hyphæ. Microconidia (Cephalosporium) and macroconidia (Fusarium) were found as in the previous cases.

It is highly probable that the disease is a Fusarium wilt.

SERIES XIII.

(*a*) *Gram inoculated with Neocosmospora vasinfecta from gram.*

The cultures were part of the regular series mentioned above under Series X and bore numerous perithecia.

The plants were grown in pots, pots, soil and seed being sterilised in the usual way. The first sowing was made in July, but all the plants, inoculated as well as control, died from heat, gram being a cold weather crop in India. They were resown at the beginning of the cold weather. At the same time a second series of inoculations was carried out, the sterilisation being very carefully attended to. The seed used in both cases was local seed, as wilt occurs sometimes in the local crop.

The inoculations were made in the usual way by sprinkling the seed and soil after sowing, but before covering, with the culture broken up in distilled water.

(*b*) *Gram inoculated with Neocosmospora vasinfecta from cotton.*

The culture was one of the regular series as before.

The plants were grown in pots and sterilisation carried out as before. As in (*a*) the first sowings were killed by heat and resowings made at the beginning of the cold weather.

The inoculations were as usual.

(*c*) *Gram inoculated with Neocosmospora vasinfecta from indigo.*

The cultures used were part of a regular series maintained from the second culture mentioned under Series XII, *i.e.*, that derived from perithecia on the roots of Indigofera arrecta.

The plants were grown and sterilisation effected as in (*a*) and (*b*) above.

The inoculations were as usual.

(*d*) *Gram inoculated with Neocosmospora vasinfecta from pigeon-pea.*

The culture was the same as that used in Series IX above.

The plants were grown, sterilisation effected and inoculations made as in (*a*), (*b*) and (*c*) above.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.
57 plants in 4 pots.	Inoculated with Neocosmospora from gram.	Sown and inoculated 1-11-08.	No deaths up to 5-3-09.
36 plants in 2 pots.	Not inoculated (control).	Sown 1-11-08.	Ditto.
44 plants in 2 pots.	Inoculated with Neocosmospora from gram.	Sown and inoculated 7-7-08. Resown 3-11-08.	Ditto.
30 plants in 2 pots.	Not inoculated (control).	Sown 7-7-08. Resown 3-11-08.	Ditto.
30 plants in 2 pots.	Inoculated with Neocosmospora from cotton.	Sown and inoculated 7-7 08. Resown 3-11-08.	Ditto.
25 plants in 2 pots.	Inoculated with Neocosmospora from indigo.	Ditto.	Ditto.
23 plants in 2 pots.	Inoculated with Neocosmospora from pigeon-pea.	Sown and inoculated 3-11-08.	Ditto.

These experiments show quite as conclusively as Series XI and XII, that Neocosmospora vasinfecta, though common on the roots of wilted plants, is purely saprophytic.

Summary of experiments with Neocosmospora vasinfecta Smith.

To sum up the experiments described under Series V to XIII above, the parasitism of Neocosmospora vasinfecta has been tested on four of the six crops hitherto found in India to be subject to wilt, and with this fungus common on the dead roots. These are pigeon-pea, cotton, indigo and gram. The diseases in pigeon-pea, cotton and gram are very similar, not only in their field characters and in their morbid anatomy, but also in the characters of the organism presumably the cause of the disease. This is a fungus with usually hyaline but occasionally brownish hyphæ, found predominantly in the xylem vessels but also penetrating the other tissues. In the vessels it often forms dense masses of matted hyphæ, which almost fill the lumen of the tube and must, of themselves, offer a considerable impediment to the flow of the ascending current. This stoppage is largely increased by a gummy exudation into the vessels, which commonly results from the presence of the fungus. On short lateral branches within the larger vessels, and also on hyphæ at the surface of the root, microconidia are formed. These are usually formed singly when within the vessels, but in culture, or at the surface of the root in moist air, several are successively produced and remain bound together into a head by a watery or slightly viscid exudation from the tip of the sporophore. They thus belong to the form-genus Cephalosporium. On the surface of diseased roots and the base of the stem, beds of macroconidia of the type characteristic of the form-genus Fusarium are found. Fusarium spores, produced in this case singly, may also be derived from cultures of the microconidia, whether from within the vessels or from the bark.

On the dead roots, especially after incubation in a moist atmosphere, perithecia of Neocosmospora vasinfecta can frequently be found. From the ascospores of these, micro- and macroconidia, indistinguishable from those just mentioned, can be obtained by cultivation. In some cases wilted pigeon-pea stems also bear perithecia of a Nectria, which again has micro- and macroconidia similar to the above. The indigo disease is in some respects (which need not be entered on here) somewhat unlike the others. Here also, however, the morbid anatomy is similar, and the same micro- and macroconidia and perithecia of Neocosmospora are common.

The experiments described above resulted in not a single case of wilt being developed in cotton, indigo or gram when inoculated with cultures originating from the ascospores of Neocosmospora vasinfecta, whether from the same host or from any of the other three. In pigeon-pea apparent infections resulted in some cases, but these can all be accounted for by accidental inoculation from some other source and were not obtained when sterilisation of all the material used was rigidly carried out. The pigeon-pea wilt is very prevalent both on the Pusa Farm and in the surrounding neighbourhood, and sources of external infection are numerous and difficult to exclude. On the other hand, the cotton wilt has not been observed in this district and the danger of external contamination is negligible. Indigo wilt has occurred on the Farm, but there was little of it either on the Farm or near by, and the same applies to gram wilt, so that in neither of these cases was the danger of accidental infection considerable.

Taking the whole of the experiments together, the conclusion is irresistible that Neocosmospora vasinfecta is a common soil saprophyte, which develops its perfect form on rotting roots of several (perhaps many) different plants and is wholly unconnected with the wilt diseases of the particular plants investigated so far in India. One might be tempted to go further and state that there is considerable doubt that the fungus is parasitic even in the United States. It seems at any rate clear that experiments intended to demonstrate the parasitism of polymorphic species of Nectria or Neocosmospora are useless unless carried out with pure cultures derived unmistakably from the perfect form of the fungus, and so far as I know, this has not previously been done in the case of Neocosmospora.

There are two questions which must now be answered. First, what evidence is there that the Indian Neocosmospora is identical with that of the United States, and second, if Neocosmospora is not the cause of wilt, what is the true cause ? In answer to the first I shall give a rather detailed account of the morphology and cultural characters of the Indian fungus which will leave no doubt as to its identity with that of the United States.

The second question can as yet only be answered in one of the four wilts referred to above, that of pigeon-pea. The ground has, however, been cleared for the study of the cotton and gram wilts, and I hope that it will be possible to ascertain definitely the cause of these diseases. The indigo disease is likely to prove more difficult, but a remarkable diminution in its intensity in the current season gives some ground for the hope that it may prove a passing outbreak of some half parasite, whose virulence may wane as the Java variety of plant gets acclimatised in its new home.

The identity of the Indian and American Neocosmospora.

Macroscopically and microscopically no difference can be detected between Neocosmospora vasinfecta from the United States and the Indian species. The description and illustrations of the former in Smith's paper(2) are so full as to leave little to be desired for purposes of comparison.

The perithecia are of the same tone of bright red in both cases as a comparison of plate I of Smith's paper, and plate I below will show. They are formed, in India as in America, on the roots below ground, rarely above ground, and are quite superficial. Smith gives their size as from 210 to 400μ high, by 150 to 328μ broad, mostly 250 to 350 by 200 to 300μ. About the same limits have been found in the Indian forms, the most usual being from 250 to 350μ high by 175 to 280μ broad. The surface is almost smooth in both, being slightly irregular from the projection of individual cells only, not groups of cells as in many Nectrias. The neck is usually short, that figured in plate II, fig. 9 (cotton Neocosmospora), where it is about $\frac{1}{8}$th of the total height of the perithecium, being perhaps the most common type. Sometimes it is longer (plate II, figs. 7 and 8), occasionally quite long as in plate I, fig. 3. Smith gives 30 to 40μ as the usual length (or rather more than 1/10th of the total height), but says it may reach 80μ. I have found the greatest variability in this respect even in the same culture.

The asci are numerous, cylindrical, shortly stipitate, the spore-bearing part measuring from 70 to 100 by 12μ. They dissolve so as to liberate the spores within the perithecium when over-ripe. Paraphyses are present and consist of a chain of several rather large, irregularly oval, thin-walled cells, which are loosely connected. The figures in plate V, fig. 2, of Smith, and plate I, fig. 5, below, may be compared to show these characters.

The ascospores are eight in each ascus, arranged in one row, globose to shortly elliptical, and with a brown thick wall of peculiar construction. This consists of an outer layer which is irregular in thickness and often wrinkled, giving the mature spore an irregular contour, and an inner layer of moderate and quite regular thickness. These two layers are not tightly fused together, as macerated or ruptured spores show. Viewed in surface focus, the wall appears as if pitted (the appearance is shown in an exaggerated form in plate I, fig. 4), but I have not been able to satisfy myself as to the exact structure of the markings seen, and they are not visible in optical section which tells against their being pits. Immature spores are colourless and with the outer wall little developed. The spores measure 10 to 15·5 by 10 to 15μ, usually about 12μ, if globose. The average of 100 spores from an agar culture of the cotton fungus gave 13·5 by 12μ. Fifty-four spores measured directly from pigeon-pea gave 10 to 14·5 by 10 to 12·5μ, the average being 11·9 by 11·5μ. Smith gives 10 to 12μ, if globose, and 8 to 12 by 11 to 14μ, if ellipsoidal, and notes that spores from a potato culture of the cow-pea fungus were generally larger than 12μ in diameter, and also larger than those measured directly from the host plant. In all the ascospore characters there is the closest possible agreement between the Indian and American forms, if we except the slight markings of the spore wall, which are not mentioned by Smith. They are only visible under high powers and are sometimes very difficult to make out, so that much importance does not attach to them.

