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ANNALS

OF THE

ROYAL BOTANIC GARDENS, PERADENIYA.

EDITED BY

J. C. WILLIS, M.A., F.L.S.

DIRECTOR.

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ANNALS

OF THE

ROYAL BOTANIC GARDENS,

PERADENIYA.

EDITED BY

J. C. WILLIS, Sc.D., F.L.S.

AND (PART III.) BY

HERBERT WRIGHT, A.R.C.S., F.L.S.

(ACTING DIRECTOR, ROYAL BOTANIC GARDENS.)

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The Genus Diospyros in Ceylon: its Morphology, Anatomy, and Taxonomy.

BY

HERBERT WRIGHT.

Part I.

THE original portion of this paper deals exclusively with the genus Diospyros, *L.*, as represented in Ceylon by some twenty species, of which Trimen remarks: "Very little is known about many of our species, which are rare or local in the forests of the wet region and seem to flower but seldom. The native Sinhalese names are vaguely applied or very local, and refer more to the wood than to the trees themselves; and one is rarely able to obtain both wood and herbarium specimens from the same tree, in which way alone it is possible to be justified in definitely deciding the source of the former. The various rare mottled cabinet-woods, which appear to be produced only by very old trees, and are known as calamander (kalu-mediriya, wal-mediriya, ho-mediriya, &c.), have mostly yet to be referred to their respective species." In view of this lack of definite knowledge and the commercial value of ebony, calamander, and other timbers, the present investigation, which has occupied much time during the last three years, both in the forests and in the laboratory, was undertaken.

The present contribution is divided into two parts, the first part containing a general statement of, and a discussion on, the various subjects investigated; the second part a detailed

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description of each species. In Part I. the following arrangement has been adopted :—

I.—History.
II.—Distribution in Ceylon.
III.—Vegetative Characters.
IV.—Anatomy ; Timber Properties, &c.
V.—Seedlings.
VI.—Reproductive Organs.
VII.—Affinity.

I.—HISTORY.

Diospyros is the largest and most important genus of the Ebenaceæ, and since most papers dealing with this order contain a description of many of our species, it is necessary to trace the history of the literature on the whole subject to gain a better grasp of the general bearing of the particular species with which we are concerned.

The accumulation of knowledge regarding the Ebenaceæ has not been rapid, probably on account of the difficulty of obtaining representative material of a natural order so widely spread, and also in virtue of the comparatively unattractive nature of this group of plants. Though in 1753 Linnæus published the names of a few species, no work of a representative kind was published until that of Hiern in 1873. During that interval the work consisted mainly of collecting and describing species, remarking on fossil forms and affinities, and discussing the ebony yielded by this group of plants.

It was not until the latter part of the nineteenth century that any internal characters were used for systematic purposes, but since that time the majority of contributions have dealt extensively with the internal or microscopical construction of the vegetative parts. The only lines of study which have hitherto been neglected are those connected with the development and anatomy of the embryos and seedlings.

In 1753 Linnæus* described five species of the Ebenaceæ, two of which belonged to the genus Diospyros. New species and genera were subsequently described by Linnæus,† C. Linnæus,‡ and Loureiro,§ and others were figured and described by Roxburgh‖ and König in 1795. It was not until 1799 that the natural order Ebenaceæ was established by Ventenat ;¶ subsequently it received considerable attention, many species and genera being quickly added from Mauritius by Poiret,** from Australia by Brown,†† from Java by Blume, from India by Wallich,‡‡ and from the Philippines by Blanco.§§

The Ebenaceæ of Ventenat, revised by Jussieu,‖‖ had by this time greatly enlarged, and the necessity for a further revision was obvious ; accordingly, G. Don¶¶ undertook this work and gave a description of every species known to him.

This was speedily followed by more collecting, and finally A. de Candolle*** wrote a monograph on the whole of the Ebenaceæ. Having formed some definite ideas as to the external morphology of the Ebenaceæ, many botanists of that period turned their attention to the possible affinities of the order, and in 1845 we have the first fossil species described by Braun, and subsequent contributions on fossil species by Unger, Ettingshausen, Zollinger, and others.

The phylogeny of the order was discussed by Miers††† and Choisy,‡‡‡ the former proposing that the Ebenaceæ be

* Linnæus, Species Plantarum, 1753.
† Linnæus, 13th Edition of Systema, 1774.
‡ C. Linnæus in Supp. Spec. Plt., 1781.
§ Loureiro, Flora Cochinchinensis, 1790.
‖ Roxburgh, Coromandel Plants, 1795–1819.
¶ Ventenat, Tableau du Regne Végétal, 1799.
** Poiret, Encyclopédie méthodique, 1804.
†† Brown, Prodomus floræ novæ Hollandiæ, 1810.
‡‡ Wallich, East Indian Plants, 1828, 32.
§§ Blanco, Flora de Filipinos, 1837.
‖‖ Jussieu, Ann. du Museum, Vol. V., 1804.
¶¶ G. Don, General System of Gardening and Botany, Vol. IV., 1837.
*** Alph. de Candolle, Prodr. Syst. Nat. Regni Veget., Vol. VIII., 1844.
††† Miers, Contributions to Botany, Vol. I., p. 24. 1851.
‡‡‡ Choisy, Memoires des Ternstrœmiaceæ, p. 9, 1855.

regarded as a polypetalous group allied to the Anonaceæ, and the latter contending that they showed strong affinities to the Ternstrœmiaceæ.

The technical value of the timber had also gained a high reputation, and many botanists discussed the origin of the term "ebony," Bertolini* contending that the ebony of the ancients was not furnished by the Ebenaceæ.

From the time of publication of the monograph by A. de Candolle in 1844 up to 1873 no work of great systematic importance was produced. In the meantime several species had been described or figured by Wight (1850), Dalzell (1852), Martins and Miguel (1856), Thwaites (1854–64), Beddome and Kurz (1871), Mueller and Bentham (1864–9), Oliver (1868–77), Eichler (1870–80), Bentham and Hooker (1872–3), and Grisebach in 1872. These, together with short accounts of the fossils, affinity, and the timbers, were all that appeared in the thirty years subsequent to the monograph by A. de Candolle.

In 1873, however, Hiern† published his monograph, which is without question the most comprehensive work on the subject. This work is purely systematic, and deals with the characters of the floral and vegetative members, the distribution of the species, their probable affinity, and the several uses to which the parts of certain species are put. Hiern distinguishes five genera, two being endemic in Africa (Royena and Euclea), one (Tetraclis) in Madagascar, and the others (Maba and Diospyros) represented in many parts of the world. The genus Diospyros, as described by Hiern, contains 160 species, and is therefore by far the most important in the order. With it Hiern has united the genera Cargillia, *R. Br.*; Leucoxylum, *Blume*; Noltia, *Schum.*; and Gunisanthus and Rospidios, *DC.* The second largest genus—Maba—includes Macreightia, *A. DC.*, and Rhipidostigma, *Dalz.* The three remaining genera contain a total of

* Bertolini, Miscellanea Botanica, XII., 1849.

† W. P. Hiern, A Monograph of Ebenaceæ, Trans. Camb. Phil. Soc. Cambridge, 1873.

thirty-three species, and since they are not represented in the flora of Ceylon, they need not be considered here.

The Brazilian genus Brachynema, *Benth.*, and the Javanese Drebbelia, *Zoll.*, are regarded by Hiern and others as being non-Ebenaceous, and as probably of Olacinaceous affinity.

The five genera recognized by Hiern are so closely associated with one another that many botanists have suggested the advisability of uniting all into one genus.

Hiern bases his classification of the genera mainly on the sex of the flowers, having the genus Royena with hermaphrodite or rarely subdiœcious flowers; the remaining genera, including Diospyros, with diœcious or rarely polygamous flowers. The observations were made upon material from the recognized herbaria of Europe, and a small quantity of spirit material obtained from Dr. Thwaites, Ceylon.

As will be shown later, the sex of the Ceylon species of Diospyros has been imperfectly and often erroneously described as a consequence of examining only herbarium specimens instead of the fresh material in the jungle.

The effect of Hiern's admirable monograph is well seen if one considers the history of the development of our knowledge prior and subsequent to its publication. Since 1873 but little has been contributed to our systematic knowledge of the Ebenaceæ, and from that time the anatomists have been at work on the basis laid down in Hiern's monograph. Their investigations have resulted in more definite knowledge regarding the structure of the leaves, the secondary tissues of the stem, and the nature of the causes leading to the discolouration of the timbers.

Wiesner* described the internal characters of the stems of some Ceylon species of Diospyros, and gave details of an onerous method of preparing sections of ebony, which was subsequently adopted by Molisch. His work was succeeded by contributions from Moeller,† in which the anatomy of

* Wiesner, Ebenholz, 1870.

† Moeller, Holzanat., in Denkschr. Wiener Akad., 1870–3.

the axis was more thoroughly dealt with, and a theory was set forth explaining the enhanced durability of ebony as a consequence of the walls of the elements being impregnated with a colouring substance of unknown chemical constitution.

A much more instructive paper was then issued by Molisch,* who prepared his sections by the method of Wiesner. Molisch described the anatomy of the stem of two of our species, D. Ebenum, *Koen.*, and D. sylvatica, *Roxb.*, together with three others, and a species from each of the genera Maba, Euclea, and Royena. He attempted to combine the facts of internal construction with external morphology, believing with Radlkofer that this would provide the best basis for a systematic grouping of the plants. He also laid stress on the striking anatomical resemblances of the species he examined, and endeavoured to discover whether the reason of the high technical value of the ebony woods lay in the anatomical construction or in the chemical changes going on within the tissues.

In connection with the colouring matter of the timbers, he believed that the initial deposits were true gums, and that the suspected resin was a product of a slow process of humification going on within the elements. He further endeavoured to show that seasonal rings of growth were found in the secondary xylem of trees of D. Virginiana, *L.*, which had been grown in Europe, whereas those grown in the tropics showed no such histological differentiation. The various points raised by Molisch will be subsequently discussed under their respective sections in the present contribution.

Hartig† has given an account of the timber of several species, and has discussed the views of Moeller and Molisch as to the nature of the colouring substance in ebony. He

* H. Molisch, Vergleichende Anat. des Holzes der Ebenaceen und ihrer Verwandten. Sitz. Akad. Wiss. zu Wien, Bd. 80, Abth. 1, 1879.

† Hartig, Bot. Ztg., p. 108, 1859, and also Lehrbuch für Förster, I. Theil, p. 256, 1861.

believed that the coloured body filling the lumina of the secondary xylem elements was neither a gum nor a resin, but one of unknown and singular chemical composition. This subject was then taken up by Belohonbek* and Höhnel,† the former concluding, after a detailed chemical analysis, that the black contents of the timber, soluble in alkali, were mainly humus acids, and the remaining material, insoluble in alkali, more or less pure carbon.

Moeller made another contribution at about the same time dealing with the anatomy of the bark, and the origin layer of the phellogen. Solereder‡ also made additions to our knowledge on the same subject, and described the histological details of the secondary elements and the papillæ on the under surface of the leaves of many species. Radlkofer§ discussed the value of internal characters, and stated that in the Ebenaceæ the affinity so apparent in the flowers may be reflected in the anatomical construction of the vegetative parts. In the same year Weiss‖ and Gürke¶ published works on the Ebenaceæ ; the former dealing with the nature and origin layer of the phellogen and its products, and the latter discussing the leading anatomical and morphological characters as known to him.

In 1892 the last anatomical contributions to our knowledge of the Ebenaceæ were made by Pomrencke** and Parmentier,†† the former dealing comparatively with the timbers, and the latter giving a detailed account of the anatomy of the vegetative members of very many species. The contribution

* Belohonbek, Ebenholz, in Sitzb. K. böhm. Gesellsch. d. Wiss in Prag., 1883.

† Höhnel, Stockwerkart Holzk., in Sitzb. Wiener Akad., Bd. LXXXIX., Abs. 1, p. 42, 1884.

‡ Solereder, Holzstruktur, 1885, pp. 68–169.

§ Radlkofer, Durchs. P. in Sitzb., Münch. Akad., 1886, p. 323.

‖ Weiss, Korkbild., in Denkschr. Regensb. bot. Gesellsch., 1890, p. 57.

¶ Gürke, in Nat. Pfl., IV. Theil, Abth. 1, 1890.

** Pomrencke, Holz. einig. symp. Fam. in Arb. bot. Gart. Breslau, 1892, p. 49–51.

†† Parmentier, Histologie comparée des Ébénacées, Paris, 1892. 155 figs., 4 pls.

by Parmentier contains a general discussion of the anatomical and morphological characters of the genera, and a detailed description of the anatomy of the leaves of seventy species of Diospyros and of other fifty species belonging to the remaining genera. Several complicated and ingenious tables are given, intended to show the relationships of the species of each genus to one another, the conclusions being based on the work of Hiern and the anatomists previously mentioned. Analytical tables for the genera and species are constructed on the sex characters of the flowers as determined by Hiern, together with the pericyclic or sub-epidermal origin of the phellogen in the stem. Parmentier believes that the genus Diospyros is characterized by a sub-epidermal phellogen in the stem, and on this ground, since D. oppositifolia, *Thw.*, and D. suberifolia, *Dcne.*, have a pericyclic phellogen, he transfers them to the genus Euclea.

Such a position is untenable, and it is unwise to lay down such rigid classifications from observations on only 40 per cent. of the species of Diospyros; furthermore, the sex of one of the species, viz., D. oppositifolia, *Thw.*, was not then known, and though it was regarded as being diœcious, I have since been able to prove that it is monœcious only. The classification put forward is further weakened by the discoveries regarding the true nature of the sex of Diospyros, and the behaviour of the phellogen in the pericycle and cortex of the primary axis.

The detailed accounts of the parts of the leaf and the grouping of species of Diospyros according to the subcentric or bifacial mesophyll, the immersion or projection of the median and lateral traces, and similar leading characters are particularly instructive, though we cannot but regard the tables of affinity, such as that on pages 56–57, as being premature, seeing that our knowledge of the whole order was then, and still is, meagre and unreliable.

We have seen that from 1873 the main work has been on the anatomy of the stem and leaves and the origin layer of

the phellogen. Smaller papers appeared during that period from Hiern* on new species and from Naudin† on the general natural history of the cultivated forms. Contributions of systematic significance were issued by Kurz‡ and Vesque,§ the latter working on the lines of Parmentier and pointing out many epidermal characters of specific importance.

The timbers also received the attention of Brandis,‖ and in more recent times were studied by Broun¶ and Ursprung.** The last-named botanist has compiled some very instructive information regarding the seasonal histological differentiation in the secondary xylem of tropical grown trees, including several Ceylon Diospyros species.

There has been only one publication dealing extensively with the Ebenaceæ during the present century, this being a purely systematic work by Hallier†† in 1901. Hallier deals with the relationships of the Tubifloræ and the Ebenales in a very general way, and from considerations upon the morphology of the flowers, fruits, and seeds, together with the phyllotaxis of the members concerned, he builds up a complicated table intended to show the polyphyletic origin of the sympetalous and apetalous flowering plants. He contends that the Ebenales show a close relationship with the Anonaceæ, Scytopetalum, Geraniaceæ, Dipterocarpaceæ, Sapotaceæ, and makes suggestive remarks as to their possible affinity to the Ancistrocladeæ, Convolvulaceæ, Quinaceæ, and many other natural orders. The contribution is full of

* Hiern, notes on Ebenaceæ, Jour. of Bot., XII., XIII., XV., 1874, 75, 77.

† Naudin, Quelques remarques au sujet des Plaqueminiers cultivés à l'air libre dans les jardins de l'Europe; in Nouv. archiv. du Mus. d'hist. nat., Paris, 1880.

‡ Kurz, Flora of British Burma, 1874–7.

§ Vesque, Gamopétales in Ann. Sc. nat., Ser. 7, 1885.

‖ Sir D. Brandis, Conf. Ind. Timbers, Col. Exh., 1886.

¶ A. F. Broun, Ceylon Ebony, Indian Forester, July, 1899.

** A. Ursprung, Beiträge zur Anatomie und Jahresringbildung tropischer Holzarten; Inaug. Disser. Hohen. Phil. Fac.; Basel, 1900.

†† Hallier, Uber die Verwandtschaftsverhältnisse der Tubifloren und Ebenalen, den polyphyletischen Ursprung der Sympetalen und Apetalen und die Anordnung der Angiospermen überhaupt. Hamburg, 1901.

interesting suggestions, and convinces one that there is no finality in pointing out the morphological resemblances between widely separated families. There is no difficulty in tracing a particular character of a floral or vegetative member through numerous non-related natural orders; in some orders the character is presented in a suppressed or enhanced form, and to deduce affinity therefrom inevitably leads to a confused notion as to the true significance of the feature dealt with.

The subject, as dealt with by Hallier, is very complicated, and in the end one gains very little precise information as to the phylogeny of any group of Angiosperms with which he has dealt.

Local History.—In connection with the history of our knowledge of Ceylon species, twenty in number, there are several interesting facts to record.

Though some of the species of Diospyros occurring in Ceylon are to be found in Malaya, Burma, Tropical Australia, Peninsular India, Anamalai hills, Tinnevelly, and South India generally, there are several endemic forms.

D. Ebenum, *Koenig*,* was the first species found in Ceylon, in 1776, but it has since been discovered in many parts of Southern India and in Malaya. It is the chief source of ebony in Ceylon, and the high commercial value of the timber was probably the reason of its being the first species to be recognized. It was not until five years later that the next species was discovered, D. hirsuta, *L.*,† an endemic form very common in the wet low-country.

In 1795 Roxburgh‡ discovered on the Coromandel Coast three species which were subsequently found wild in this Island, viz., D. Melanoxylon, *Roxb.*, the source of most of the Indian ebony, but nearly extinct in Ceylon; D. montana, *Roxb.*, a species abundant in the low forests of the

* Koenig, in Phys. Salsk. Handl., Vol. I., p. 176, 1776.

† Linnæus, Suppl. Plant., p. 440, 1871.

‡ Dr. Roxburgh, Coromandel Plants, Vol. I., pp. 36, 37, 38, t. 46, 48, 47, 1795.

hot dry country in Ceylon ; and D. sylvatica, *Roxb.*, now only rarely met with in this Island. In 1807 D. Embryopteris, *Pers.*,* and in 1827 D. Toposia, *Ham.*,† were found, the former first in the East Indies and the latter in Bengal, but both subsequently found in very many parts of Ceylon. Nearly a quarter of a century passed before the next Ceylon species was found, and this discovery—D. ovalifolia, *Wight*‡—was first made in Madras. This was speedily followed by the discovery of D. pruriens, *Dalz.*,§ first in Bombay by Dalzell, and subsequently in the Sabaragamuwa Province by Thwaites.‖ By that time Dr. Thwaites, then Director of the Royal Botanic Gardens, Peradeniya, had commenced the work of collecting the plants of Ceylon, and his discovery of D. pruriens, *Dalz.*, in Ceylon, so soon after that by Dalzell, was followed by the discovery of ten¶ species of Diospyros in 1860 ; seven of these have not yet been found out of Ceylon, and some of them are at the present time exceedingly rare. The species found were :— D. crumenata, D. affinis, D. quæsita, D. oocarpa, D. insignis, D. oppositifolia, D. Gardneri, D. Moonii, D. acuta, and D. attenuata. Since then only one species has been added to the Ceylon group, viz., D. Thwaitesii, by Beddome** in 1871, a form peculiar to this Island.

Locally, no further original work has been done on the genus Diospyros other than what is represented in Dr. Trimen's "Handbook of the Flora of Ceylon."

II.—DISTRIBUTION IN CEYLON.

The forest vegetation in Ceylon varies according to the rainfall and elevation, and as far as the genus Diospyros is concerned we may speak of the species as being dry, wet,

* C. H. Persoon, Synopsis Plantarum, Vol. II., p. 624, 1807.
† Hamilton, Trans. Linn. Soc., Lond., Vol. XV., p. 115, 1827.
‡ Dr. Wight, Icones Plant. Ind. Orient., t. 1,227, 1850.
§ Dalzell, Kew Journal of Botany, Vol. IV., p. 110, 1852.
‖ Trimen, Flora of Ceylon, Vol. III., p. 95.
¶ Thwaites, Enum. Plant. Zeyl., pp. 179-182, 1860.
** Beddome, Ic. Pl. Ind. Or., p. 27, t. cxxxv., 1871.

or intermediate zone plants. In the dry zone, where the rainfall ranges from 35 to 70 inches, we have seven species, viz., D. Ebenum, D. Embryopteris, D. Melanoxylon, D. oocarpa, D. montana, D. affinis, and D. ovalifolia. The majority of these species, particularly D. Ebenum, D. ovalifolia, and D. Embryopteris, are to be found in abundance in local areas of the dry zone. D. oocarpa is less common, though at Mihintale, Dambulla, Haragama, Maturata, and Kalugala it is abundant in many of the forests. Of the dry zone species D. Melanoxylon has the most limited distribution. It was first found by Dr. Trimen* between Bibile and Ekiriyankumbura in 1888, and the fact that its existence was not determined by Dr. Thwaites is sufficient to show its rarity. In 1901 its presence was again noted in this locality, and in addition a large number of plants were found on the patana and in the coarse forests at Elukapudena and Diggalrana to the south-west of Bibile. Many large trees were also found along the roadside from Bibile to Bintenna, and in the forest along the side and at the base of Bibile hill.

The remaining thirteen species occur in the wet zones, where the rainfall is never less than 80 inches, and in places often reaches over 300 inches per annum, and at elevations from sea level to 4,000 feet. The most generally distributed species are D. insignis and D. Toposia. In the districts around Ratnapura, Sinha Raja forest, Pasdun korale, and Hiniduma, the species D. hirsuta, D. Moonii, and Thwaitesii are specially abundant. In the higher parts of the wet zones, as at Ambalawa, Hantane, Kadugannawa, and Gangaruwa, abundance of D. crumenata, D. Gardneri, and D. sylvatica is met with. The remaining species are rare, and occur in the low-lying wet forests of the Southern and Western Provinces.

The rarest of the wet zone species is undoubtedly D. oppositifolia. Specimens of this species were collected at Hiniduma in 1853 by Dr. Thwaites, and this was the only material which Dr. Trimen ever saw. This species is

* Flora of Ceylon, Vol. III., p. 99.

limited to the upper part of Hinidunkanda, a hill in the Southern Province some 2,200 feet high. The upper part of this hill is for the greater part of the year enveloped in clouds, and it is only between 1,500 and 2,000 feet that this species occurs. It is particularly abundant, together with D. quæsita, on the north-west flank, and is entirely absent from the eastern part of the hill. The species D. acuta and D. attenuata are the next in point of rarity, they being limited to the low wet country between Hinidunkanda and Pitigala. Both species occur in abundance in the damp forests of Wewella, Pasdun korale, and D. acuta extends to the Wirakanda forests near Hewessa.

The remaining wet zone species—D. pruriens and D. quæsita—occur in the wet forests of Karawita, Sinha Raja, Hiniduma, and Yagirala. D. pruriens reaches its maximum dimensions and is most abundant in the forests of the Adam's Peak Wilderness, and thrives best on the rccky soils in the vicinity of Magala, Kadawatta, and Eratna, where the rainfall is very heavy.

In the intermediate zones, where the rainfall varies from 70 to 80 inches, the whole of the dry zone species, excepting D. Melanoxylon, occur, but of the wet zone species, however, only two—D. Gardneri and D. sylvatica—occur.

Intermingling of Dry and Wet Zone Species.

One rarely meets with any of the thirteen species of the wet zone in a purely dry zone. D. Moonii, a species possessing relatively thick fleshy leaves, is reported from dry places along the coast, though it is most characteristic of districts where the rainfall is great. Again, D. insignis, a species generally distributed in the wet zone, occurs in the Pindeniya and Kegalla districts. None of the wet zone species have ever been reported from the arid zones of the Island.

On the other hand, at least two of the dry zone species—D. Ebenum and D. Embryopteris—constantly recur in

truly wet zones. These two species, though attaining their maximum distribution in the dry areas around Anuradhapura, Trincomalee, Vavuniya, &c., may also be found in the low-lying forests of Sabaragamuwa and the Central Province, sometimes being very plentiful along the banks of streams. In the moist regions D. Ebenum may extend up to 4,000 feet, many occurring at Hantane, Ambalawa, Gangaruwa, Hinidunkanda, Borulugoda, Eratna, and Hewessa. The dimensions of trees of these two species when in the wet zone are usually but not always less than those from a dry zone. Specimens of D. montana, D. oocarpa, D. ovalifolia, or D. affinis have not yet been recorded from any wet zone area, though D. oocarpa is known in the intermediate zone.

III.—VEGETATIVE CHARACTERS.

Dimensions, Habit, &c.—As far as the Ceylon representatives of the genus Diospyros are concerned, every species assumes an arborescent habit.

It is characteristic of the dry zone species to attain huge dimensions. D. Ebenum, being the main source of ebony in the Island, is usually felled after attaining a breast-height circumference of 6 feet, but further increments are possible, and many trees are known with a circumference of 9 to 10 feet. Specimens of D. affinis in the Viriniya and Bibile districts and of D. Embryopteris at Anuradhapura often attain a circumference of 9 feet and possess an unbranched bole over 50 feet in length. The total height of the dry zone species is often over 100 feet, and the huge dimensions are only departed from when the plant occurs in the wet zone areas.

There is, however, one district in the wet zone where trees of D. Ebenum and D. Embryopteris attain dimensions which outrival those known in the dry zones. I refer to the Ambalawa district on the boundary between the Central and Sabaragamuwa Provinces, where the rainfall is over 100 inches a year and the elevation varies from 2,000 to 3,500

feet. Here there is one specimen of D. Embryopteris measuring no less than 16½ feet in circumference, not allowing for the undulations in outline, which, if taken into account, would give a total circumference of over 20 feet and a height of 130 feet. Specimens of D. Ebenum also occur in the same forest which have a circumference of nearly 13 feet and a total height of 100 feet.

With the wet zone species there is likewise a wide range of variability, though only few species attain the huge dimensions of the dry zone plants.

Among the smallest trees we may place D. pruriens, since in the Sinha Raja district a single plant is often of convenient size for a herbarium sheet. This species, when it attains its maximum dimensions along the rocky slopes of the Peak Wilderness, rarely exceeds a total height of 9 metres (30 feet) and a circumference of 30·5 cm. (12 inches).