The conidial stages are, as pointed out above, practically valueless for purposes of comparison. Their variability is such that it is hardly possible to separate by microscopic examination and measurements alone many of the different species of Fusarium from one another, and still less those of Cephalosporium. Smith gives the spores of the former stage of Neocosmospora vasinfecta as lunulate, 3 to 5-septate, and 30 to 50 by 4 to 6μ in diameter, and of the latter as oval to narrowly elliptical, straight or slightly curved and 4 to 25 by 2 to 6μ. I have found that the majority of the Fusarium spores are from 35 to 40μ long, but the lower limit is very elastic, as all gradations down to the Cephalosporium type can be found. The breadth of the spores and the number of septa agree with the data given by Smith, but the intermediate types between Fusarium and Cephalosporium often have one or two septa. These types develop chiefly in culture, the spores formed in stromata on the bark of the host being more regular. The Cephalosporium spores average about 6 to 10 by 2 to 4μ, and their mode of formation is shown in fig. 5, plate II, which may be compared with fig. 3, plate III of Smith's paper.

Chlamydospores are not uncommon in the vessels of old diseased roots, and are also formed on the surface and in old cultures. They are figured on plate II, fig. 4, which may be compared with fig. 12, plate III of Smith.

The cultural characters of Neocosmospora vasinfecta are very fully described by Smith. The greater part of his observations relating to pigment production were, however, carried out with cultures of the watermelon fungus originating from conidial forms on the host, not from ascospores ; there is, therefore, no certainty that they belonged to Neocosmospora. They never developed perithecia though continued for five years on a variety of media. On the other hand, his observations regarding the influence of different media on perithecia formation were made with ascosporal strains of the Cow-pea Neocosmospora. The following table gives a comparison between some of the results noted by Smith and those observed in ascosporal cultures of the Indian fungus from pigeon-pea, indigo and cotton.

Cultural characters of American and Indian Neocosmospora from different hosts.

Cow-pea (Smith).	Pigeon-pea.	Indigo.	Cotton.
Steamed potato. 6th day, colour of substratum dark lead grey. Perithecia roseate by 6th to 9th day, then bright coral red.	*Steamed potato.* In about a week surface growth pink, no violet or purple. Below a pale green stromatic line. Brown stroma in contact with glass. Perithecia light red. 14 days, perithecia darker, some brown.	*Steamed potato.* 7 days, growth white to dark greenish grey. Perithecia numerous, scattered, pale red to deep red. 16 days, mycelium chiefly dark grey. Perithecia mostly rose.	*Steamed potato.* 7 days, flocculent, growth white, stromata scanty pale green to pale purple. 16 days, perithecia many, bright red.
Pearl tapioca. 8th day, not 1/1000th as much growth as on potato. Perithecia few, appear slowly, at first pale red, then black. Remain sterile.	*Tapioca.* 14 days, no growth.	*Tapioca.* 7 days, no growth. 16 days, growth hardly visible. No perithecia.	*Tapioca.* 7 days, no growth, 16 days growth scanty. No perithecia.

Cow-pea (Smith)	Pigeon-pea.	Indigo.	Cotton.
Banana Groth slow and perithecia appear after some weeks, then many, pale yellowish red or ochraceous buff after 20 days. After 2 months one culture with red perithecia, and fertile, others with dark brown or black and sterile.	*Plantain.* 7 days, growth good, white tinged with pink. No perithecia. 34 days, perithecia visible, dark red.	*Plantain.* 7 days, growth less than on potato, white to grey. Perithecia few, pale. 16 days, perithecia yellow, a few pink.	*Plantain.* 16 days, growth not good, no perithecia.
Spanish Onion. Perithecia appear slowly, then many, pale red to bright coral.	*Onion.* 7 days, growth pinkish, flocculent, numerous perithecia, light red. 14 days, perithecia darker.	*Onion.* 7 days, growth white to greenish, no perithecia. 16 days, numerous bright red perithecia.	*Onion.* 7 days, growth white, no perithecia. 16 days, perithecia rather scanty, pale.
Acid rice. (5 drops very dilute HCl added to each tube). 16 days, substratum dark purplish red. Perithecia numerous, full grown, colourless to yellowish red. No bright red.	*Acid rice.* (5 drops $\frac{1}{2}$% HCl added to about 10 c.cs. boiled rice). 7 days, growth feeble, upper part pinkish. 14 days, colour deeper, no perithecia. 34 days, numerous perithecia.	*Acid rice.* (As in column 2). 7 days, growth dark purple or claret, perithecia many, yellow to black. 16 days, perithecia mostly dark purple, none red.	*Acid rice.* (As in column 2). 7 days, growth copious, pale pink to bluish purple. 16 days, mostly pink, no perithecia. With more strongly acid rice (10 drops acid), a few pale perithecia appeared after 56 days.
Alkaline rice. (10 c.cs. rather dry boiled rice, with 2 c.cs. cold saturated solution bicarbonate of soda). After 40 days growth sparing, no perithecia.	*Alkaline rice.* (5 drops saturated solution of sodium bicarbonate added to about 10 c.cs. of boiled rice), 7 days, growth moderate, stromata dark brown, no perithecia. 14 days, a few light red perithecia.	*Alkaline rice.* (As in column 2). 7 days, growth greenish to brownish, no perithecia. 16 days, mycelium almost black above, yellow to brown below, no perithecia.	*Alkaline rice.* (As in column 2). 7 days, growth white, no perithecia. 16 days, lower part dirty green, no perithecia. 56 days, a few light red perithecia.

The characters given above agree particularly closely in the case of the cow-pea fungus of Smith and the indigo fungus. In the other cases some divergencies occur, but the general behaviour corresponds fairly well. The differences, such as they are, are as general between the three Indian strains as between these and the American, and are such as are inseparable with working with media of the indefinite composition of those mentioned.

No one could think of separating as distinct species, fungi agreeing so generally in their microscopic characters and cultural behaviour as the Neocosmosporas studied in the United States and in India.

CHAPTER III.

FUSARIUM UDUM N. SP., THE CAUSE OF PIGEON-PEA WILT.

The repeated examination of the roots of wilted pigeon-pea plants in all stages of the disease, carried on during the course of the investigations described above, left practically no doubt that the disease was a typical Fusarium wilt. Attempts to prove its connection with Fusarium stages of the two Hypocreaceous fungi found on the bark, the Nectria found at Dehra Dun and Neocosmospora vasinfecta, having failed, it remained to look elsewhere.

The number of soil organisms that may be obtained from dead vegetable matter in the soil (such as the surface of the roots of a dead or dying plant) is greater than would be anticipated by any one not accustomed to the specific examination of soils for fungi. In any locality several are sure to be so common as to be found on almost any root examined, and amongst these are Fusaria probably belonging to several different species. It appeared an endless matter to hunt through these for possible parasites. If, however, the superficial forms could be excluded or destroyed, it seemed likely that the true cause could be induced to give a comparatively pure surface growth by appropriate treatment. The following procedure was, therefore, adopted to isolate any truly internal organisms that might occur in diseased roots.

A short length of tap root from a just wilted seedling was cut off with a flamed scissors and the presence of the internal mycelium determined by sectioning the end of one or other of the rejected pieces. The root was washed thoroughly, first in tap water and then in several changes of distilled water, being well rubbed between the fingers to remove irregularities where particles of soil might lodge. It was then seized in sterile forceps, dipped in absolute alcohol for about 5 seconds, the alcohol flamed off and the root rapidly dropped into a tube of sterile prepared medium. In this manner it was hoped to destroy all but organisms deep in the tissues. All the roots thus treated gave rise to the growth of a bacillus which gave characteristic colonies on nutrient agar. In some the fungus known to be present within the root was killed by the treatment, and no mycelial growth occurred. In others a filamentous fungus appeared on the surface or at the cut ends, and was easily got into pure culture free from the bacillus. Only these two organisms, a bacillus and a fungus, were thus obtained and work was continued with them.

SERIES XIV.

The culture was obtained from a wilted pigeon-pea root grown in soil which in part originated from pot V of Series V above (p. 10). On August 21st, 1907, all the plants in this pot had wilted and were pulled out. The soil was then mixed with some fresh potting earth in equal parts, and filled into two pots. In these pigeon-pea and indigo respectively were sown. Wilt appeared in the former on October 10th, and all the plants were dead by November 21st. They were pulled out and perithecia of Neocosmospora developed on some of them after 10 days in a moist chamber. Pigeon-pea was resown in the pot immediately. On November 25th, the indigo plants in the other pot (still perfectly healthy) were pulled out and pigeon-pea sown in the pot, after adding as usual an equal bulk of fresh potting soil. The pigeon-pea after pigeon-pea developed wilt during January, 1908, and that after indigo at the end of the same month. Eight plants in each pot were dead by March 28th. The rest were then pulled out and the soil from the two pots mixed, part being used to grow yet another pot of pigeon-pea. This showed wilt in a month, being the fourth generation of seedlings that had succumbed to the infective material of pot V.

On May 19th, 1908, a very recently infected root was selected from a wilted plant of the last batch, washed in water and alcohol and flamed as described above, and dropped into a tube of nutrient agar. On the 2nd day the contents of the tube, now clearly showing a growth of hyphæ and bacteria around the root, were plated and the fungus transferred in pure culture from a single-spore colony to an agar tube three days later. The resulting growth differed considerably in appearance from any stage of Neocosmospora, though on examination it was found to consist of Cephalosporium microconidia. Subcultures from this tube on steamed carrot and potato were used for the inoculations below.