In point of size, D. acuta and D. attenuata come next to D. pruriens. In the wet forests of Pasdun korale these species occur in the form of small trees, from 20 to 30 feet in height and 1 to 4 inches in diameter. The leaders have often a weeping habit, particularly in D. attenuata, and though only 1 inch in diameter, may bear abundance of flowers and fruits. One specimen of D. attenuata was obtained in flower in the Wewella forest which had a short straggling leader only 14·0 cm. in diameter. Trees of these species frequently occur in groups of three to fourteen trunks matted together by dense woody roots at the common base of the trunks, and this, together with the weeping habit, is suggestive of the bamboo clumps growing in the same area.

D. hirsuta, though occurring so abundantly along the streams around Ratnapura, Eratna, and Hiniduma, rarely exceeds 9 metres (30 feet) in height and 20 cm. (8 inches) in diameter. When the stem is only 7·5 to 10·2 cm. (3 to 4 inches) in diameter the plant bears fertile seeds.

D. Thwaitesii, except in the Hiniduma district, is a tree similar in size to D. hirsuta, and in the Hewessa and Palakete

forests rarely exceeds a total height of 30 feet and a diameter of 5 inches. In the Hiniduma district, however, particularly along the north-west side at an elevation of 1,000 feet, many specimens of D. Thwaitesii attain a total height of 15·2 to 18·3 metres (50 to 60 feet) and a breast-height circumference of 50 to 76 cm. (20 to 30 inches).

D. insignis, characterized by its straight leader unbranched to a height of 6·1 metres (20 feet), is likewise of comparatively small dimensions. The breast-height circumference rarely exceeds 64 cm. (25 inches), and many plants having a main stem less than 12·7 cm. (5 inches) diameter bear a considerable amount of fruit.

The above-mentioned species may be regarded as those in the wet zone, which are characteristically of small dimensions. Commencing with the class possessing species of relatively large dimensions, we may for the sake of a continuous series first consider the smaller members, D. Moonii and D. oppositifolia, which thrive best along the banks of streams or along damp precipitous slopes, and usually attain a total height of 12·2 to 18·3 metres (40 to 60 feet) and a breast-height circumference of 610 to 915 mm. (2 to 5 feet). Nevertheless, specimens of D. Moonii in the Hewessa district and D. oppositifolia on the western side of Hinidunkanda occur as clumps of thin leaders matted together at the base by a common system of roots.

Next to these we may place D. quæsita, D. Toposia, and D. Gardneri, since they often attain a total height of 30·5 metres (100 feet), and many exceed a breast-height girth of 1·8 metres (6 feet).

The remaining wet zone species, D. crumenata and D. sylvatica, may attain dimensions which rival the colossal species of the dry zone. The largest specimen of D. sylvatica in Ceylon is probably at Ambalawa, near Gampola, since it consists of a main stem 4·2 metres ($13\frac{1}{2}$ feet) in circumference which remains unbranched for a distance of 24·4 metres (80 feet). At this height the stem branches, one fork then

continuing its upward course through a distance of over 30·5 metres (100 feet). In the Ambalawa and Dambalagalla districts there are some very fine patches of forest in which trees of Diospyros species are very abundant and attain huge dimensions.

Branch System.—The branch system is invariably well developed. Though the conditions of canopy do to a very great extent determine whether the branches shall grow erect, horizontal, or assume a weeping habit, yet it seems characteristic of certain species to possess branch systems of a fixed type. For instance, under conditions of open or close canopy, *i.e.*, either exposed equally on all sides or in dense forest, trees of D. Embryopteris have a branch system usually nearly horizontal. Again, D. quæsita has a branch system spreading at an angle of 40° to 50,° and according to Hiern the branch system of D. sylvatica spreads at 60° to 70°. Specimens of D. attenuata growing in dense forest have invariably a weeping habit, though the weight of foliage, &c., is never great.

Phyllotaxy.—In the majority of the Ceylon species the alternate arrangement of the leaves is characteristic on twigs of the mature plant. Small shoots of D. Moonii have often large leaves arranged alternately along the length of the thin stem. The final disposition of the mature leaves is usually one which ensures the maximum of light on their upper surfaces, and many leaves in their attempts to attain this position have undergone much twisting, particularly in the region of the petiole. There are, however, three of our species in which the phyllotaxy departs from the alternate type.

The leaves of D. Melanoxylon are usually opposite; sometimes they are sub-opposite and occasionally alternate. In very many instances the leaves are densely crowded, either at the end of a twig or near the main stem. D. insignis has the majority of its leaves disposed alternately

and the remainder sub-opposite. D. oppositifolia resembles D. Melanoxylon in the opposite and sub-opposite arrangement of the leaves. In the former species, however, many twigs have their leaves crowded together to form large rosettes.

Form and Size of Leaves.—The leaves conform to the usual tropical type in that they are simple, entire, and petiolate. The shape may be ovate (D. ovalifolia), lanceolate (D. hirsuta), or lanceolate oblong, with a tapering or abrupt apex, and a rounded or tapering base.

The size varies considerably, being smallest (30 to 70 mm.) in D. oocarpa and D. pruriens, and largest (190 to 350 mm. long) in D. Moonii, D. insignis, and D. Embryopteris. Within the same species there is often a considerable variation in size, the young leaves arising on offshoots from the main stem being many times the size of those occurring on the normal twigs. A case in point is in the large leaves of D. Melanoxylon, these occurring on the young shoots arising from the base of small trees and measuring 100 to 240 mm., whereas the normal dimensions for this species are 50 to 100 mm. Heterophylly occurs to a marked degree in D. Gardneri, D. oppositifolia, and D. sylvatica.

Venation.—The vascular bundles in the leaf form a central stout midrib with several smaller lateral factors connected alternately along its length, these in their turn being made up by the coalescence of the very small bundles scattered between them. Sometimes the vascular bundles project strongly on the upper surface (D. Embryopteris), sometimes on the lower surface (D. insignis), but are often relatively inconspicuous (D. affinis, D. montana, and D. oocarpa).

The midrib may be very conspicuous, as in D. Moonii and D. acuta, or it may be insignificant as in D. oocarpa and D. attennata.

The lateral and reticulate bundles are invariably pellucid; sometimes this character is not very conspicuous, as in D. affinis; in other species, particularly D. Embryopteris, D. Ebenum, and D. Toposia, the translucent character of the small bundles is the most striking feature of the foliage.

The reticulate meshwork is of a closely knit nature in D. Toposia; and in D. Embryopteris, particularly var. nervosa, the meshwork is wide.

The pellucid venation, though characteristic of every Ceylon species of Diospyros, is not limited to this group of plants. It is prominent throughout the Anonaceæ, and also characterizes the foliage in species of Anacardium.

Climatic Types.—The majority of the Ceylon species have tough coriaceous leaves, this being particularly characteristic of D. insignis, D. Embryopteris, and D. Ebenum. The coriaceous type of leaf is prevalent in nearly every one of our dry zone species. In the wet zone species we may have the fleshy type of leaf, as in D. acuta and D. Moonii; the densely pubescent and thin type, as in D. pruriens; or the normal tender leaves, as in D. attenuata and D. Thwaitesii. The fleshy type and the densely pubescent type are, as far as the Ceylon species of Diospyros are concerned, limited to the very wet zone. The pubescent type, as exemplified in the leaves of D. pruriens, is found in a part of the Island where the rainfall is never less than 300 inches per year; D. hirsuta, which in point of pubescence comes next to D. pruriens, likewise thrives best in the wet districts of Eratna and Ratnapura.

Persistence of Foliage.—The Ceylon species of Diospyros are of the evergreen type. This is characteristic of the genus throughout the world, there being very few exceptions, notably D. Tupru, *Buch*., which according to Beddome sheds all its leaves in the cold season and produces new ones in the beginning of the hot weather. The twigs of D.

montana and D. ovalifolia become partially leafless every year in the dry northern districts of Ceylon.

In Ceylon the leaves of most species of Diospyros drop at irregular intervals, and if one tree be selected for observation there is hardly a week passes without a shedding of a few leaves. The leaf-fall in most species is not sufficient to render the tree even partially bare, and the nett result of the leaf production, which repeatedly occurs, is an increase of foliage from year to year. The production of new leaves takes place during nearly every month of the year, if one considers the whole of the Diospyros species in the Island. If, however, one selects a district where the force of each monsoon and the intervening lulls is felt, a regularity in the leaf production is noticeable.

In the Peradeniya district there is an annual production of leaf in flowering trees of D. Gardneri, D. Embryopteris, D. Ebenum, D. affinis, D. Toposia, D. sylvatica, and D. crumenata. In non-flowering trees of D. Embryopteris there is a production of new leaf twice yearly, this occurring during the months of April to June and October to November.

The production of new leaf on any particular tree may be completed within one month, or new foliage may appear for several months in succession. The prolonged period of active growth occurs in one tree of D. Toposia from December to June, and again in trees of D. Ebenum leaf production may commence in December and continue for four or five months. Other trees of D. Toposia and D. Ebenum in the same and also adjacent districts may not produce any new leaves until well on in the months of February and March.

Respecting other species of Diospyros, particularly D. hirsuta and D. Thwaitesii in the wet zone, I have never visited the forests without finding some trees in new leaf during nearly every month of the year.

In the wet zone it is impossible to speak of any month as being specially noticeable for leaf production within the

Diospyros genus. The leaf production is apparently not of such a nature as to severely tax the resources of the plant, and its occurrence is probably to be correlated with individual requirements rather than with climatic conditions.

This can only obtain in the vegetation of the tropics where the temperature and rainfall are relatively equable throughout the year.

IV.—ANATOMY, TIMBER, &c.

Stem.—In the genus Diospyros the phellogen is often said to be of sub-epidermal origin, and this is considered by Parmentier and Solereder to be of taxonomic importance, the former using this as one of the main characters in his proposed grouping of the genera. The phellogen, however, actually arises either immediately beneath the epidermis or from the pericycle, the latter origin being conspicuous in the primary axis or hypocotyl of the seedlings.

The sclerotic or stone cells of the cortex are conspicuous in D. Ebenum, and the various stages of their formation and degeneration are shown. (See pl. XIX., figs. 1–4); they are relatively short, thick walled, and well pitted; finally they lose their definite outline and form hyaline masses of tissue, which do not respond to the commoner staining reagents. In longitudinal section they are seen to be surrounded with parenchyma and long sclerenchymatous fibres. The phloëm and cambium are of the ordinary type, and we may proceed to deal with the anatomy of the secondary xylem.

The observations of Molisch, Möller, Solereder, and Parmentier, already referred to, all agree as to the regular composition of the secondary xylem, the scarcity of tracheids, and the distribution of the elements.

Molisch obtained his sections of the hard brittle ebony by the method of Wiesner, which is briefly as follows: A thin slip of ebony, 2 to 3 cm. square, is cut by a fret-saw and fastened by means of sealing wax to a cork; both sides of the section are then polished on a smooth rotating wheel,

and when sufficiently thin the section is removed and finally polished on a razor stone. This method allows one to obtain fairly large sections, though smaller sections cut by hand in the ordinary way provide ample material for obtaining all points in detail.

Histology of the Timbers.—The anatomy of the secondary xylem of the Ceylon species of Diospyros is of the ordinary arborescent dicotyledonous type. The differentiation of the tracheal elements and fibres is remarkably uniform, but the parenchymatous tissues exhibit sufficient variation to allow of a grouping of the various species under different types. In dealing with the distribution, size, form, and percentage number of the secondary xylem elements one must allow for variability even for members of the same species, since they may have developed under quite dissimilar climates and their internal requirements are probably at great variance. As far as possible the statements have been made in a general sense, and where it has been possible to obtain material of the same species in the dry, wet, and intermediate zones, this has been done.

Tracheal Elements.

The tracheal elements are almost wholly represented by vessels; tracheids are never abundant, and when present usually occur alongside a large vessel.

Vessels.—The distribution of these elements varies according to the species, the age of the secondary xylem, and the climatic conditions under which the plants have grown. Usually the vessels occur in a more grouped condition in the xylem of the first few years than in the sapwood of old trees.

In some species the heartwood appears to be characterized by an equal number of isolated vessels and radial groups of two or three cells. Usually the members of vessels, when occurring in groups, form rows two to four cells in radial thickness; in others, notably D. attenuata, the groups may contain twenty members arranged one to two cells in

tangential width. Sometimes one group is separated from its neighbour only by a single line of medullary ray cells; usually, however, there is a wide band of fibres and parenchyma between parallel rows of vessels.

There does not therefore appear to be much regularity in the distribution of the vessels in the secondary xylem, and one may find as many as eight radial groups in one field, while adjacent parts of the same section may not show a single vessel, though the field of view is 0·6 mm. in radius. Usually, in passing from within outwards the vessels become more widely separated, tend to be more as single members, and are considerably increased in size.

In the sapwood of D. Moonii the vessels are nearer to one another tangentially than in the heartwood, yet in other species the space between the vessels increases from within outwards.

They are usually surrounded with fibres or flanked with short wood parenchyma or medullary ray.