The plants were grown in pots sterilised by immersion in ·001 per cent. corrosive sublimate for about 5 minutes before filling with soil. The soil was sterilised by intermittent steaming on three days, the internal mass being maintained at about 87° C. for two or three hours each day. The seeds were sterilised as usual by steeping in ·1 per cent. formaldehyde for 2 hours. About 25 plants grew in each pot.

The inoculations were made by sprinkling the seeds and soil with the cultures broken up in distilled water, after sowing but before covering.

No. of pot.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
1	Inoculated with Cephalosporium from pigeon-pea.	Sown and inoculated 13-6-08.	Wilt appeared.	1st death on 16-7-08, typical wilt.
2	Ditto	Ditto	Ditto	1st death on 1-8-08, typical wilt.
3	Ditto	Ditto	Ditto	1st death on 12-8-08, typical wilt.
4	Ditto	Ditto	Ditto	1st death on 19-7-08, typical wilt.
5	Not inoculated (control).	Sown 13-6-08.	No death up to September 4th, '08.	...
6	Ditto	Ditto	Ditto	...

All the plants, except one, in the four inoculated pots were dead by October 26th. On this date those left were pulled out and examined. The number of dead plants in the four pots was 18, 18, 16 and 19 respectively, several in each pot having been pulled out for examination on previous occasions. Most had no surface growth of fungi on the roots, though about one-third showed whitish patches with single-celled spores on a fine mycelium resembling Cephalosporium. Several were placed in the moist chamber and gave rise to Cephalosporium and in some cases also Fusarium after some days. None gave perithecia, nor were any observed on any plant, whereas those that had wilted in soil taken from pot V of Series V developed perithecia of Neocosmospora vasinfecta when similarly incubated. This series, therefore, combined with Series VI above, showed that the soil of pot V contained a harmless fungus, Neocosmospora vasinfecta, with which it had been inoculated, and a virulent parasite, the fungus now under consideration, which must have entered accidentally either from the pot walls, the seed or the air.

A macroscopic and microscopic examination of the diseased roots was carried out. The characters of the wilt and the gross appearance of the tissues were found to be exactly similar to those of cases of wilt occurring naturally on the Farm. In section the conditions were just as described in my previous paper on this disease, the hyphæ being found chiefly in the vessels, where also microconidia and chlamydospores were observed. As this experiment coincided in time with the gram inoculations mentioned under Series XIII, in which plants inoculated with Neocosmospora (as well as the controls of the same series) died, the death being from heat and not from Neocosmospora as was proved by the further sowings in the same pots later in the year, when the temperature had fallen, a comparison was made between the roots in the two cases. In both the conditions were sufficiently alike to lead to considerable difficulty in distinguishing between them. The gram roots were permeated with the hyphæ of Neocosmospora which attained their chief development in the vessels. On the surface, while still in the soil, or after some days in the moist chamber, nearly all the gram plants developed perithecia of Neocosmospora. From this it is apparent that Neocosmospora, though a saprophyte, penetrates freely into roots killed from other causes and fills the vessels with a mycelium closely resembling that of the true wilt fungus.

SERIES XV.

The culture used was obtained from the third batch of plants grown in the soil from pot V of Series V. A very recently attacked root was selected, washed carefully in several changes of distilled water and rubbed well between the sterilised fingers to remove adhering soil and dead bark. It was then placed in distilled water on a sterile slide. In 24 hours a fine growth was visible on the surface and a trace of this aerial mycelium was transferred to an agar tube. On the 6th day there was a distinct growth along the streak and a subculture was made from one point on this to another agar tube. This proved microscopically pure and was used for the inoculations after 13 days.

The plants were grown in pots, twenty-five seeds being sown in each.

The seeds, soil and pots were sterilised and the inoculations made as in Series XIV.

No. of pot.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
1	Inoculated with Cephalosporium from pigeon-pea.	Sown and inoculated 17-4-08.	Wilt appeared.	1st death on 6-6-08, all dead by 12-9-08.
2	Ditto.	Ditto.	Ditto.	1st death on 12-5-08, all dead by 8-9-08.
3	Not inoculated (control).	Sown on 17-4-08.	No death up to September, 15'08.	..
4	Ditto.	Ditto.	Ditto	...

Here, again, the wilt was typical and virulent. All the plants (nearly 50) in the inoculated pots were dead by the early part of September, the control plants remaining perfectly healthy.

SERIES XVI.

The cultures were obtained as in Series XV, and were grown on carrot, onion, plantain and rice.

The plants were grown in a small plot in my garden, 8 by 4 feet in size, the seeds being steeped in formaldehyde as before.

The inoculations were made as in the last two series.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
Contents of a plot 8×4 feet.	Inoculated with Cephalosporium from pigeon-pea.	Sown and inoculated 1-7-08.	Wilt appeared.	1st death on 10-8-08. A large number were dead by 26-10-08.
Ditto	Not inoculated (control).	Sown on 1-7-08.	No deaths up to March, '09.	...

The two plots were side by side, separated by a small trench about a foot in depth. It is somewhat remarkable that there was no spread from the inoculated to the control part by aerial conidia, as other experiments seem to show that such a spread occurs not uncommonly in nature.

SERIES XVII.

The cultures used were the same as in the last series.

The plants were two clumps over a year old, growing in open soil in my garden, and were the contents of pot No. 3 (inoculated previously with Neocosmospora) and pot No. 7 (not previously inoculated) of Series V above (page 10). These had been cut back when about 9 months old and had given a second vigorous growth, being still perfectly healthy.

The inoculations were made by scraping away the soil down to the finer roots and burying part of the culture in contact with the latter

No. of plants.	Treatment.	Date of inoculation.	Result.	Remarks.
About 5 plants out of a clump of about a dozen which had been a year previously inoculated with Neocosmospora.	Inoculated with Cephalosporium from pigeon-pea.	Inoculated 1-7-08.	Wilt appeared.	The first death was on 29-7-08. All in the clump were dead by the end of the year.
The same in a clump not previously inoculated.	Ditto.	Ditto.	Ditto.	The first death was on 24-7-08. All were dead by November, '08.

The disease spread from the inoculated clumps to those belonging to pots 2, 4, 6, 8, 9, 10, 11 and 12 of Series V, all of which were near together and not separated by any obstacle from the inoculated clumps, and were perfectly healthy at the time of inoculation. Hence, though the plants from pot 3 had flourished for more than a year after being inoculated with Neocosmospora, they succumbed without exception to the attack of the Cephalosporium in from one to five months, though they were very large plants, mostly over 8 feet high.

The proof is therefore complete that the Cephalosporium isolated from the roots of wilted pigeon-pea plants in the manner described under Series XIV above, is a virulent parasite and that it, and not Neocosmospora, is the cause of the wilt disease commonly found in this crop.

SERIES XVIII.

An experiment was carried out to test whether the presence of Neocosmospora in any way altered the course of the disease induced by the Cephalosporium isolated from the interior of wilted pigeon-pea roots.

The culture of the Cephalosporium used was a subculture on steamed potato from that used in Series XIV. That of Neocosmospora was an agar subculture originating from the culture on pigeon-pea used to inoculate pot 2 of Series V above.

The plants were grown in pots; pots, soil and seeds being sterilised as in Series XIV, and the inoculations were made as in that Series.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
About 25 plants in 2 pots.	Inoculated with Cephalosporium isolated from the interior of pigeon-pea roots combined with Neocosmospora from the surface of the roots.	Sown and inoculated 18-6-08.	Wilt appeared.	The first death was on 24-7-08.
Ditto.	Not inoculated (control).	Sown 13-6-08.	No deaths up to 4-9-08.	...

The presence of Neocosmospora appeared to make no difference in the rapidity of onset or characters of the disease.

As mentioned on page 53 above, a bacillus was constantly obtained from the interior of the roots of pigeon-pea plants affected by wilt, after flaming. The action of this bacillus on healthy plants, both alone and in conjunction with Neocosmospora and the parasitic Cephalosporium, was tested.

SERIES XIX.

The culture of the bacillus used was obtained as described under Series XIV above and isolated by plating. That of the Neocosmospora was the same as in Series IX. That of the parasitic Cephalosporium the same as in Series XIV.

The plants were grown in pots; pots, seeds and soil being sterilised as in Series IX and XIV, and the inoculations made as in those Series.

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
About 25 plants in 2 pots.	Inoculated with bacillus isolated from the interior of wilted pigeon-pea roots.	Sown and inoculated 13-6-08.	No deaths up to 2-9-08.	.....

No. of plants.	Treatment.	Date of sowing and inoculation.	Result.	Remarks.
About 25 plants in 2 pots.	Not inoculated (control).	Sown 13-6-08.	No deaths up to 4-9-08.	......
22 plants in 2 pots.	Inoculated with a mixture of the above bacillus and Neocosmospora from pigeon-pea.	Sown and inoculated 1-11-08.	No deaths up to 16-3-09.	......
About 25 plants in 2 pots.	Inoculated with a mixture of the above bacillus and the parasitic Cephalosporium.	Sown and inoculated 13-6-08.	Wilt appeared.	1st death on 10-7-08. All were dead by October, '08.

The bacillus itself or in conjunction with Neocosmospora is unable to cause disease. When combined with the parasitic Cephalosporium it causes no apparent change in the rapidity of appearance and nature of the disease caused by the latter. It has not been seen in the tissues and so presumably is present in small numbers. A quite similar bacillus was obtained from the roots of healthy jute plants in the same manner. What part these organisms play when present in such roots is unexplained.