The size of the members is never very great. The transverse and longitudinal dimensions show a regular increase as one passes from the heartwood to the sapwood, and it may be taken for granted that the larger the dimensions of the trunk the larger will be the dimensions of the vessels in the youngest part of the sapwood. This regular increase occurs in all our species, and is probably correlated with the physiology of the plant, particularly the storing and conducting of water. This increase of dimensions in the products of the old cambium is not characteristic of all the secondary xylem elements, and with the vessels we have to note that the increase of dimensions is concomitant with a decrease in percentage number and a more complete isolation from like elements. The fact that there is in every case a decrease in the percentage number when there is the maximum amount of foliage, and therefore probably maximum transpiration, renders some increase in size absolutely necessary when the heartwood is blocked up with gum and resin.

Dimensions of Vessels.

[Tw. = twig ; Sw. = sapwood.]

		Diameter. mm.	Radial Diameter. mm.	Tangential Diameter. mm.	Length. mm.
D. Ebenum	Tw. 6		0·045	0·034	**0·31**
	Sw. 360		0·085	0·081	0·45
D. quæsita	Tw. 15		0·04	0·04	0·22
	Sw. 190		0·13	0·07	0·43
D. oocarpa	Tw. 23		0·027	0·025	0·23
	Sw. 255		0·07	0·06	0·42
D. affinis	Tw. 9		0·03	0·03	0·22
	Sw. 200		0·12	0·08	0·45
D. montana	Tw. 8		0·04	0·07	0·34
	Sw. 175		0·07	0·05	0·36
D. Embryopteris	Tw. 9		0·04	0·04	0·31
	Sw. 360		0·14	0·09	0·43
D. Moonii	Tw. 15		0·06	0·05	0·27
	Sw. 165		0·18	0·10	0·35
D. attenuata	Tw. 6		0·025	0·028	0·21
	Sw. 140		0·09	0·06	0·32
D. pruriens	Tw. 9		0·038	0·04	0·26
	Sw. 80		0·11	0·10	0·44
D. acuta	Tw. 7		0·034	0·028	0·31
	Sw. 60		0·10	0·09	0·50
D. hirsuta	Tw. 10		0·03	0·026	0·41
	Sw. 75		0·18	0·09	0·45
D. Thwaitesii	Tw. 11		0·027	0·02	0·30
	Sw. 203		0·14	0·09	0·42
D. crumenata	Tw. 20		0·05	0·04	0·27
	Sw. 210		0·16	0·10	0·54
D. sylvatica	Tw. 9		0·03	0·028	0·20
	Sw. 405		0·13	0·09	0·36
D. Gardneri	Tw. 14		0·05	0·045	0·30
	Sw. 170		0·09	0·06	0·46
D. oppositifolia	Tw. 11		0·03	0·026	0·32
	Sw. 170		0·14	0·09	0·4–0·6
D. Melanoxylon	Tw. 10		0·023	0·03	0·36
	Sw. 270		0·13	0·09	0·46
D. ovalifolia	Tw. 22		0·024	0·024	0·20
	Sw. 240		0·05	0·05	0·40
D. Toposia	Tw. 14		0·027	0·03	0·27
	Sw. 250		0·09	0·05	0·30
D. insignis	Tw. 12		0·03	0·034	0·21
	Sw. 185		0·11	0·073	0·42

The dimensions of the vessels in the heartwood vary to a slight extent ; in the first three or four years' wood the radial diameter varies from 0·024 to 0·05 mm., the tangential diameter from 0·024 to 0·06 mm., and the length from 0·20 to 0·35 mm.

In the sapwood of the whole of our species the variation in radial diameter is from 0·05 to 0·18 mm., and the variation in

length of the members of the vessels from 0·30 to 0·54 mm. This constancy in size throughout the genus in Ceylon is one of the main characters of the timbers. When one considers the climatic differences between Mannar and Adam's Peak Wilderness, one is led to expect that there will be great differences in the size of the water storing and conducting tissues in the species growing at these places, but such differences are by no means pronounced.

There is very little variation in the form of the members of vessels. In the heartwood the small-lumined vessels are, when isolated, approximately spherical or crudely hexagonal in transverse outline, but as one passes to the sapwood the increase in dimensions is more in the radial than the tangential direction, and as a consequence a radially elongated element presents itself. When the members are grouped, however, the spherical or elongated outline is rarely met with, one or more sides become straight, and the tangential diameter of each member is usually considerably more than the radial.

The sides of each member are characterized by a straight vertical course, and the original transverse partitions are only slightly inclined to the horizontal.

The walls of the vessels vary in thickness from 0·002 to 0·0035 mm. They are usually very well pitted. They are composed mainly of lignin, which continues to respond to the safranin and fuchsin tests even when considerably discoloured, and the lumina partially filled with coloured materials.

The function is probably that of storing or even conducting water, but when once the lumina are filled with gum and resin this function must be taken up by the younger tracheal elements. The vessels do not undergo depletion of coloured contents, the infiltrating materials increasing from time to time until the vessels are completely blocked.

Tracheids.—There is not very much to be said about these elements. They are only very sparsely distributed, and in

transverse sections only differ from the vessels in being usually of smaller diameter. They are generally limited to the neighbourhood of large vessels, frequently flanking the tangential surface, but in D. Embryopteris they may occasionally be seen among fibres.

The transverse dimensions are often only a trifle in excess of the largest wood parenchyma cells, but in some instances they attain a radial diameter of 0·04 to 0·08 mm. In length they come next to the fibres and may attain 0·27 to 0·90 mm. When of great length the ends taper very strongly, and in such cases it is difficult to distinguish them from the more abundant fibres, and the term "fibre-tracheids" would be very appropriate. The commonly small and constant transverse dimensions of true fibres seems to differentiate them from tracheids, but otherwise it often becomes well nigh impossible to distinguish a short fibre from a narrow lumined, long tracheid.

Parenchymatous Elements.

This includes the wood parenchyma, fibres, and medullary rays of the secondary xylem. It is in the distribution of these elements that the maximum variation occurs, and even in our Ceylon species it is sufficient to allow of a grouping of the species into sections according to—

(1) Whether the medullary rays are one cell in tangential breadth.

(2) Whether the medullary rays are more than one cell in tangential breadth.

(3) The presence of special radial groups of parenchyma.

As with the tracheal elements, the general features of distribution, histology, and function may be subject to all manner of variation according to the internal and external forces at work.

The parenchymatous tissues compose the greater part of the secondary xylem and increase considerably with the age of the cambium. It is obvious that the value of the timber

is greatly due to the percentage composition of elements of the parenchyma type and the structure and form of these elements.

In the poorer timbers the wood parenchyma is usually of the thin walled, wide lumined type, and this alone is often responsible for the inferior quality, for no matter how thick and long the surrounding fibres may be, the soft bands of parenchyma, when present, lead to early cracking and decay.

Wood Parenchyma.—In transverse sections the presence of these elements is usually determined by the abundance of carbohydrate and mineral contents, together with their relatively thin walls and wide lumina. Often, however, they are not easily distinguishable, sometimes because their transverse dimensions are similar to those of the neighbouring cells, as in D. quæsita; sometimes on account of the proximity of adjacent medullary rays, and again because the surrounding fibres may not have undergone much lignification; the latter is often the case in the secondary xylem of young twigs. In some species they are always very conspicuous, either on account of their lumina being very large, or because adjacent medullary rays are separated by patches of fibre of considerable tangential width.

The difficulty of distinguishing these elements, however, is only when one is limited to transverse sections; the great length of these elements and their numerous contents serve to isolate them in any longitudinal section.

The distribution of these elements is somewhat complex, and is such that a continuous system of elements of the parenchyma type is established, together with frequent direct and indirect contact with the tracheal elements. The wood parenchyma cells are distributed as tangential bands, oblique bands, and around large tracheal elements. The tangential bands usually extend from one medullary ray to another, and their significance varies according to the width of this gap; the tangential bands between adjacent rays in xylem of

the same age are connected by the intervening parenchymatous medullary ray cell, and a fairly continuous circumferential circulation of food materials can therefore be effected through such elements. In a few cases, however, the tangential line of parenchyma only reaches half way from one ray, the terminal cell appearing in transverse section to be surrounded by unlike elements; it is conceivable that there may be some connection in the vertical course.

In the majority of our species the tangential lines of parenchyma are only one cell in radial thickness; in some species, notably D. affinis they are very often two, and are occasionally grouped in the middle of a patch of fibres. In some specimens of D. hirsuta the bands—two cells in radial thickness—often run together through a vertical distance of over 0·8 mm. These tangential bands of wood parenchyma are separated from one another radially by patches of fibres from 0·06 to 0·18 mm. in thickness. These elements are therefore in communication with like elements or those of the medullary ray by means of their radial surfaces, with fibres by their tangential surfaces, and with tracheal elements by any surface.

The oblique bands of wood parenchyma are obvious in many species, and it is very probable that if sufficient material were examined they would be found to occur in all species.

The components of these bands, instead of being arranged to form one line parallel to the circumference, are arranged in radial series, one slightly internal to the next, and thus result in what may be described as a terraced system of parenchyma. Adjacent cells are usually in contact with one another by a part of their radial surfaces, and the terracing is therefore very gradual. Such systems of parenchyma connect one medullary ray to the next, but it is obvious that they tend to bring into direct communication the successive tangential bands between the same medullary rays, and therefore to establish a more thorough communication between like elements in tissues of different ages.

In some specimens of D. montana from Trincomalee I observed that some oblique bands of wood parenchyma were connected at the outer end to the median cells of a tangential band of parenchyma, and within, to a medullary ray at a point opposite to another tangential line of parenchyma. By this means tangential bands of one zone can be connected, almost directly, with a band in an older zone, along a different radius. Such an arrangement must greatly facilitate the transference of food materials through the parenchymatous system.

The tangential and oblique bands of wood parenchyma therefore effect an excellent communication with all elements, excepting perhaps the vessels and tracheids. The remaining part of the wood parenchyma is, however, specially associated with these elements. In most of our species the large vessels are surrounded or flanked on their tangential surfaces with relatively wide lumined but short wood-parenchyma cells. These are in communication with the other cells of wood parenchyma or medullary rays, and therefore a complete communication is effected with every element of the secondary xylem.

The vertical distribution of these elements is easy to follow since they are arranged one above another through a considerable vertical distance. They form very long columns of cells, often as many as twelve cells in the same row. The majority form single straight lines with the components exactly above one another; frequently one cell abuts on to another, not end to end, but by the radial walls, thus giving the terraced system in the vertical direction.

There is nothing unusual in the form of these elements. In transverse outline they may be any shape from circular to crudely four-sided, but only rarely do they exhibit sharp corners. They are elongated considerably in the vertical direction, the vertical walls being straight and the end walls flat or occasionally tapering at one end when in contact

with unlike elements. When one end tapers the appearance is very similar to that of a short fibre.

There is a little variation in the transverse, but considerable in vertical dimensions throughout the species. In some species the relatively large transverse dimensions aid materially in distinguishing them in the wood of young twigs.

The following are the dimensions of these elements in the sapwood of the respective species :—

Species.	Radial Diameter. mm.	Length. mm.
D. Ebenum	0·015	0·03 to 0·12
D. quæsita	0·009	0·04 to 0·15
D. oocarpa	0·013	0·06 to 0·13
D. affinis	0·016	0·09
D. montana	0·02	0·07 to 0·20
D. Embryopteris	0·01	0·09 to 0·13
D. Moonii	0·015	0·08 to 0·20
D. attenuata	0·014	0·08 to 0·18
D. pruriens	0·015	0·08 to 0·14
D. acuta	0·013	0·09 to 0·15
D. hirsuta	0·018	0·05 to 0·13
D. Thwaitesii	0·013	0·05 to 0·18
D. crumenata	0·016	0·06 to 0·12
D. sylvatica	0·014	0·07 to 0·20
D. Gardneri	0·016	0·07 to 0·18
D. oppositifolia	0·014	0·08 to 0·13
D. Melanoxylon	0·017	0·07 to 0·13
D. ovalifolia	0·011	0·09 to 0·13
D. Toposia	0·013	0·06 to 0·15
D. insignis	0·014	0·06 to 0·19

The thickness of the wall varies from 0·001 to 0·0016 mm. These are the average radial dimensions and variations

length of the wood parenchyma cells in the sapwood of the several species. The age of the trees and the climates under which they have grown are widely different, though the above does not show any remarkable variation.

Wood Fibres.—These compose the greater part of the secondary xylem, and are responsible to a great extent for the durability of the timber. The occurrence in large numbers of these elements of great length, with thick walls and narrow lumina, enhances the value of any timber.

These elements form large patches of tissue, often entirely filling the gap between adjacent medullary rays; at other times scattered with intervening wood parenchyma. In the heartwood the fibres form much larger and more compact areas, in radial and tangential thickness. In the sapwood one meets with relatively narrow bands of fibres, often only a single radial line of fibres existing between adjacent medullary rays.

In their vertical distribution one notes the wavy outline of individual fibres and the deviation from the vertical of their tapering ends.

The fibres are mainly in contact with like elements, or with those of the wood parenchyma on their tangential surfaces and medullary ray cells on their radial surfaces; they are rarely in direct contact with vessels, since the latter are usually surrounded by short parenchyma cells.

There is nothing remarkable in their form; they possess the normal thick or thin walls, small transverse dimensions, great vertical length, and strongly pointed ends.