In all these inoculation experiments, carried out with no less than four distinct organisms found more or less regularly associated with the disease, one and one only of the four has been found definitely parasitic. The other three are harmless. Were it not that two of these three possess stages in their life-history closely resembling the true parasite, and frequently occur intermingled with it, there would have been no need for the laborious testing in pure separate cultures of the various organisms. It appears clear that much of the work that has been done with Fusarium wilts has met with the same difficulties, and in so far as these difficulties have not been allowed for, so to the same extent the work is unreliable. It may be said definitely that no case of parasitism attributed to Fusarium or Cephalosporium stages of Hypocreaceous fungi can be accepted unless successful inoculations have been carried out with ascosporal strains. Similarly none of these conidial types of soil fungi can be considered a proved parasite unless successful inoculations have been obtained in each case with pure cultures of the fungus concerned. The mere presence of a fungus in the tissues of the diseased plant with conidial stages agreeing with those of a recognised parasitic form of Cephalosporium or Fusarium counts for nothing without successful cultivation and inoculation.

Description of the parasite of pigeon-pea wilt.

The characters of the internal growth in diseased roots have been described in the previous paper. When such roots are well washed, flamed and placed in water on a slide, an external growth appears on the surface in a day or two. This has at first consisted only of the Cephalosporium type in the cases observed, but subsequently Fusarium spores appear. The Cephalosporium is characterised by a rather scanty creeping mycelium, with very many short conidiophores, often whorled, and bearing great numbers of microconidia. There is ordinarily little tendency for the growth to extend into the air ; most of the conidiophores remain immersed in the liquid and therefore do not show the characteristic heads of spores bound in a drop of water. These occur, however, in cultures on solid media and may be studied in agar drop cultures on slides or in glass cells (plate IV, fig. 3).

The following description is taken from pure strong cultures of the fungus, the parent of which or subcultures from which have been proved to be parasitic by inoculation. The cultural characters on different media will be given in detail below.

The hyphæ are fine, copiously branched, septate and colourless under the microscope. Anastomoses occur rarely in vigorous cultures, but are common when a portion of the growth in an old culture is sown in water, and also between the germ tubes of both sorts of conidia (plate IV, fig. 10). Cephalosporium spores begin to form when the mycelial growth is still scanty, and are found in great numbers by the third day in most good cultures. Singly they are colourless but in the mass range from flesh colour to deep salmon pink on most media. They give a peculiar moist, almost oily, appearance to the surface of the growth from their great numbers. They are formed either on single conidiophores arising directly from the creeping mycelium (plate IV, fig. 2), or on special whorled branches in dense clusters (fig. 1). If there is any morphological character which distinguishes this species from its allies, it is this formation of crowded whorled conidiophores. I have not observed them in other species seen. They are not, however, always formed and the other type, which is always present, is not distinguishable from that of several allied species.

Even at an early stage of the cultures septate spores are formed. The typical forms found at this period are straight or slightly curved, continuous and measure 5 to 15 by 2 to 4μ. The other forms which occur mingled with these are falcate or strongly lunulate, single-celled spores, larger than the last (up to 21μ in length), and one, two or sometimes three-celled spores, which may be straight or curved and with pointed or rounded ends. Examples of all the types seen in a single culture on the third day are shown on plate IV, fig. 4.

In a few cultures on potato and plantain, small round sclerotia, bearing microconidia, appeared. These seem to correspond to the Tubercularia stage of Nectria cinnabarina.

Many of the cultures, especially some of those on liquid media, formed no other kind of spore but the above. In others Fusarium spores develop. They appear later than the other forms and are figured in plate IV, fig. 7. Quite similar spores may be got from any culture by inoculating a drop of agar on a slide, and it appears probable that they occur regularly in all good solid-medium cultures that are well aerated, but less frequently in liquid media or in badly aerated cultures.

The Fusarium type of spore may be formed either singly on short lateral conidiophores, or in clusters. A true tuberculariaceous stroma bearing macroconidia has not developed in any of the cultures, but it almost certainly does so in nature on the bark of the host plant. I have not been any more successful in the prolonged cultures of Neocosmospora on a large variety of media in obtaining conidial stromata. Such stromatic beds are common on the bark of wilted plants and some, at least, would appear to belong to the parasite.

The Fusarium conidia are formed in a manner quite like that of the microconidia, except that the spores successively abjuncted from the apex of the conidiophore, drop off at once, and are not bound in a drop of water into a head. They are falcate or more rarely nearly straight, with pointed ends, 3 to 5-septate, slightly swollen between the septa and measure 30 to 50 by 3 to 5μ.

In several cultures, particularly on potato, a second type of Fusarium spore developed. This was nearly as long as the first but much narrower and produced on whorled conidiophores resembling the clustered type often found in the microconidial stage.

Both micro- and macroconidia germinate readily in water, putting out one or more germ tubes, which may grow out into a mycelium or may be of limited growth and give rise to secondary spores, usually of the microconidial type, but sometimes of the other. Several of those figured in fig. 7, plate IV, arose from the germ hyphæ of the microconidia figured in fig. 6 of the same plate.

Chlamydospores are found on the mycelium within the vessels and also develop in culture. They are usually round or oval swellings of a hypha, either at the end or in its length, and are sometimes in short chains of two or three. The wall is thick but not, so far as seen, coloured, in this differing from the similar bodies of several of the common soil Fusaria. In old cultures portions of the mycelium may become segmented into thick-walled, irregular cells, which appear to be of the same nature as chlamydospores.

The above description is not sufficient to separate this species from conidial stages of more than one species of common soil fungi. In comparing it with conidial stages of Neocosmospora vasinfecta the only character which appears to be of diagnostic value is the clustered conidiophore of the microconidial stage, which, however, is not a constant character in culture. The species named Fusarium Dianthi Pril. and Del.(17), the cause of the carnation disease in the south of France, is evidently closely similar to the conidial stages of Neocosmospora, since Delacroix in a subsequent paper(5) stated that they appeared to be identical. This same fungus was referred by Mangin(18) to Fusarium roseum, one of the commonest members of the genus, and hence this must also be considered as a close ally of the pigeon-pea parasite. Similarly, Fusarium oxysporum Schlect., with its numerous possible synonyms, is hardly to be distinguished morphologically from this species except in the more regular, coloured chlamydospores. The latter are, however, very variable bodies. Fusarium Lini Bolley (19), another of the proved wilt-producers, is also probably a close ally. It is true that Bolley does not specifically mention a microconidial stage, but from his figures on pages 37 and 45 it would appear probable that one exists.

In the absence of the perfect fruit it appears therefore necessary to rely on cultural characters for some of the chief diagnostic features of the pigeon-pea parasite.

Cultural characters of the pigeon-pea parasite.

The following media were inoculated from an agar tube culture originating from a single spore and being part of the material used for the successful inoculations in Series XIV.

Nos. 1 to 10 consisted of a standard solution made up of ammonium nitrate 10 grms., potassium phosphate 5 grms., magnesium sulphate 2·5 grms., and distilled water 1,000 c.cs., to which were added the substances specified below. The liquid cultures were in Pasteur flasks containing 30 c.cs. of the medium, the solid cultures in tubes.

A. Liquid media.

1. Glucose 3% added to the standard solution.
2. Saccharose 3% „ „ „

3. Maltose 3% added to the standard solution.
4. Glycerine 5% ,, ,, ,,
5. Gum acacia 5% ,, ,, ,,
6. Peptone 1% ,, ,, ,,
7. Asparagin 1% ,, ,, ,,
8. Citric acid 1·5% ,, ,, ,,
9. Sodium carbonate 1% ,, ,, ,,
10. Absolute alcohol ·5% ,, ,, ,,

B. Solid media.

11. Potato boiled in distilled water.

12. Acid potato, prepared by soaking for 20 minutes in 1% sulphuric acid, then rinsing quickly in water and boiling in distilled water to sterilise.

13. Alkaline potato, as 12, but 1% sodium carbonate used in place of sulphuric acid.

14. Carrot boiled in distilled water.

15. Acid carrot, as 12.

16. Alkaline carrot, as 13.

17. Rice boiled in a paste with distilled water.

18. Acid rice, about 10 c.cs. rice moistened with distilled water and with 10 drops of ·5% hydrochloric acid added.

19. Acid rice, as 18, but only 5 drops acid added.

20. Alkaline rice, as 18, but 5 drops of saturated solution of sodium carbonate added in place of the acid.

21. Alkaline rice, as 20, but only 2 drops alkali added.

22. Plantain boiled in distilled water.

23. Onion boiled in distilled water.

24. Sugarcane pith boiled in distilled water.

25. Tapioca boiled in distilled water.

26. Nutrient agar; agar 15 grms., beef extract (Liebig's) 4 grms., peptone 10 grms., sodium chloride 5 grms., distilled water 1,000 c.cs., neutralised by sodium carbonate.

27. Glucose agar as last but with 20 grms., glucose added. The characters of the growth on these media are given below.

1. *Standard solution + glucose.*—After a week the growth in this flask was ahead of that in any other of the series. The surface growth was dense and of a moist pink appearance from spore production. The deep growth entirely filled the solution. After 15 days this was still the best flask, the submerged growth being very dense. Neither in this nor in any other of the liquid media was there any appreciable aerial growth. After two months the surface colour had faded to a dirty flesh colour with some creamy patches. All three spore forms were produced.

2. *Standard solution + Saccharose.*—The growth was slower than with glucose, the surface growth after 15 days being only about one-half that of the latter. After two months the colour was a deep pink, much brighter than in 1. All three spore forms were produced.

3. *Standard solution + maltose.*—The growth was patchy at the surface though dense below after a week. The surface patches were salmon pink from spore formation. The latter had increased by the 15th day but still did not cover the whole surface as in 1 and 2. In two months the colour was intermediate between 1 and 2, but the growth still less than in either. All three spore forms were produced.

4. *Standard solution + glycerine.*—Growth fairly dense after a week but no colour. In 15 days the superficial growth was greyish white. In two months a little colour had appeared, and this gradually developed into a uniform pale creamy pink which persisted for many months. All three spore forms were produced.

5. *Standard solution + gum acacia.* — Growth of the same character as in glycerine but denser and the pink tinge appeared in 15 days, and was about No. 16 of Saccardo's "Chromotaxia" after two months. Macroconidia not developed.

6. *Standard solution + peptone.*—Surface growth slight, white. Submerged growth less than in any of the above, flocculent, not in sheets. No colour developed after many months. Few spores were formed and all of the microconidial type.

7. *Standard solution + asparagin.*—Surface growth better and submerged growth worse than with peptone, after a week. Then improved and after 15 days the surface was nearly covered with a moist white growth with well defined margins and concentric, slightly raised, lines of growth. In two months all growth had apparently ceased. Spores not numerous, only microconidia.

8. *Standard solution + citric acid.*—The only growth visible after a week was a number of minute flocculent colonies. These increased subsequently but little and never developed any colour. A moderate number of all three kinds of spores developed.

9. *Standard solution + sodium carbonate.*—No visible growth at the end of two months.

10. *Standard solution + alcohol.*—No surface growth resulted at any time. The submerged growth was thin and filmy but fairly abundant. Microconidia abundant, macroconidia and chlamydospores few.

11. *Normal potato.*—After three days the surface was practically covered with a dense rough growth, grey or white at the base, but with dirty pink patches over a considerable portion. After two months the whole slab was covered with an even, moist, non-filamentous growth of a dirty cream colour. All the potato cultures bore eventually all three types of spore.

12. *Acid potato.*—After three days the whole slab was covered with a dense moist growth, mostly salmon pink from copious spore formation (see plate III, fig. 2). The growth in this tube remained one of the best of the series. After some months the upper part of the slab was nearly black from a development of thick-walled brittle hyphæ, with short segments and brown walls. A few small pink sclerotoid bodies, similar to those described under No. 22 below, were found after about four months.

13. *Alkaline potato.*—After three days the growth was in isolated white woolly tufts with no trace of colour and without the moist appearance of 12 (see plate III, fig. 1). A pink tinge

appeared about the 7th day and was well developed, though still paler than on acid potato, by the 12th day.

14. *Normal carrot.*—After 15 days the growth was good, colour pale salmon, surface moist, submerged growth in the water at the bottom of the tube colourless and flocculent. Spores very numerous, mostly slightly falcate, unicellular but also some with one or more septa. No macroconidia after a month.

15. *Acid carrot.*—Growth as in 14, but colour tint deeper in 15 days. Submerged growth in the water at the bottom of the tube in a dense pale-yellow sheet. Spores as in 14.

16. *Alkaline carrot.*—Growth as in 15.

17. *Normal rice.*—After 15 days the growth was considerable, surface colour salmon pink and dry, with numerous coremial-like strands extending to the glass, and copious spore-formation. Deep colour in contact with the substratum orange-red. This was the deepest colour produced in any culture. In the lower part of the tube, where aeration was deficient, the colour varied from salmon pink to pale orange.

18. *Acid rice.*—10 drops acid, after 15 days colour as 17 but more brick-red (see plate III, fig. 3).

19. *Acid rice.*—5 drops acid, not distinguishable from 18.

20 & 21. *Alkaline rice.*—5 and 2 drops alkali respectively, as 18 but growth less and colour paler.

22. *Plantain.*—After 15 days growth copious, woolly not moist, dirty flesh-colour, coremial strands as in No. 17. Where the growth was confined between the medium and the glass a thick yellow or white stroma formed. A surface sheet, almost colourless, covered the liquid in the bottom of the tube and on this several sclerotial bodies were formed. These consisted of pseudo-parenchyma, lined on the surface with crowded, erect, short conidiophores from which microconidia were budded off. The whole arrangement corresponded to the Tubercularia stage of some Nectrias. On the rest of the culture the spores were broader than usual.

23. *Onion.*—In one tube the growth resembled that on plantain, but the surface growth on the liquid below was brick-red in colour, and no sclerotia were formed. In another tube the growth was moist and pink as on normal potato and there were no coremial strands.

24. *Sugarcane pith.*—Growth very feeble and scarcely visible after a week. It ceased entirely soon after. A few microconidia only were formed.

25. *Tapioca.*—After 15 days growth slight and confined to the point of inoculation. Colour pale salmon pink. A few microconidia.

26. *Nutrient agar.*—In streak cultures the growth appears slowly, being visible on the third day, and forming a raised distinct band by the 6th day. The band is strongly convex, limited closely to the neighbourhood of the streak, and the rest of the surface of the agar long remains free from the fungus. There is usually little aerial growth, the streak being not unlike a bacterial growth. In the centre it is from salmon pink to brick-red, and around this is a zone of scanty superficial growth distinctly filamentous under a lens. The raised part of the streak is uniformly moist and shiny as soon as spore-formation becomes considerable. After about 2 weeks portions of the streak become greyish black and this may gradually extend to the whole growth. The spores are very variable even in young cultures, those figured on plate IV, fig. 4, being sketched from a single culture 3 days old. In old tubes macroconidia occur, but they are never numerous on this medium. Chlamydospores form on agar, as on most of the other media, after some months.

27. *Glucose agar.*—The addition of glucose does not appear to affect the character of the growth to any extent. It is rather more vigorous, and the black colour may develop more quickly.

In seeking for diagnostic characters in the above series of cultures, most weight naturally attaches to such characters as appear more or less regularly in the media on which the fungus grows satisfactorily. Of these the most striking is the moist, bacterial-like surface growth which developed sooner or later in all the cultures in which growth was considerable, except rice and plantain. It is most strongly developed in ordinary agar streak cultures, which would be taken on a cursory examination for bacterial growths. It is quite unlike the growth of the conidial stages of either Neocosmospora vasinfecta or of the Nectria mentioned in the early part of this paper. The second character of importance is the colour. In almost all the successful cultures this developed first with spore-formation and was largely confined to the spores. It ranged from pale flesh colour to salmon pink in these cases, and examination of spores in the mass never indicated a deeper tone than the latter. On rice, however, the substratum and the mycelial layers in contact with it developed a much deeper orange-red (plate III, fig. 3). This was altogether independent of spore-formation, and examination showed that the colour was contained in the hyphal contents not in the walls. In no cases were any green, blue, purple or carmine tones developed and this fact serves at once to distinguish the species from Neocosmospora (*cf.* plate III, figs. 4 and 5).

Of less important characters, because less constant, the chief is the formation of Tubercularious stromata observed in cultures on acid potato and on plantain. The formation of coremial strands on rice, plantain and onion is a character of the same nature, but is not constant even on these media, as the onion cultures showed.

Of other cultural characters it may be said that the fungus grows equally well when carbohydrate is supplied as sugar (in the liquid cultures) or as starch (in the solid cultures). In the former case glucose is the most suitable, saccharose next and maltose least of the three tried. Similarly of starchy media potato, carrot, rice and plantain were the best in the order named, while tapioca was hardly capable of utilization at all. As regards reaction, acid potato, carrot and rice gave better results than normal, and in potato and rice the normal was better than the alkaline culture. In carrot the two were about equal. Though in the standard solution with $1^{0}{}_{0}$ sodium carbonate no growth took place, the tolerance for alkali is shown in the alkaline cultures on solid media and was also evident in some field experiments mentioned below, in which the disease was not diminished by heavy liming. Most Fusaria so far investigated agree in this respect.

For the fungus possessing the characters above described I propose the name Fusarium udum, without prejudice to the question, which I hold to be unanswerable, whether it has been previously included amongst the named members of the genus. The following diagnosis should serve to identify it with sufficient accuracy.

Fusarium udum n. sp.

Mycelium parasitic within the roots of the host plant or saprophytic and then creeping ; hyphæ hyaline, slender, much branched, usually with little aerial growth ; microconidia of the Cephalosporium type, produced successively on the ends of short simple or clustered conidiophores and remaining bound in a drop of liquid after abjunction, unicellular or with 1 or more septa, elliptical or falcate, hyaline singly, salmon pink in mass, occasionally developing from the surface of minute spherical stromata and then of the Tubercularia type, 5 to 15 by 2 to 4 μ in diameter ; microconidial stage in culture usually moist and bacteria-like, white to salmon pink, occasionally (on rice) orange-red, never green, blue or purple ; macroconidia of the Fusarium type, formed as the microconidia but on shorter conidiophores and becoming free as soon as abjuncted, falcate, 3 to 5-septate, hyaline, 15 to 50 by 3 to 5 μ in diameter, usually late in appearing ; chlamydospores, round or oval, rather thick-walled, hyaline, sometimes in short chains, 5 to 10 μ in diameter.

Parasitic in roots of Cajanus indicus and saprophytic in soil, India.

Other biological characters of Fusarium udum.

The fungus remains alive in soils, even in the absence of the host plant, for a considerable period. The pot experiments have not been of sufficient duration to indicate how long this period may be, but it certainly exceeds a year. Most of the conidia found in cultures nearly a year old were still capable of germination, and then usually formed secondary spores very rapidly. The chlamydospores are likely to retain their vitality for a still longer period. The prevalence of the disease and the extent of damage caused by it are largely due to soil infection from the preceding crop. It is on this account that sufficient rotation is of such paramount importance in pigeon-pea cultivation in India. Spread within a field takes place chiefly through the soil. It is, however, dependent largely on the space between the plants and the size of the latter. It is noticeable that extension occurs much more rapidly where the plants are crowded in pots than in the field. Similarly the extension is more rapid the larger the plants are. It cannot be doubted that this is due in both cases to extension occurring more rapidly along the roots than across the intervening soil. Hence the nearer together the roots of different plants are, whether as a result of overcrowding or of extensive lateral growth in the roots of large plants, the more rapid the spread of the disease.