The transverse outline is usually strikingly angular, and the lumina may be only partially or almost completely closed by the secondary thickening of the walls. As previously mentioned, the vertical outline is often wavy and deviates considerably from the vertical near the tapering ends.

The constancy in transverse dimensions is exhibited in these elements better than in any others; the maximum variation is however seen in the length of these elements, since they vary from that of a cambium cell to over 1 mm. in length. The thickness of the wall varies from 0·001 to 0·003 mm.

The range of variation in transverse dimensions as one passes from the heartwood to the sapwood in very old trees is very small, and this relative constancy allows one to readily distinguish the scattered fibres from other elements. A list

of measurements of transverse dimensions of the fibres in the sapwood and heartwood is given below :—

	Radial Diameter in mm.	
	Heartwood.	Sapwood.
D. Ebenum ...	0·013 ...	0·013
D. quæsita ...	0·0076 ...	0·008
D. oocarpa ...	0·009 ...	0·010
D. affinis ...	0·009 ...	0·008
D. montana ...	0·010 ...	0·009
D. Embryopteris ...	0·009 ...	0·009
D. Moonii ...	0·013 ...	0·013
D. attenuata ...	0·011 ...	0·012
D. pruriens ...	0·013 ...	0·012
D. acuta ...	0·010 ...	0·009
D. hirsuta ...	0·001 ...	0·014
D. Thwaitesii ...	0·011 ...	0·011
D. crumenata ...	0·010 ...	0·010
D. sylvatica ...	0·012 ...	0·011
D. Gardneri ...	0·014 ...	0·012
D. oppositifolia ...	0·013 ...	0·013
D. Melanoxylon ...	0·010 ...	0·011
D. ovalifolia ...	0·0075 ...	0·008
D. Toposia ...	0·010 ...	0·010
D. insignis ...	0·012 ...	0·011

The above table would perhaps lead one to believe that our wet country species had generally larger transverse dimensions than our dry zone species. It is also to be noticed that there is not, in every case, an increase in transverse dimensions as one passes into the sapwood, and that the maximum variation in transverse dimensions for the fibres in the whole of our species is about 0·006 mm. and for fibres of the same species less than half this amount. The transverse dimensions, thickness of wall, &c., may be greatly modified by individual forces, stress, windage, &c.

Medullary Rays.—These elements are, as far as the genus Diospyros is concerned, the most variable of all the components of the secondary xylem. Fundamentally they are similar to the wood parenchyma cells since they possess thin cellulose walls and contain abundance of starch, tannin, and oxalate of lime. Their presence in abundance tends to lower the value of the timber, their thin walls and wide lumina rendering shrinking more certain.

The medullary rays occur as radial rows of cells throughout the secondary xylem. They are, in the majority of our species, only one cell in tangential width, but in some species they may be two or even three cells wide, as in D. crumenata, D. Toposia, D. insignis. D. pruriens, D. Thwaitesii, D. attenuata, and others. The occurrence of rays more than one cell in width is never general throughout the xylem, and very frequently when the double ray is traced outwards or inwards it is found to be continuous with a ray only one cell broad. There seems every probability of discovering these broader medullary rays in the xylem of nearly all our species, providing sufficient material is examined. It is usual to find that the differentiation of a medullary ray has been going on for many years without a break, but, nevertheless, several cases have been seen where the differentiation of a medullary ray has been discontinued and where new rays have appeared ; in such cases the last or first formed cell respectively is usually surrounded with fibres only, and only occasionally with a wood parenchyma cell. As one passes into the younger wood the number of rays, not necessarily the individual cells, increases, and in the sapwood of very old trees it is not unusual to find the medullary rays separated by only one or two rows of fibres, whereas in the heartwood they are usually separated by broad bands of fibres.

This increase of parenchymatous tissue lowers the value of the sapwood timber, even though the elements may be more or less filled with the brown products so abundant in the old wood. In some specimens of D. Ebenum the continuity of a medullary ray is destroyed by the intrusion of fibres on either side of the ray ; this, however, is only local, for the same ray can be seen abutting on the inner and outer surfaces of such intrusive fibre patches.

In D. insignis, where the double rays probably reach their maximum development, the distribution is very irregular, there being from two to twenty single rays between a pair

of double rays. In tracing one ray from the younger to the older wood it was first seen to be three cells broad, and very gradually one marginal row was replaced by a row of fibres, and finally, the double ray passed into a single ray, each component having a tangential diameter equal to the sum of those forming the double ray. It has also been noticed in specimens of D. attenuata, that whenever the ray is more than one cell broad the component cells are invariably of the horizontal type, and at each end of such a ray the components are of the vertical type with large tangential diameters.

It is to be noted that whenever the ray is more than one cell broad the components have always a small tangential and large radial diameter, and many sections show a double ray superposed on a broad single ray, each ray extending vertically through a distance of many cells.

The medullary rays form large vertical strands of tissue from twelve to over thirty cells in height, the components having very variable dimensions and forming part of single, double, and triple rays.

The medullary rays, since they pass through all the secondary xylem, come into direct communication with every other type of cells, but the most striking communication is with the wood parenchyma, which they so closely resemble (particularly the vertical type) in structure, thin walls and crowded contents.

Form and size can be treated better in a combined description of the differentiation of medullary ray tissue.

In nearly every species there is a well marked differentiation into (*a*) horizontal cells characterized by large radial and short tangential and vertical diameters, and (*b*) vertical cells having short radial and large tangential and vertical diameters. In many cases one feels strongly inclined to introduce yet another type having approximately the form of a cube.

In specimens of some species, notably of D. acuta and D. Gardneri, this differentiation is only feebly exhibited.

The same ray may possess members belonging to each category, but often one type exists alone throughout a considerable length of a particular ray, and is superposed vertically on a group of the opposite type.

The vertical cells usually predominate in the very old wood, and as one passes outwards the number of horizontal cells increases until in the peripheral sapwood of very old trees they are the predominant type. Sometimes the heartwood, as in specimens of D. crumenata, shows a fairly equal proportion of horizontal and vertical cells. This increasing differentiation of the horizontal type with the age of the cambium is worthy of note.

The size of the medullary ray cells invariably increases from within outwards, and this increase, since it usually results in a radial extension of the cells, leads to an increase in the number of horizontal cells. The local occurrence of rays more than one cell in width also leads to a rapid increase in the percentage number of horizontal cells.

In the sapwood of D. insignis it appears very probable that many of the horizontal cells are parts of double rays and the vertical cells parts of single rays, the volume of the two types being nearly the same. Nevertheless, one must realize that both types of cells may be differentiated in single rays, as in D. Ebenum and others, where double rays are very scarce or do not exist.

In the sapwood of old trees the outline of the cells is usually sharply angular ; the walls are straight, and the tangential walls are frequently inclined at an angle of 45° from the vertical ; in young twigs the outline is not as sharply cornered, and tends to form a crude ellipse in transverse section.

The following table of measurements will serve to indicate the differentiation in wood of various ages in all

our species. Only the average dimensions are here given :—

Dimensions of Medullary Ray Cells in mm.

[V. = vertical. H. = horizontal, medullary ray cells.]

Species.		Radial Diameter. mm.		Tangential Diameter. mm.		Vertical Length. mm.
D. Ebenum	V.	0·015	...	0·02	...	0·06
	H.	0·06	...	0·012	...	0·035
D. quæsita	V.	0·012	...	0·015	...	0·09
	H.	0·05	...	0·010	...	0·03
D. oocarpa	V.	0·015	...	0·014	...	0·05
	H.	0·04	...	0·012	...	0·018
D. affinis	V.	0·02	...	0·017	...	0·048
	H.	0·08	...	0·015	...	0·018
D. montana	V.	0·024	...	0·02	...	0·034
	H.	0·07	...	0·01	...	0·022
D. Embryopteris	V.	0·025	...	0·012	...	0·070
	H.	0·07	...	0·009	...	0·032
D. Moonii	V.	0·02	...	0·02	...	0·08
	H.	0·036	...	0·02	...	0·03
D. attenuata	V.	0·03	...	0·026	...	0·09
	H.	0·07	...	0·014	...	0·03
D. pruriens	V.	0.02	...	0·018	...	0·05
	H.	0 038	...	0·010	...	0·025
D. acuta	V.	0.017	...	0·02	...	0·054
	H.	0·050	...	0·015	...	0·027
D. hirsuta	V.	0·022	...	0·012	...	0·12
	H.	0.04	...	0·009	...	0·06
D. Thwaitesii	V.	0·024	...	0·018	...	0·078
	H.	0·08	...	0·012	...	0 023
D. crumenata	V.	0·019	...	0·02	...	0·06
	H.	0·05	...	0·012	...	0·02
D. sylvatica	V.	0·02	...	0·023	...	0·07
	H.	0.07	...	0·01	...	0·02
D. Gardneri	V.	0·03	...	0·02	...	0·07
	H.	0·07	...	0·015	...	0‘02
D. oppositifolia	V.	0·019	...	0·02	...	0·07
	H.	0·055	...	0·012	...	0·015
D. Melanoxylon	V.	0·02	...	0·02	...	0·056
	H.	0·05	...	0·01	...	0·027
D. ovalifolia	V.	0·018	...	0·016	...	0·06
	H.	0·07	...	0·012	...	0·025
D. Toposia	V.	0·02	...	0·02	...	0·09
	H.	0·05	...	0·01	...	0·035
D. insignis	V.	0·03	...	0·016	...	0·08
	H.	0·056	...	0·012	...	0·018

There is, in addition to the foregoing types of parenchyma, still another which, though of rare occurrence, is worthy of description. In specimens of calamander from Karawita

forest the xylem is characterized by large radial strands, 0·09 mm. in tangential width, of very large parenchyma. These often commence at the pith and run inwards for a distance of several millimetres; they die out gradually, but frequently at the pointed end another radial patch commences and extends a considerable distance into the younger secondary xylem.

Similar strands occur in D. Gardneri from Peradeniya, the component cells being about twice the size of ordinary parenchyma and surrounded by fibres or flanked by a medullary ray. When more than one cell broad the cells are usually irregularly disposed, occasionally they exhibit a radial arrangement, though in no cases do the components exhibit the radial regularity of other elements of the secondary xylem.

The cells are parenchymatous with transverse dimensions often equal to those of the neighbouring vessels; they possess thin walls, and their contents include starch and oxalate of lime. These strands may be purely pathological, or they may perform some part in the physiology of a secondary xylem of such slow rate of growth. They cannot be regarded as parenchyma drawn from the perimedullary zone, because they appear in the sapwood of old trees; their presence in radial groups suggests an origin from the cambium similar to the broad medullary rays, and accepting this as the interpretation one must regard the final irregular disposition of the component cells as a consequence of active growth evidenced in their abnormal dimensions and numerous contents.

The Percentage Composition of the Secondary Xylem.

These calculations have been arrived at by examination of transverse sections of the secondary xylem of young twigs and the sapwood of old trees. The number of elements of each type within a fixed field of view have been counted, and after several areas have been so examined for

each species the percentage composition has then been calculated.

Percentage Number of Elements in Diospyros Woods.

	Tracheal Element.	Fibres.	Wood Parenchyma.	Medullary Rays.
D. hirsuta.				
Young twig, 10 mm. diameter ...	1·3	74·8	7·0	16·9
Old stem, 80 mm. diameter ...	0·60	78·8	7·1	13·5
D. acuta.				
Young twig, 7 mm. diameter ...	2·1	79·8	4·9	13·2
Old stem, 60 mm. diameter ...	0·4	84·4	7·6	7·6
D. oppositifolia.				
Twig, 11 mm. diameter	2·5	75·6	5·2	16·7
Old stem, 170 mm. diameter ...	0·8	79·6	6·6	13·0
D. oocarpa.				
Twig, 6 mm. diameter ...	1·9	74·9	10·7	12·5
Stem, 255 mm. diameter	1·0	81·8	8·9	8·3
D. ovalifolia.				
Twig, 7 mm. diameter...	2·3	75·5	6·3	15·9
Old stem, 240 mm. diameter ...	1·4	85·5	6·3	6·8
D. montana.				
Twig, 8 mm. diameter ...	3·0	76·9	5·9	14·2
Old stem, 175 mm. diameter ...	1·4	81·9	7.8	8·9
D. insignis.				
Young twigs ...	3·43	75·43	2·73	18·41
Average of timber, 130 mm. diameter ...	0·85	79·00	7·90	12·25
D. Ebenum.				
Young twigs ...	2·95	73·95	8·25	14·85
Old timber, 360 mm. diameter ...	0·76	85·4	6·14	7·7
D. Moonii.				
Young twig ...	1·70	76·11	8·45	13·74
Old timber, 170 mm. diameter ...	0·94	83·60	6·53	8·93
D. pruriens.				
Young twig, 9 mm. diameter ...	1·20	74·7	12·2	12·1
Old timber, 80 mm. diameter ...	0·84	79·64	10·24	9·28

	Tracheal Element.	Fibres.	Wood Parenchyma.	Medullary Rays.
D. attenuata.				
Young twig, 6 mm. diameter ...	2·7	77·6	4·7	15·0
Old timber, 140 mm. diameter ...	0·88	83·84	3·94	11·34
D. Thwaitesii.				
Young twig, 3 mm. diameter ...	1·33	81·3	4·6	12·77
Old stem, 200 mm. ...	0·44	85·86	6·6	7·1
D. Toposia.				
Twig, 14 mm. diameter...	0·9	80·0	7·8	11·3
Old stem, 250 mm. diameter ...	0·5	81·2	7·6	10·7
D. sylvatica.				
Twig, 9 mm. diameter ...	0·8	81·0	7·1	11·1
Old stem, 405 mm. diameter ...	0·55	82·05	7·35	10·05
D. Melanoxylon.				
Twig, 10 mm. diameter...	2·9	81·2	5·1	10·8
Old stem, 270 mm. diameter ...	1·2	81·6	7·1	10·1
D. Embryopteris.				
Twig, 9 mm. diameter ...	1·2	83·3	4·3	11·2
Old stem, 310 mm. diameter ...	0·6	85·1	7·1	7·2
D. quæsita.				
Twig, 15 mm. diameter...	1·03	80·0	3·1	15·87
Old stem, 190 mm. diameter ...	0·90	85·9	5·7	7·5
D. Gardneri.				
Twig, 14 mm. diameter...	0·9	83·0	5·8	10·3
Old stem, 170 mm. diameter ...	0·7	83·0	7·5	8·8
D. crumenata.				
Twig, 20 mm. diameter...	1·0	81·4	8·8	8·8
Old stem, 210 mm. diameter ...	0·6	83·1	9·9	6·4
D. affinis.				
Twig, 9 mm. diameter ...	1·5	84·5	5·8	8·2
Old stem, 200 mm. diameter ...	0·3	91·6	3·7	4·4

This table is instructive as affording data to show the change which takes place in point of percentage number, as one passes from the oldest to the youngest xylem, and also

to give a systematic value to the percentage composition of the xylem.