Aerial spread by wind-borne spores probably occurs, though to a lesser extent and much more slowly than through soil. The following observations bear on this point. Up to the present no direct attempt to isolate the parasite from the bark of the stem of wilted plants has been made, though it is proposed to do so shortly. Fusarium beds and microconidial colonies are common on such places, but they have not been separated and their parasitism tested. Some at least belong to other species. The control pots growing in the neighbourhood of infected pots have in several cases ultimately developed the disease. This has not occurred until the plants were a good size, from three to five months after sowing. The control plot of Series XVI remained free from wilt for eight months, though only separated from the inoculated plot by a narrow trench a foot deep. Aerial infection is not likely to be responsible for much loss since it occurs rather late in the season, and though isolated plants may be killed before harvest, centrifugal spread in the soil to surrounding plants has not time to occur to any great extent.

There is no definite evidence that the disease is conveyed in the seed, and this appears to be unlikely. The control plants in the earlier series, before seed disinfection was practised, indicate that it does not happen commonly.

To determine the exact locality of infection a series of water cultures was tried, the plants being germinated under sterile conditions, and transferred to plugged sterile cylinders containing von Crone's solution,[1] when the shoot was from $1\frac{1}{2}$ to 2 inches high. Arrangements were made for daily aeration of the solution and stirring up the precipitate of salts. The inoculations were made from a glucose agar culture. The results bore out, what was already fairly evident from examination of the pot cultures, that infection begins ordinarily through the fine lateral roots. These were rapidly attacked and shrivelled, whether they arose below the seed, or above it, in those cases where the seed was well below the cork. On the other hand, inoculation of the stem gave no result, nor did one or two inoculations made on the main root just below the seed and above the origin of the first lateral root. The water cultures were remarkable in some respects. Though infection occurred on the white lateral roots, even more than an inch behind the growing point, provided the part inoculated was above the level of the solution, none occurred in any case below the liquid. The filaments in the former case penetrated the cortex and led to browning of the cortical cells, visible externally as a distinct brown mark at the point of inoculation. They did not, however, reach the vascular system, no case of penetration of the central cylinder having been observed. Hence there was no stoppage of the upward current and death did not result in any of the six plants inoculated at the roots, though two of them shed many of their leaves and looked very pallid, and a third was less markedly affected. In two of these the observations extended for over three months, in the other four for two

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[1] Potassium nitrate 1 grm., ferrous phosphate ·25 grm., tri-calcic phosphate ·25 grm., magnesium sulphate ·5 grm., calcium sulphate · grm., water 1 litre.

months. Schikorra [(14) p. 16] similarly found that the parasitism of the "St. Johannis" disease parasite in water cultures was less than in soil. In inoculations below the liquid the explanation may simply be that the destructive enzymes by means of which penetration is effected are diluted as soon as formed and never reach a concentration sufficient to injure the roots. This does not explain, however, why the vascular system was not penetrated in the cases inoculated above the water level, and the problem involved is evidently of great physiological interest.

Treatment.

In the case of an internal root parasite widely distributed in the ordinary cultivated soils of the parts of India where pigeon-pea is grown, nothing short of extensive sterilisation of the soil will free it from the germs of the disease, if frequently cropped with the host plant. Such sterilisation is usually not practicable on account of the high cost, and is besides very difficult in the wilts hitherto investigated. Orton (3) tested the effects of a large number of soil fungicides in the allied cotton wilt, and failed to obtain satisfactory results with any. Delacroix (5) advocates the use of formaline injected into the soil, but the cost of his treatment, which he claims was perfectly efficacious against carnation wilt, works out to nearly an anna per square yard, or Rs. 300 per acre. I have tried sulphate of iron and also lime, with results agreeing with those of Orton. The sulphate of iron was applied directly to the soil around each plant, half a pint of a $2\frac{1}{2}$ per cent. solution to each of 323 plants. No benefit whatever resulted. The lime was applied at the rate of one ton to the acre, the plots being 400 square feet in area. In the two limed plots 70 and 45 plants respectively had wilted at the end of 5 months, quite as many as in the similar unlimed plots near by. Bolley (19) working with the flax wilt Fusarium found it was rather more virulent in limed than in ordinary soils.

No application made to the above-ground parts of the plant can possibly do any good, since the fungus lives in the soil and attacks the plants through the roots.

There remains only, in our present knowledge of plant therapeutics, the method of breeding resistant strains. This method has already proved extremely fruitful in the United States. In India the introduction of *buri* cotton into wilt affected parts of the Central Provinces promises equally well. In any case it is the only method at present available and must therefore be fully tried.

Preliminary work was commenced in 1906, under the care of Mr. J. B. Knight, Professor of Agriculture, Bombay Department of Agriculture. The number of varieties of pigeon-pea grown in India does not appear to be large. All those that could be found were collected and sown on the Poona Farm in 1905. In 1906, nine of the varieties that promised best were resown on the same plot. The following year four varieties were retained. The purpose of continuing the growth of certain varieties on the same plot, prior to single plant selection, was twofold. It was desired to learn something of their value, and it was necessary before definite selection work was commenced, to make sure that all the plants had been exposed to the disease.

In 1908, the control of the selection work was taken over by Mr. W. Burns, Economic Botanist to the Government of Bombay, who is continuing it on the lines of pedigree breeding from single plants.

The most recent work in plant improvement has shown that individual plants which possess a given character, frequently transmit this character unaltered to their progeny. Individual plants differ greatly in regard to this ability, and these differences may apply to a whole variety (*e. g.*, the Egyptian varieties of cotton are generally more resistant to the American cotton wilt, than the indigenous Upland varieties, and the same seems to apply to *buri* cotton in regard to the cotton wilt in India). No variety of pigeon-pea obtained has shown itself to be specially resistant to the disease. More usually the inherent resistance is confined to individual plants and the behaviour of the other plants in the variety need not be considered.

Pedigree breeding consists simply in separating out once for all the individual plants possessing the required character, and multiplying rapidly, under isolation, their progeny.

The first step in pedigree breeding for disease resistance is to choose a considerable number of plants which are both resistant to the disease, and possess otherwise desirable qualities, such as productiveness, etc. This is simple enough in the case of a disease which spreads rapidly by air-borne spores, since in any year of considerable disease the individual plants in a plot will be all equally exposed to infection. In a disease of the type of wilt, where spread occurs comparatively slowly through the soil, it is not possible to be sure, in an experiment lasting through one season only, that healthy plants are resistant to the disease or have merely escaped infection through not coming into contact with the parasite. Hence in the experiments at Poona the seed of selected healthy plants was resown on the same plot for several seasons, until the whole of the soil was thoroughly infested and the possibility of any plant not being reached by the parasite was reduced to a minimum. It was early apparent that there was little hope of any *variety* proving resistant, as the plots became a mass of mixed types, presumably through free intercrossing. In the last season or two the crossing, if effected between plants within the plot, has been probably in most cases between more or less resistant individuals, and the individual plants possessing the quality of resistance inherent in them are, it is hoped, now fairly numerous.

The seed of the selected plants will be harvested separately and planted separately next season. The resulting growth and behaviour in regard to the disease will be critically examined. If the desired character of resistance appears definitely in any of the plots, combined with other desirable characters sufficiently to make the variety suitable for general cultivation, it will be rapidly multiplied and tested on a large scale for distribution. Should the first selections not prove successful, they must be repeated. Ultimately, though experience is as yet comparatively limited with regard to this method of combating disease, it may be hoped to obtain a variety that is truly resistant to wilt.

It is only in this direction, so far as our knowledge at present extends, that a practical means of fighting the disease can be sought.

PUSA, *March 30th*, 1909.

DESCRIPTION OF THE PLATES.

PLATE I. *Neocosmospora vasinfecta Smith, from indigo (Indigofera sumatrana).*

Fig. 1. Perithecia on a root. × 4.

,, 2. Pure culture on nutrient agar from an ascosporal colony, showing concentric formation of perithecia in culture. × 4.

,, 3. A perithecium from pure culture on nutrient agar. × 170.

,, 4. Ascospores from the same culture as fig. 3. The projections of the outer wall are shown too regular. The right hand spore is focussed in surface view to show the superficial markings. × 1100.

,, 5. Asci with spores, and paraphyses, from the same culture as above. ×580.

(All painted by H. Hormusji).

PLATE II. *Neocosmospora vasinfecta Smith, from ascosporal cultures.*

Fig. 1. Fusarium spores (macroconidia). Indigo fungus. × 300.

,, 2. Germination of ditto, with secondary formation of microconidia from the upper spore and of a macroconidium from the lower spore. Pigeon-pea fungus. × 300.

3. Intermediate types between micro- and macroconidia. Indigo fungus. × 300.

,, 4. Chlamydospores. Indigo fungus. × 300.

,, 5. Formation of microconidia. From a continuous observation. Pigeon-pea fungus. × 325.

,, 6. Mycelium bearing microconidia formed from germination of the ascospores. Cotton fungus.

,, 7, 8 & 9. Perithecia and ascospores of the gram, pigeon-pea and cotton fungus respectively. Perithecia × 114, spores × 730.

PLATE III.

Fig. 1. Fusarium udum n. sp., pure culture on alkaline potato (see text). × $1\frac{1}{2}$.

,, 2. Ditto on acid potato. × $1\frac{1}{2}$.

,, 3. Ditto on acid rice. Natural size.

,, 4. Neocosmospora vasinfecta Smith, pure culture on acid rice. Natural size.

,, 5. Ditto on bread. Natural size.

,, 6. Germination of the ascospores of Neocosmospora vasinfecta from cotton.

(All painted by A. N. Banerji).

PLATE IV. *Fusarium udum n. sp.*

Fig. 1. Whorled conidiophore with microconidia. × 730.

,, 2. Simple lateral conidiophores on the creeping mycelium, with microconidia. × 730.

Fig. 3. Aerial conidiophore with microconidia in heads (Cephalosporium type). × 730.

„ 4. Types of microconidia from a single culture on nutrient agar 3 days old × 730.

„ 5. Formation of microconidia. From a continuous observation. × 730.

„ 6. Germination of the microconidia. × 730.

„ 7. Fusarium stage (macroconidia) with mode of attachment. The lower four spores were formed from the microconidia figured in fig. 6. × 730.

„ 8. Chlamydospores. × 730.

„ 9. Germination of the macroconidia with formation of secondary spores. From an old maltose culture. × 330.

„ 10. Anastomosis between the germ tubes of two macroconidia. × 330.

PLATE V.

Fig. 1. Early stage of root infection in pigeon-pea wilt. The seedling was sown in infective soil on November 21st, 1907, and was removed on March 28th, 1908. Eight seedlings had wilted between January and March. × $1\frac{1}{4}$.

„ 2. Stages in pigeon-pea wilt. From a photograph.

PLATE VI.

Fig. 1. Two of the pots of Series XV. One inoculated with Fusarium udum n. sp. and one not inoculated (see text). From a photograph.

„ 2. Three of the pots of Series XIV, two inoculated with Fusarium udum n. sp. and one not inoculated (see text). From a photograph.

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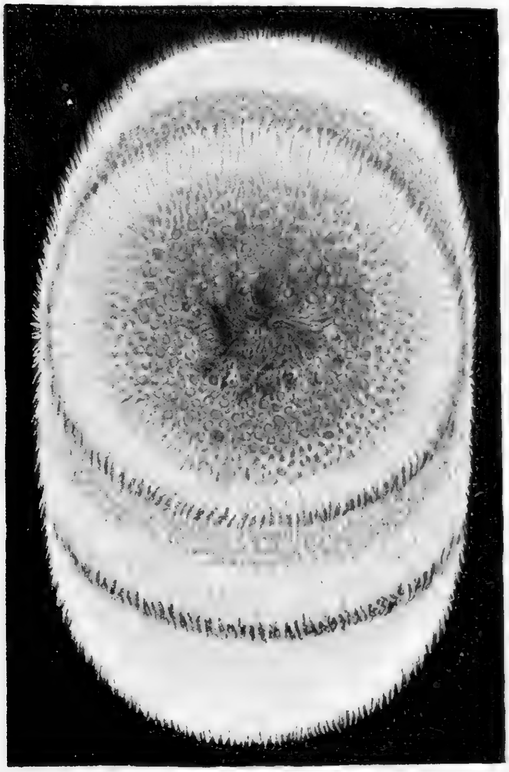

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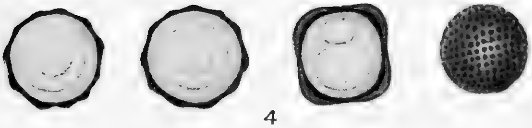

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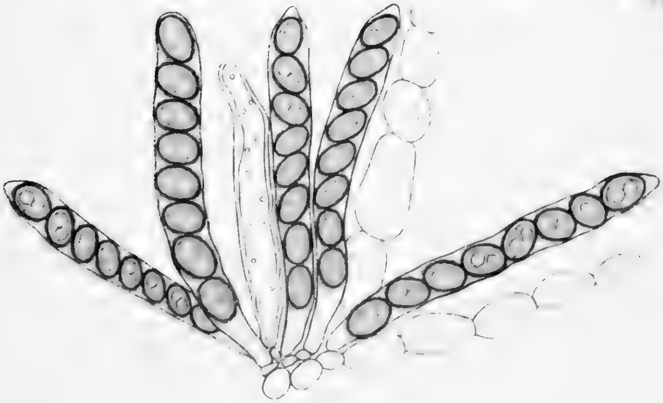

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NEOCOSMOSPORA VASINFECTA.

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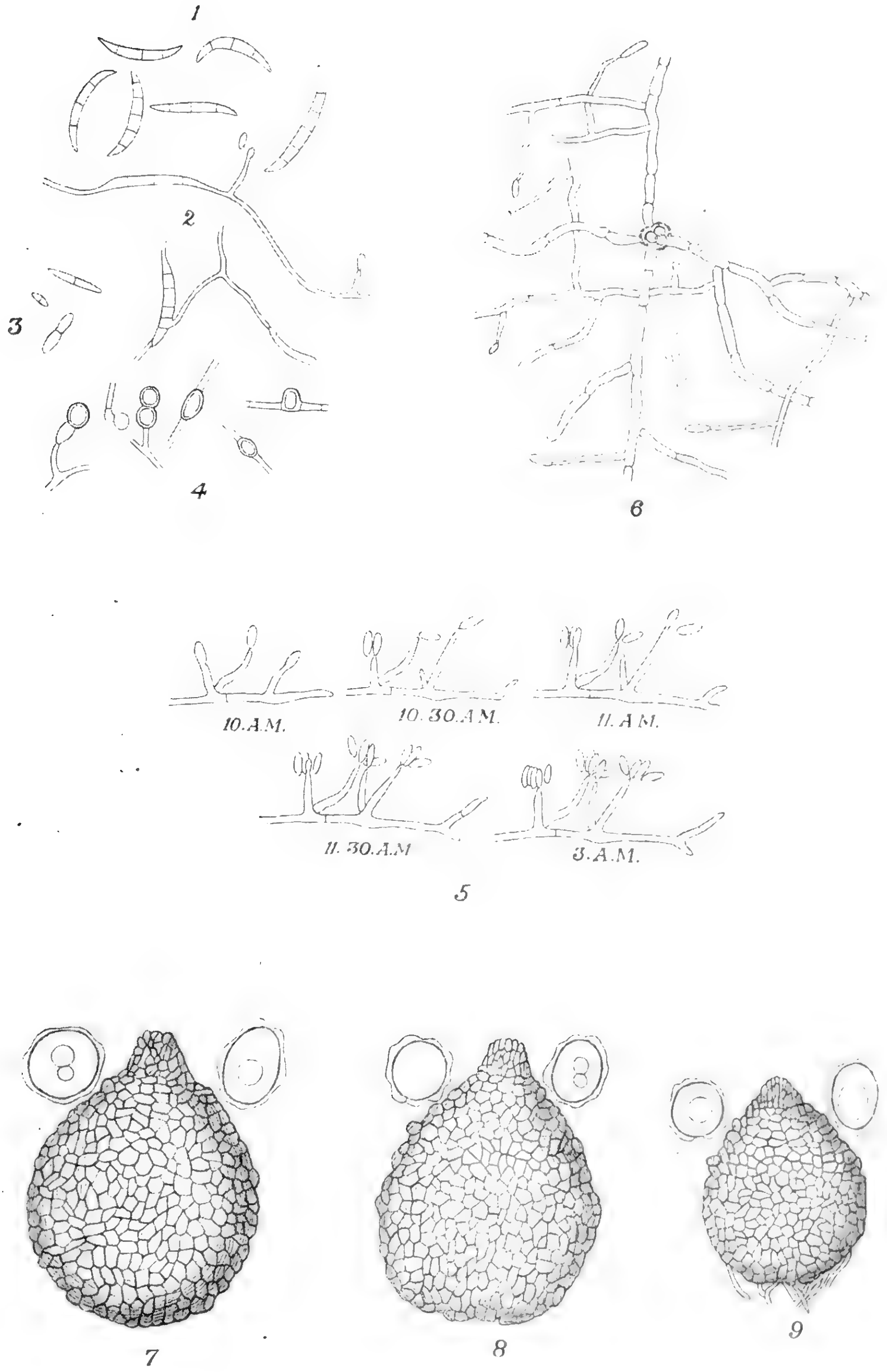
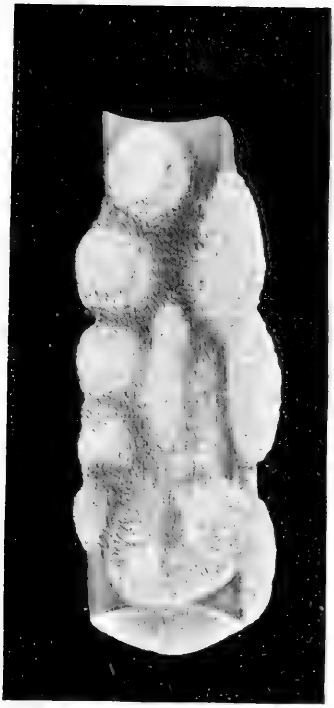


NEOCOSMOSPORA VASINFECTA.

PLATE. III.