Change in Percentage Number of Elements in Old and Young Xylem.—In every species the percentage number of tracheal elements decreases with the age of the cambium, the first formed xylem having the maximum percentage number and the last formed the minimum. The number of tracheal elements in the heartwood may reach 3·43 per cent. as in D. insignis, or be as low as 0·8 per cent. as in some specimens of D. sylvatica ; this is a very low number, but in the sapwood it is still lower, the maximum being 1·4 per cent. in D. ovalifolia and D. montana and the minimum 0·3 per cent. in D. affinis.

Hence we see that the percentage number of tracheal elements in young and old xylem of all our Ceylon species does not vary more than 3 per cent., and the relatively low percentage number will serve to systematically diagnose the secondary xylem of our species of Diospyros. The tracheal elements are represented by a lower percentage number than any element of the parenchyma type, and this is to be correlated, perhaps, with the evergreen nature and very slow rate of growth of all the Ceylon species.

The thickest leaved species have a very low percentage of tracheal elements in the sapwood of the mature tree, as for instance D. acuta with 0·4 per cent. and D. affinis with 0·3 per cent. The thinnest leaved species in the dry zone is D. montana, with a percentage number of 1·4 in the sapwood, whereas the thinnest leaved species in the wet zone, where the temperature is never very high and the air is always moist, is D. attenuata with a percentage number of 0·88 in the sapwood of stems 140 mm. diameter.

Though knowledge of the individual variations prevents one from attaching too much importance to similar features in different species, yet it is worthy of note that in every species growing in the wet zone the percentage number of tracheal elements is approaching the minimum, as in D.

Gardneri, 0·7 per cent., D. hirsuta 0·63 per cent., and D. Thwaitesii 0·44 per cent.; whereas in the majority of our dry zone species the percentage number is considerably increased, *e.g.*, D. montana 1·4 per cent., D. ovalifolia 1·4 per cent., D. Melanoxylon 1·2 per cent.

The facts of histological differentiation are therefore in general accord with the varying climates and the transpiration which probably occurs under these conditions.

As previously shown, the decrease in percentage number from within outwards is concomitant with a regular increase in transverse dimensions.

The parenchymatous elements compose the remaining part of the secondary xylem, and are mainly represented by fibres. The fibres constitute from 74 to over 90 per cent. of the total secondary xylem elements.

The wood parenchyma, together with the medullary ray cells, tend to form an approximately constant proportion in the xylem of different ages within the same tree. Generally speaking, the percentage number of medullary ray cells decreases from within outwards, this decrease being concomitant, as in the case of the tracheal elements, with an increase in size; whereas the percentage number of wood parenchyma cells, though generally increasing from within outwards, is apt to show a steady percentage number, or even a decrease from within outwards. The approximation to a constant proportion in the old and young wood is seen in D. insignis (20·15 and 21·14), and, as pointed out in a previous paragraph, it is often very difficult, owing to feeble lignification of surrounding fibres, to be absolutely certain, in transverse sections, whether one is dealing with fibres or wood parenchyma.

Though the percentage number of wood parenchyma cells, in the majority of our species, increases in the younger wood, the difference in percentage number is rarely over 3 per cent. of the total number of xylem elements. In the xylem of D. ovalifolia, the percentage number in the wood of a young twig and the sapwood of a tree 240 mm. diameter proved

to be the same, viz., 6·3 per cent., and in other cases a reduction in percentage number has occurred in the sapwood. It is therefore obvious that the percentage number of wood parenchyma cells is the most unstable of the secondary xylem elements, since all other elements show a definite increase or decrease.

The fibres in virtue of their abundance and constitution are the most important from an economic point of view. The most parenchymatous woods, such as those of D. insignis, rarely contain less than 79 per cent. of fibres, and, on the other hand, the xylem of several species contain over 90 per cent. fibres.

From the table quoted it will be seen that the percentage number of fibres gradually increases from the heartwood to the sapwood, and in this respect is almost alone among the secondary xylem elements. The gradual increase in percentage number in passing into the younger wood is concomitant with a decrease in the percentage number of tracheal elements and medullary ray cells. The increased weight of foliage, &c., consequent on age and development is perhaps sufficient reason for the production of an increased percentage number of fibrous elements.

The percentage number of medullary ray cells comes next to those of the fibres, and varies from 6 to over 18 per cent. of the total number of xylem elements.

The highly parenchymatous woods are characterized by a particular abundance of these elements, and in all such cases the quality of the timber is inferior, as in D. insignis, D. hirsuta, and D. oppositifolia.

As with the tracheal elements, a decided reduction in percentage number occurs as one passes from the heartwood to the sapwood, but this is accompanied by an increase in dimensions, especially in the radial direction. In the sapwood of most species the enormous size of these elements is apt to create an erroneous idea of their percentage number; the decrease in the latter is fully compensated by the increased dimensions.

Rings of Growth.

These are inconspicuous in the majority of our species. According to Ursprung the timber of some species of Diospyros presents well defined rings of growth when the trees have been grown under a subtemperate climate.

The whole of our Ceylon species are characterized by a slow rate of cambial activity, and, with the exception of the partially deciduous trees of D. montana and D. ovalifolia, may be regarded as typical evergreens. Nevertheless, the majority of our species are characterized by foliar periodicities which recur, fairly regularly, year by year, and these together with the independent effects of a hot dry season, are perhaps responsible for the zoned differentiation often met with. We have also to allow for the possibility of special periods of activity determined by internal forces and expressed in the differentiation of irregular patches of xylem. In the majority of the specimens examined the inconspicuous rings have been difficult to follow throughout the whole of any transverse section, many being tangential bands in association with a neighbouring branch, and therefore roughly limited to the side on which the branch occurred. In timber of D. insignis and D. Thwaitesii rings of growth are visible to the naked eye, and consist of broad dark bands alternating with narrower bands of a lighter colour. The narrow light rings vary from 0·2 mm. to 1·2 mm. in radial diameter, and are disposed at very varying distances—radially—from each other.

The rings of growth are often present in one part of the section and gradually merge into adjacent rings of growth, and in consequence of this, and the varying radial distances (2 to 8 mm.) between successive rings, we find that the number of rings along different radii is subject to great variation. It is impossible to at present determine in our Ceylon ebonies the exact representation of time of each ring of growth.

Rate of Growth.

The genus Diospyros, in Ceylon, possesses some of the most slowly-growing tropical trees. In the seedling and sapling stages, up to the first ten or twelve months the growth takes place at a fairly rapid rate ; seedlings two months old may measure, above ground, from 30 to 150 mm. according to the length of the hypocotyl, but in two and a half years the total height may exceed 3,300 mm. ; saplings ten years old may measure less than this, and the subsequent growth takes place at a slow rate. The following are the dimensions of two and a half years old saplings raised in the same plot at Peradeniya :—

Species.	Height.	Circumference.
	mm.	mm.
D. montana ...	3,610 (11 ft. 10 in.)	... 111
D. Ebenum ...	1,828 (6 ft.)	... 84
D. Embryopteris ...	1,220 (4 ft.)	... 81
D. quæsita ...	610 (2 ft.)	... 38

Some species never develop into large trees, *e.g.*, D. acuta and D. pruriens, but the majority of Ceylon species attain huge dimensions, particularly D. sylvatica, D. crumenata, and D. affinis. There are, however, very few trees of known age, and exact information cannot therefore be obtained. There is one specimen of D. quæsita in the gardens, which, though known to be over sixty years old, measures only 472 mm. in circumference and a total height of about 14 metres ; this, however, is one of our slowest growing species ; other species, notably D. Embryopteris and D. montana, probably grow at a much quicker rate.

Sample plots for observing the rate of growth have been established by the Ceylon Forest Department, and yearly observations have been made on selected trees in the various forests ; the results are, however, at great variance.

Broun states that after reaching a circumference of 914 mm. (3 feet) D. Ebenum is very slow growing, and that the tree may reach a circumference of 457 mm. (1 foot 6 inches) at the age of 25 years, 914 mm. (3 feet) at 75 years, 1,372 mm. (4

feet 6 inches) at 135 years, and 1,828 mm. (6 feet) at the age of 200 years.

The following observations were made on trees growing in the Peradeniya Garden :—

Circumference of Trees in Millimetres.

Date of Observation.	Species. D. Embryopteris. mm.	D. Gardneri. mm.	D. Ebenum. mm.	D. quæsita. mm.
August 13, 1900...	585	467	147	370
January 1, 1901 ...	587	468	147	382
July 2, 1901 ...	600	468	156	400
August 6, 1902 ...	630	474	162	430
August 12, 1903...	673	496	179	472
Increase in circumference in three years ...	88	29	32	102

The selected trees were of unknown age, and, as is shown in the first measurements, of widely different dimensions; it is, nevertheless, of interest to know that in trees of the selected species the increase in circumference may be from 29 to 102 mm. in three years' time. This increase may be due to phellogenetic activity as much as that of the vascular cambium, but assuming that the increase in circumference is due to the production of secondary xylem only, we find that that in D. Ebenum is equal only to 62 vessels, or an average of one to two vessels along each radius, per month during the three years in question.

Timber.

The genus Diospyros has obtained its widespread recognition mainly in virtue of the valuable timber yielded by several of its species. The term *ebony* is loosely applied to any black heavy wood capable of taking a good polish, and from time to time there has been considerable discussion as to the exact botanical source of the ebony of the ancients. Many plants are known to yield timber which in colour and density resembles the real ebony, and botanists have been found who assert that the ebony of the ancients was not

obtained from the genus Diospyros, but from a leguminous species, called Fornasinia ebenifera, Bertol. The natural order Leguminosæ has long been known to yield variously coloured timbers, and in some countries the respective species furnish a marketable ebony, *e.g.*, Dalbergia Melanoxylon, G. and P., the ebony of tropical Africa, and Brya Ebenus, DC., the Jamaica ebony.

In Ceylon, however, the ebony of export is obtained exclusively from species of Diospyros, and mainly from the trunks of D. Ebenum. This ebony has been known from distant times, and some botanists believe that the ebony mentioned in the Bible was obtained from this Island.

According to Trimen* the tree was not known to Hermann, and only the timber of it to Burmann,† who quotes from Grimm‡ as to its medicinal virtues.

Rumph§ states that ebony trees are abundant about "Trinkenemale," and Trimen believed this to be the earliest record of our most important ebony-yielding trees in Ceylon.

The ebony is obtained by felling the tree and stripping off the peripheral sapwood. It is usual to fell all those trees which have attained or exceeded a breast-height circumference of 2 metres ($6\frac{1}{2}$ feet), providing the preliminary examination indicates the existence of a good proportion of solid black heartwood. The preliminary examination usually consists of making an incision and determining the extent to which the discolouration has proceeded; in some cases an apparatus known as Pressler's increment borer is used, as by this means only the minimum damage is done to the timber, and the tube can be easily withdrawn and the cylinder of wood extracted from the stem. In Ceylon the felling of the ebony trees is carried out on definite principles, each officer clearing only those trees which have

* Trimen, Flora, Vol. III., p. 95.
† J. Burmann, Thesaurus Zeylanicus, 1647.
‡ Grimm, Laboratorium Ceylanicum, 1679.
§ G. E. Rumphius, Herbarium Amboinense, 1750.

attained the standard dimensions, and at such a rate that only one-fortieth to one-sixtieth of the forest acreage under his charge is cleared each year.