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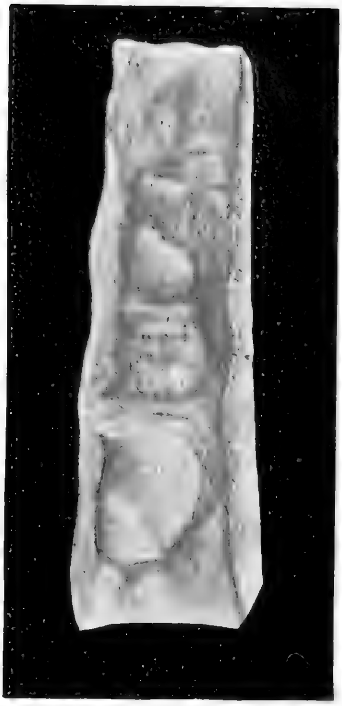

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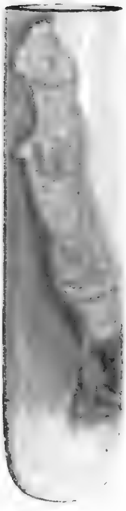

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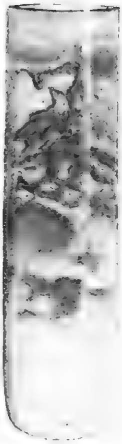

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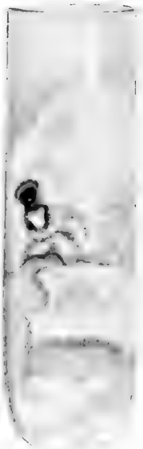

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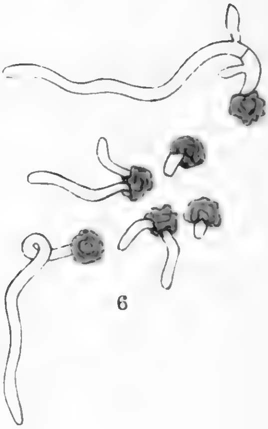

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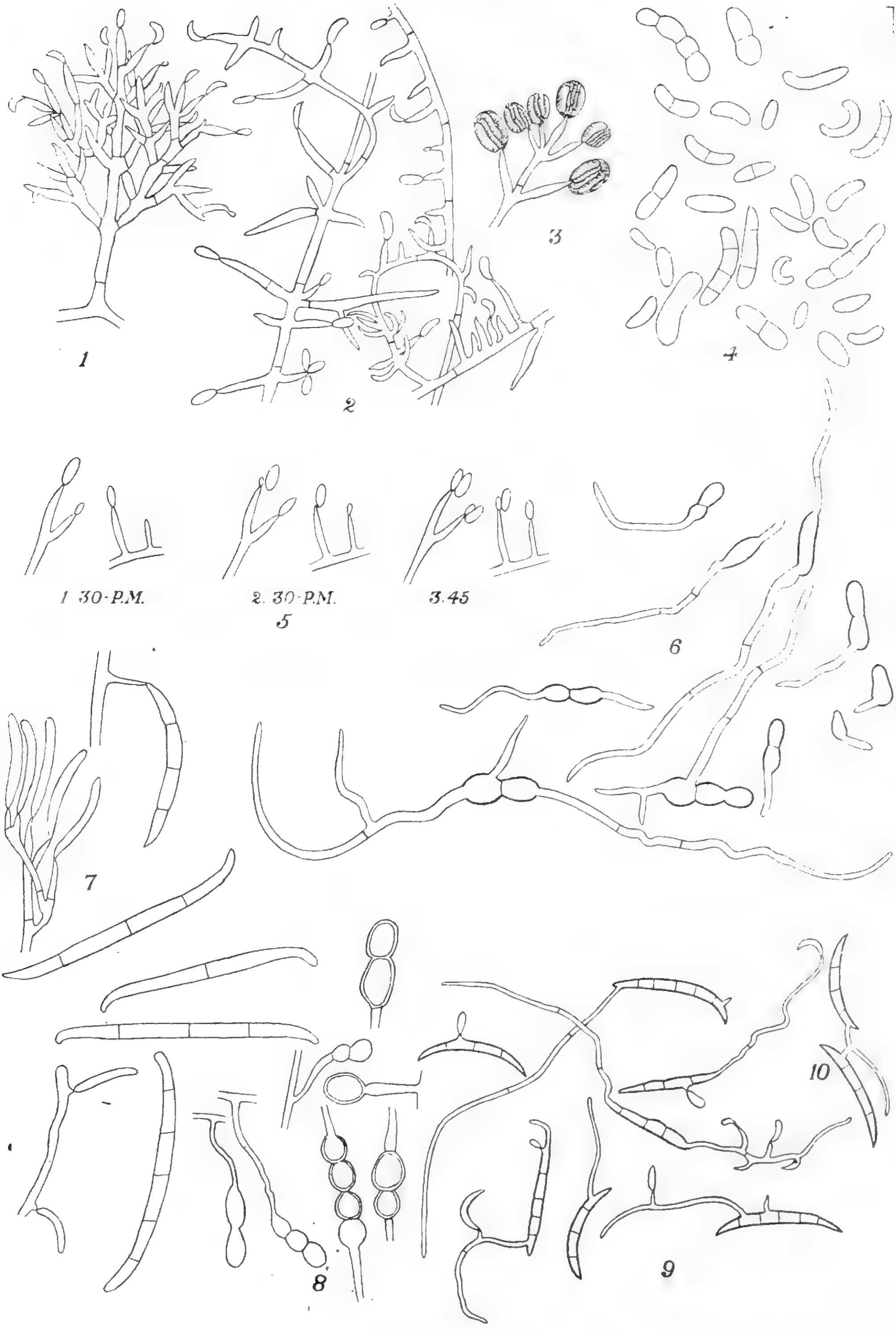
FUSARIUM UDUM (FIGS. I TO 3) AND NEOCOSMOSPORA VASINFECTA. (FIGS. 4 TO 6).

PLATE IV.



Fusarium udum.

PLATE V.

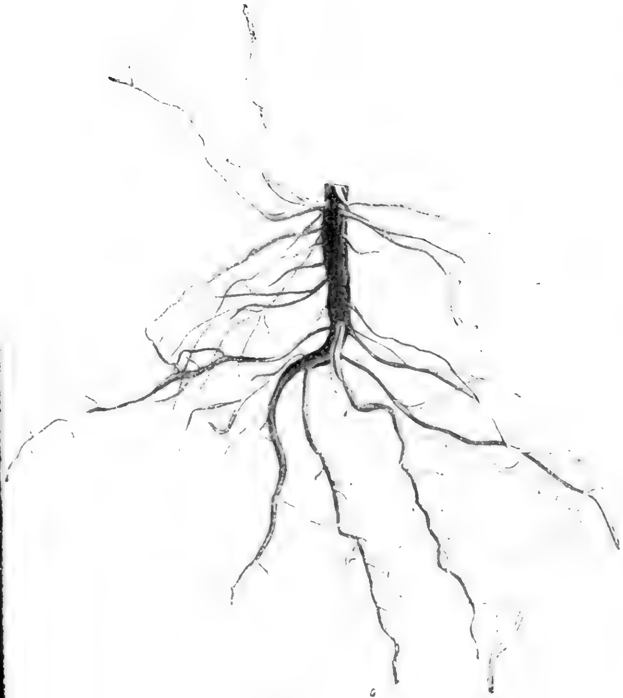


Fig. 1.

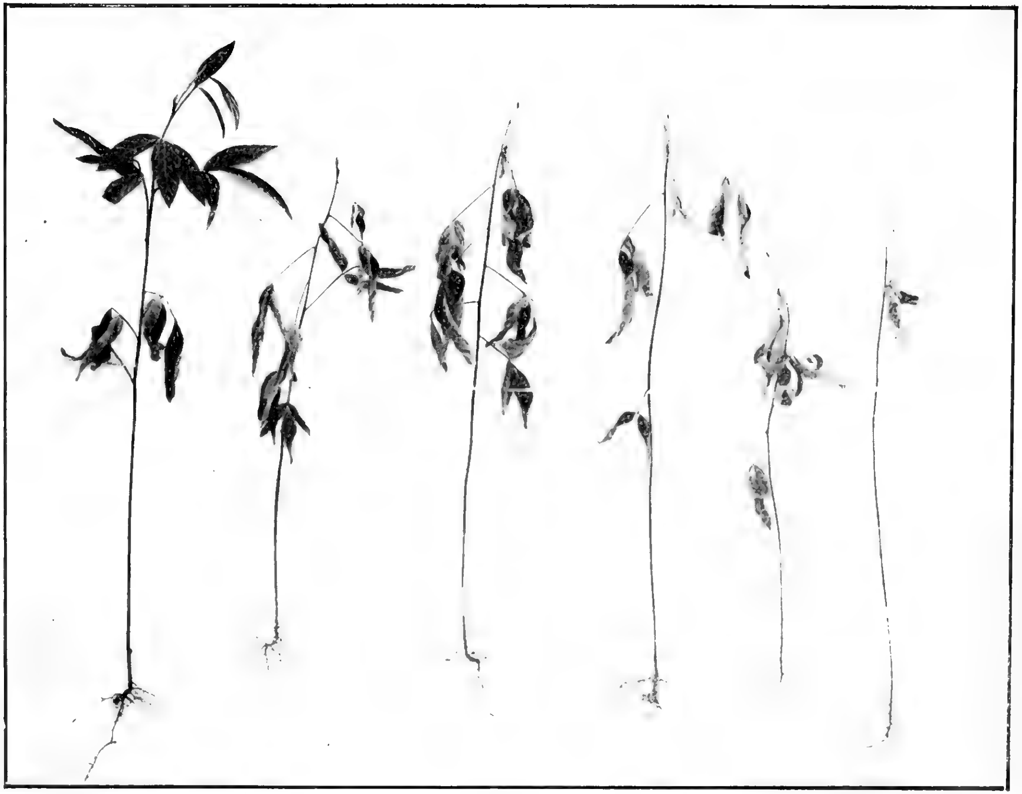


Fig. 2.

Pigeon-pea Wilt.

PLATE VI.

Fig. 1.

Fig. 2.

Pigeon-pea Wilt.

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