The occurrence of ebony within the plant cannot be stated in terms of the age of the tree, the dimensions of the stem, or the climatic conditions under which the plants have been grown, though a few facts capable of a very general application may be here given. The black heartwood occurs usually in the stem, but is often present in young twigs and roots. In the majority of our species the discolouration commences in the perimedullary zone and spreads from within outwards. The discolouration is usually of an uniform black in D. Ebenum, streaked in D. oocarpa, D. affinis, D. quæsita and others, red in D. Moonii, and a dirty white in such species as D. insignis and D. attenuata. The discolouration may occur in the oldest central wood only, or it may appear in local strands throughout the secondary xylem of the stem. In many young stems the only areas where ebony has been produced are directly associated with insect punctures, wounds, &c.

The occurrence of the central black wood within the length of the stem is often erratic, though most usually it decreases in volume from below upwards.

The eccentric formation is where the central column of black wood widens and narrows repeatedly at different points along the stem, and in consequence of this one cannot accurately estimate the volume of ebony in a stem by external observations alone. In some instances, particularly in young stems and twigs, the black heartwood repeatedly dies away and reappears at different points along a given length.

The age of a particular tree or the dimensions it has attained do not afford a sure criterion as to the quantity of ebony it will possess, though the probabilities are that the older the tree and the larger the dimensions, the greater will be the proportion of discoloured heartwood. This

uncertainty has long been recognized by persons engaged in financial speculations, and too much stress cannot be laid on the individual variation which occurs in trees of the same species from the same or different localities.

On the other hand, there can be no question as to the specific tendencies to produce a definite type of heartwood, though even here one has to allow a wide range of variability for each species. For instance, the heartwood of D. Melanoxylon and D. Ebenum is almost invariably jet black, and on this account these two species provide the greater part of ebony from India and Ceylon; D. insignis, on the other hand, never yields a black heartwood, D. Gardneri always produces a yellow wood, and D. Moonii a timber which is of a red tint spotted here and there with small black strands. There could be no possible doubt of the species were the timbers of D. Ebenum, D. Kurzii, D. insignis, and D. quæsita to be mixed with one another, as their macroscopic characters are so pronounced.

The specific colour tendencies are somewhat difficult to explain. The two factors which determine the colour of the timber in the respective species are: (1) the means of distribution of the coloured substances; (2) the proportion of coloured gum and resin present in the tissues.

It is perhaps safe to assume that the best or most general distribution of coloured substances will be effected in those xylems the elements of which are freely communicating with one another, and therefore those species the timbers of which contain a high percentage of medullary ray cells and wood parenchyma should show the most general distribution of colouring substances. The fact that the xylem of D. insignis is highly parenchymatous and is really white points to the conclusion that for the production of ebony the superabundance of colouring material is the first desideratum, rather than profusely pitted elements. An open type of pit communication between the elements will tend to prevent the formation of central ebony in timbers where the colouring

substances are not abundant. The central timber will tend to become dark in colour when the communication between the elements is not frequent, as the substances must then remain in approximately the same area in which they were formed.

The jet black colour of the timber of species such as D. Ebenum is due to the coloured substances being present in large quantities in the oldest wood and remaining approximately in that area. If a more open communication existed between the elements in this species the colouring materials would be more widely distributed and the central timber deteriorate in consequence.

The red, yellow, or white colour of many Diospyros timbers is due either to the more complete distribution of the colouring substances throughout the wood in the respective species or to the relative scarcity of coloured substances.

The climate does not appear to have any appreciable influence on the production of discoloured heartwood, the same species showing similar characters in the dry, wet, and intermediate zones of Ceylon. The majority of our ebony is obtained from the dry zones in the northern part of Ceylon, because D. Ebenum grows more luxuriantly there than elsewhere, and not because the black timber of this species is more abundant, per tree, or of better quality than that from the scattered trees of the wet zone.

It is, however, generally believed by Ceylon foresters that the nature of the soil exerts some influence on the proportion of discoloured wood. Many cases have occurred where the trees growing on rocky hill banks possessed large quantities of black heartwood, and the proportion of ebony decreased as one got on to better soil. According to Broun the best ebony in Ceylon is found on rocky well-drained soil. It grows well on soils containing a large quantity of clay and on sandy loam with a good subsoil drainage.

The general belief is that the proportion of discoloured heartwood tends to increase in trees grown on poor rocky soil. This is substantiated by every forester I have met.

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The durability of our Diospyros timbers is due to the nature and percentage number of the elements comprising the wood, together with the presence of coloured contents partially or wholly filling the elements. In all our Ceylon species of Diospyros the cambium divides very slowly, and the elements, particularly the fibres, possess small transverse dimensions and thick walls ; the percentage number of fibres is in every case very high, and that of the tracheal elements very low, consequently the xylem is much more durable than the majority of our Ceylon timbers. Nevertheless, the histological composition of the secondary xylem is only one factor in determining the durability of these timbers, the infiltrated gums and resin providing a substantial support to the otherwise empty elements. The relative durability of the outer white sapwood and the central ebony is well seen in trunks of trees exposed to the atmosphere and vermin ; the sapwood is stripped completely in a few years, leaving a smooth black log of ebony which resists the attacks of ants and many wood borers.

Discolouration of Timber.

The discolouration of the wood is mainly due to chemical and physical changes of the materials stored in the elements of the wood, and to a less extent to a change in composition and colour of the cell walls. The coloured material entirely fills the lumina of the elements in pure ebony, and decreases in quantity as one passes to the red, yellow, and white woods. The white sapwood surrounding the central ebony contains a varying quantity of coloured material partially filling the secondary elements, and the quantity of this material increases from without inwards.

To the naked eye there appears to be a sharp distinction between the limit of the central ebony and the white sapwood. A gradual series of changes can, however, be discerned in microscopic sections, and for the conversion of the peripheral sapwood into ebony it is mainly a question of time.

Usually the ebony or heartwood occurs as a fairly regular circular mass at any particular level in the stem ; when the ebony is not limited to xylem of the same age the projections towards the sapwood are associated with wounds or old branches.

To explain why the limiting line of the central ebony is so sharply defined, or, in other words, to explain why the coloured substances occur so definitely in xylem of the same age, we must consider the distribution and pit communication between the different elements. In the first place we must admit that the wood parenchyma, medullary ray cells, and tracheal elements are abundantly supplied with large pits on all surfaces, whereas fibres are but sparsely pitted.

The tangential bands of wood parenchyma serve as excellent means for the transference of coloured substances through xylem of the same age, from like cells or those of the medullary ray to the tracheal elements or the short parenchyma surrounding them.

The frequency of the pits between the wood parenchyma, medullary ray cells, and tracheal elements is one reason why the circulation of the coloured substances, originating in the parenchymatous elements, should tend to keep within these elements. The fewness of pits in the fibres does, on the other hand, account for their sparse contents and the fact that they are the last elements to have their lumina filled with the coloured substances.

We therefore see that the maximum facility is accorded for transference of the coloured substances tangentially through the wood parenchyma and tracheal elements rather than radially through the wide patches of sparsely pitted fibres, and this will perhaps serve to explain why the coloured substances tend to first fill the elements in xylem of approximately the same age and thus lead to the sharp line of distinction between the outer limit of the ebony and the white sapwood.

At the same time the transference of coloured materials can and does take place in the radial direction, from one

medullary ray cell to another, but the proportion of these elements is so small compared with the surrounding fibres, that any contents they may possess cannot greatly change the tint of the xylem as a whole.

When the parenchymatous and tracheal elements have their lumina blocked the coloured material gradually infiltrates into the fibres. The coloured substances, under normal circumstances, first appear in the oldest elements, and therefore the blackening takes place from within outwards.

The composition and origin of the discolouring substances has been discussed by Belohonbek, Hartig, Molisch, and Moeller. They all regard the coloured materials as being singular in chemical constitution, and the terms "gum" and "resin" have been frequently applied to the separated substances.

The coloured substance is partially soluble in water, creosote, benzine, ether, and sulphuric acid. The solution varies in colour from a deep brown to claret red. In all cases microscopic examination of the sections so treated shows that only a very small proportion of the coloured substance has been extracted. If the sections are treated with strong sulphuric acid for several days the walls of the elements disappear and liberate long black rods of material which resist the attack of the strong acid even after heating. These black carbon-like rods appear to be unaffected after treatment with any reagent. Mr. Kelway Bamber has very kindly made an analysis of the coloured timber, and has allowed me to quote his results here:

Ebony Dust.

	Per cent.
Moisture ...	14·36
Organic matter...	77·84
Ash ...	7·80
	100·00

	Per cent.
Water extract (soluble gum) ...	3·60
5 per cent. NaOH extract ...	7·24
Residue (dark rods) ...	67·00
Ash in residue ...	7·02

Mr. Bamber finds that the 5 per cent. caustic soda solution contains a gum precipitable by alcohol, and a resinous body,

dark reddish brown in colour, which can be extracted from the original ebony dust with alcohol and amounts to 3·58 per cent. of the dust.

The black colouring material therefore contains two gums, one resin, and an insoluble residue composed mainly of carbon.

It has been asserted that the colouring materials arise by chemical change of the inner layer of the elements in which they occur, and even Molisch believed that the reputed thinness of the walls of some vessels was due to part of the material having been so modified. My own observations do not confirm this theory, though I have noticed a certain amount of swelling when sections of the fresh wood are placed in water. This is probably due to the absorption of water by the thin layer of gum which forms a lining to the tracheal elements, and which occurs in the yellow or white sapwood of ebony-bearing species.

From an examination of longitudinal sections of the sapwood and heartwood of our species I have concluded that the greater part, if not the whole, of the coloured materials filling the lumina of the elements is derived from the materials accumulated in the parenchymatous system of the secondary wood. Usually the discolouring substances make their first appearance in the cells of the medullary ray or wood parenchyma, then in the tracheal elements, and lastly in the fibres.

The parenchymatous elements of the sapwood are invariably packed with starch grains, tannin, and calcium oxalate. The starch grains gradually lose their regular outline and a fine granular texture becomes obvious, together with a change in colour. Finally, globules suggestive of a resin or gum appear in the parenchyma cells, and as these increase a deepening of tint from yellow to brown occurs. It would therefore appear that by a series of chemical changes the contents of these elements gradually disintegrate, and the resulting compounds are in the form of globules of coloured material. It must, however, be remembered that starch is a stable

substance, and also that the disappearance of many grains is due to their conversion into sugar for uses within the plant, and may not be associated with the coloured globules under consideration. If one examines the vessels of the sapwood one often finds the globular material entering through the pits. In one section the stream of coloured material could be traced from the medullary ray cells through the pits into the lumen of the wide vessel with which they were in contact.

In very many cases the coloured substances project into the lumen of the vessel as large globules suggesting tyloses; these swell, and are partially soluble in water. The globules may exhibit stratification according to the colour of the different parts.

In other cases the large globules are entirely absent, and the deposit appears as a thin film of a pale straw-coloured material in the area of the pits. The whole of the pits in the wall of any particular vessel do not usually present this appearance, the pits thus coloured usually occurring only in local groups along the wall of the vessel. The deposit may become very abundant, and when half filling the vessel is irregularly globular in outline. It therefore appears that the material occurring in the tracheal elements is derived from the substances stored in the parenchymatous elements, and the relative freedom of the latter from contents—a feature often noticeable in mature ebony—may be a consequence of exhaustion of store material. The infiltrating material may be of a pale straw or light brown colour; as it increases in quantity the tint deepens and the elements finally become blocked with deep brown or black material.

The gum-resin issues in large quantities from the stumps of freshly felled trees and accumulates at points of exposure. The walls of the elements from trees which have yielded large quantities of this substance do not show any reduction in thickness, and it is probable that they have been derived from disintegration of store materials in the parenchyma of the wood.

The stratification exhibited by the deposit is due to the variation in the colour of the different parts, and may be detected in the globules formed within the parenchymatous elements.

The maximum quantity of gum-resin is seen in our blackest woods, such as D. Melanoxylon and D. Ebenum, and the minimum in our whitest woods, such as D. insignis and D. hirsuta.

The mottled colour of some timber specimens is due to the gum-resin being almost limited to the medullary ray cells; these are packed with the brown-coloured substances, while the neighbouring elements, including vessels, are nearly empty. This feature is noticeable in our lighter coloured woods, such as D. Gardneri, D. sylvatica, and D. insignis.

The appearance of the material in the vessels may occur unaccompanied by any change in the physical properties of the wall, and the fuchsin and safranin reagents can still be used with advantage, even when the elements are entirely filled with the coloured substances. In many cases the coloured substances impregnate the walls of the elements, but only in few cases do the walls show signs of decay.

V.—SEEDLINGS.

In the development and anatomy of the seedlings several interesting points have been determined, and a synopsis is here given. The characters of seedlings have not yet found a prominent place, if one at all, in systematic monographs. The occurrence of specific and generic characters in the developmental phases, in the morphology of the cotyledons and epicotyledonary leaves, and in the behaviour of the leaf traces must serve as the reasons for their inclusion in the present work.

The importance of seedling characters for systematic purposes has of late been discussed by various botanists.

Miss Sargant* has stated that no doubt remains as to the systematic value of the indications given by the vascular

* Ethel Sargant, The Origin of the Seed-leaf in Monocotyledons; New Phytologist, Vol. I., No. 5, 1902.

structure of the cotyledon, hypocotyl, and primary root. At a later date* a further contribution was made on the same subject, and in it a very great significance was alleged for seedling characters. Though the examination was mainly with seedlings of the Liliaceæ and Ranunculaceæ, the evidence seemed sufficient to justify the publication of a theory of the origin of monocotyledons founded primarily on the structure of their seedlings. This theory was again discussed at the British Association meeting, September, 1903. Fritsch,† in a general discussion on the value of anatomical characters, states that though seedlings may present a very uniform type of structure throughout large groups, the anatomy of the seedling may be expected to indicate affinities more clearly than that of any other part of the plant.

The length of the hypocotyl and primary epicotyledonary axis, the phyllotaxy, and general morphology of the first formed leaves, together with the persistence or dropping of the cotyledons, provide ample material for the recognition of most Ceylon species of Diospyros. In addition to these characters we have to consider the number of traces per cotyledon, and the behaviour of the epicotyledonary and cotyledonary traces in the hypocotyl and primary root ; these in themselves afford facts sufficient to allow one to construct a useful artificial key for the identification of Ceylon species.

Germination.—The time taken for germination varies according to the condition of the seeds when gathered and sown. If sown after partial drying in air, germination usually occurs within two to four weeks. If, however, the fresh seeds are sown direct, without drying, it may take several months before the primary root projects from the micropyle. The seeds of D. ovalifolia have a particularly

* Ethel Sargant, A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings; Ann. Bot., Vol. XVII., No. LXV., January, 1903.

† F. E. Fritsch, The use of Anatomical Characters for Systematic Purposes : New Phytologist, Vol. II., No. 8, October, 1903.

hard testa and a copious horny endosperm, and many do not germinate until nine months after sowing.

The material required for the study of the vascular system prior to the production of secondary elements is best obtained by allowing the seeds to germinate on sheets of blotting paper, which are always kept moist, or on porcelain dishes partially immersed in water and covered by a bell jar.

If it is desirable to study the embryo prior to the appearance of lignification of the proto-elements, a convenient method is to first thoroughly dry the seeds until the testa begins to crack and then immerse them in water kept at 100° F. for some time. Seeds of D. Ebenum treated in this way provided excellent material, since the embryos completely emerged from the confines of the endosperm into the bath without being injured in any way.

Development of the Seedling.

When the primary root has attained a length of 2 or 3 cm. the young curved hypocotyl appears above ground. The cotyledons are embedded within the copious endosperm, and together with the testa are still below the surface of the ground. Subsequently the hypocotyl shows signs of rapid growth, the collet area increases in thickness, and the hypocotyl becomes more strongly arched and sooner or later assumes an erect position, carrying at its apex the cotyledons or epicotyledonary leaves. In every Ceylon species of Diospyros and also Maba, the seedlings are of the epigeal type, though the mode of development in those species having very short hypocotyls is suggestive of a hypogeal habit.

In a few of our species, viz., D. Ebenum, D. Gardneri, D. sylvatica, and D. montana, the pair of opposite ovate cotyledons persist for many months and function as assimilatory structures until an adequate system of epicotyledonary leaves has been established. In all such cases the epicotyledonary leaves develop very slowly. This is true for seedlings

raised from seed obtained from cultivated trees in India and Ceylon and from the jungle. The delayed epicotyledonary development is characteristic only of those species which have normal persistent cotyledons. It is also to be noticed that in all these cases the primary epicotyledonary axis, *i.e.*, axis between cotyledonary node and first epicotyl leaf, is very short, and that the first two leaves on this axis never form an opposite pair, but are always arranged alternately, and are speedily followed by many others disposed in a similar way.

The majority of our Ceylon Diospyros species exhibit a curious mode of development, and a detailed account of seedlings of D. quæsita is now given, commencing at the stage of the strongly arched hypocotyl, when the testa, endosperm, and cotyledons are still connected with the hypocotyl and partially covered with soil. At this stage the testa splits near the micropyle, and the gap thus formed gradually extends along each side of the seed to a distance of about 1 cm. The chalazal end and often the greater part of the seed is still below the surface of the soil. In consequence of the strain set up by the rapidly growing hypocotyl the sessile cotyledons now become detached and the hypocotyl frees itself from the confines of the seed, carrying the enhanced epicotyledonary leaves at its apex. The cotyledons are left behind surrounded by the bulky endosperm, and from the moment of their detachment the young seedling receives no further nutritive substances from the endosperm. At this stage there is a large quantity of endosperm, and this, together with the whole of the reserve materials contained in the parenchyma of the cotyledons, is wasted. In consequence of the detachment of the cotyledons and the enhanced development of the epicotyledonary leaves a large number of the seedlings die. This is brought about by the death and decomposition of the cells of the detached cotyledons and the endosperm, which in time leads to a diseased condition of the apex of the epicotyledonary axis. It is therefore highly desirable to apply artificial pressure and crack the

testa sufficiently to allow the cotyledons to escape prior to detachment.

The cotyledons, though they have attained their full dimensions and are exposed to light, never take on the work of assimilation as in the case of the species with normal persistent cotyledons. They are at first pale yellow in colour, but within twenty-four hours show signs of death, and within thirty-six hours become black and shrivelled. They may, however, still adhere to the cotyledonary node by the bases of their short petioles.

The point of interest in this curious suicidal mode of development is that the disconnection of the cotyledons seems to have been provided for long before the actual detachment takes place. Ungerminated embryos show a conspicuous epicotyledonary axis usually with a minute pair of interlocked leaves at the apex. In those species with persistent cotyledons such an enhanced epicotyledonary development does not present itself until three or even five months subsequent to the full exposure of the cotyledons. By the time the cotyledons are detached the epicotyledonary leaves are well developed ; they are also provided with a palisade tissue, and on exposure take on the work of assimilation usually allotted to the cotyledons. Furthermore, the first epicotyl leaves usually form an opposite pair of interlocked leaves, and thus remind one still more forcibly of cotyledons. When the epicotyl leaves form an opposite pair these usually persist alone for many months ; this suggests most strikingly that their enhanced development has really been an effort, and internal evidence indicates that it is associated with abortion of cotyledons, which appears to have been taking place through many generations.

The majority of our species show this detachment of cotyledons and enhanced development of epicotyledonary leaves which take on the work usually assigned to cotyledons. The cotyledons never acquire palisade tissue, but this layer

is laid down in the epicotyledonary leaves long before they are exposed to light.

As to the causes which lead to the detachment of the cotyledons, it is very difficult to make any definite statements. The regularity of the occurrence in seeds of all sizes, under natural and artificial conditions, is suggestive of the possibility of a definite cellular activity cutting off the cotyledons at the node in a manner similar to that in which old leaves are cut off from the parent tree. This, however, cannot be the case, as in all experiments where the cotyledons have been set free prior to detachment their dead and shrivelled tissues have persisted at the cotyledonary node for a considerable length of time.

Hence we are driven to the conclusion that the detachment is probably a case of separation under conditions of strain, and several possible factors may be quoted in support of this contention. The first is the pressure of the endosperm. In those species where the cotyledons are persistent the endosperm may be equable (D. Ebenum) or strongly ruminate (D. sylvatica); similarly it may be markedly ruminate in species with detached cotyledons (D. hirsuta) or equable (D. insignis). Hence, the pressure of the endosperm, as indicated by the absence or presence of ruminations of this substance, has probably very little to do with the detachment of the cotyledons. A second factor is probably to be obtained in the bulk of the endosperm, testa, &c.; for though D. ovalifolia may prove exceptional, it is a fact that those species with persistent cotyledons have relatively a smaller quantity of endosperm which is necessarily exhausted early, resulting in a shrinking of the testa and liberation of the cotyledons at an early date.

However, neither of the foregoing, even if coupled with the increased resistance of the irregular surface of the mature cotyledons, can completely explain the cause of detachment.

The chief cause, in my opinion, is to be found in the insufficient splitting of the testa; in D. pruriens and D.

ovalifolia there is no splitting of the testa, and it is impossible for an expanded cotyledon to effect its exit from such a small circular micropylar opening amply filled by the thin axis of the hypocotyl ; in other species there is only a partial splitting, and even in calamander seeds the gap is never large enough to allow the cotyledons to escape intact.

Since the splitting of the testa would be more complete if the endosperm were exhausted more quickly, it follows that probably all the forces mentioned above play some part in the final detachment of the cotyledons.

The mode of development just described is not a consequence of the artificial raising of the seeds ; the detachment occurs in nature, and the internal characters of the epicotyledonary and cotyledonary traces indicate that this line of development has been habitual for a considerable period of time. This mode of development is characteristic of some of our rarest species, and is probably one of the factors which is leading to the extinction of many species.

The detachment of the cotyledons is attended with the minimum disadvantages in those species having short hypocotyls (D. insignis and D. Embryopteris). In these instances the seed coat, endosperm, and cotyledons are but rarely raised above the surface of the soil, and the young though enhanced epicotyledonary parts gain easy exit.

The habit of D. insignis in particular is very suggestive of a hypogeal tendency, since the seeds are rarely raised above ground, the hypocotyl is very short, and the epicotyl stem very long and provided with small leaf rudiments suggestive of typical Garcinia seedlings.

The morphological relationships of the parts of the seedlings are also of interest. In the first case it is worthy of note that in those species possessing short hypocotyls the epicotyledonary axis is usually long (4 to 7 cm.), whereas in those having hypocotyls of normal length the epicotyledonary axis is usually only from 0·5 to 1·5 cm. in length.

By this coincidence the first series of pronounced epicotyledonary leaves are brought to approximately the same height above ground in all species.

The lengths of these axes are fairly constant in each species, the median length of hypocotyls being from 5 to 7 cm. as in D. Ebenum and D. Thwaitesii; short hypocotyls, about 1 to 2 cm. as in D. insignis; and long hypocotyls, being from 10 to 11 cm., as in D. crumenata and D. quæsita.

The cotyledons are in all cases of the broad ovate type with blunt or tapering apices and attached by very short petioles at the cotyledonary node.

The first epicotyledonary leaves are, in the majority of our species, opposite; in one species they may be opposite or sub-opposite, and in the remaining species they are alternately disposed on an elongated axis. In all cases the leaves are simple, ovate-lanceolate in shape, but show differences in size and venation in the respective species. Generally speaking, they possess the diagnostic feature of the leaves of the mature plant in all points except size.

Internal Characters of the Seedlings.

In every species the number of traces per cotyledon is constant, and we have to separate those possessing two traces per cotyledon (*e.g.*, D. Ebenum and D. Gardneri), from those with three (*e.g.*, D. crumenata and D. Embryopteris).

In those possessing two traces per cotyledon the cotyledons are usually persistent; the cotyledonary traces are prolonged into the primary root and the epicotyledonary traces die away immediately below the cotyledonary node.

In those species with three traces per cotyledon the majority are characterized by detachment of cotyledons and enhanced epicotyledonary development, and though there are three traces per cotyledon the xylem and phloem of the median trace are abortive in all species except D. pruriens.

Furthermore, in those species with deciduous cotyledons the epicotyledonary traces are continued through the hypocotyl into the primary root.

The tendency for the median cotyledonary trace to abort is what one may expect in those species where the cotyledons are defunct at such an early period, and the prolongation of the epicotyl traces into the root is rendered necessary since nutritive substances cannot be absorbed from the endosperm. The fact that the embryo shows these structures fully differentiated points to a past history in connection with these curious developments.

The traces of the cotyledons are provided for the conduction of food materials absorbed from the endosperm to all parts of the seedling; in those species with persistent cotyledons they are the only vascular tissues present during the first few weeks or months of the seedling's life. If the absorbing tissues and the reserve food are cut off from the seedling during this phase, the young plant must die if the epicotyledonary traces are not prolonged into the root to establish a connection between the growing point of the stem and the new absorbing tissues constituted by the primary root.

It is very doubtful whether such developments can be accomplished in one generation, and the definiteness of the median trace abortion and epicotyledonary prolongation are sufficient evidence that the curious mode of development has been going on for many generations past.

There are, however, several facts which point to a very unstable condition. Seedlings of the same species show considerable variation in the degree of differentiation of the different tissues, and also in the behaviour of the vascular strands in the region of the collet. In one seedling the epicotyledonary and median cotyledonary traces were absent from the primary root at a distance of 2 cm. from the apex; at this point only the four lateral cotyledonary traces were present, though in the hypocotyl the six cotyledonary and two epicotyledonary bundles were in evidence; in this case the median cotyledonary trace had apparently suffered complete abortion at a point which had not yet been reached

by the descending epicotyledonary trace, and thus indicated one of the possible stages in the establishment of a new root symmetry.

Splitting of Xylem Traces.—Another point which indicates most markedly the unstable conditions of the seedlings is seen in the splitting of the xylem of the leaf traces. This is best seen in seedlings which are very young and in which vascular cambium has not made its appearance, and for the sake of clearness a description of the behaviour in D. Embryopteris is here given. At the cotyledonary node three vascular bundles make their exit on each side and persist as three separate strands in the petiole of each cotyledon. At right angles to the cotyledons, two strands from the epicotyl leaves appear, one on each side. As these strands are traced through the hypocotyl they are seen to separate from one another, and on reaching the collet area where the parenchymatous system is large each xylem strand separates into two, three, or more parts. At the collet area I have counted as many as twenty-two groups of xylem resulting from the scattering of the original eight traces. Traced below the collet into the primary root a fusion occurs, but whether this takes place between parts of dissimilar bundles or otherwise is very difficult to determine. The fusion goes on gradually, and at certain levels the number of strands is seen to be sixteen, later twelve, and through eight and six on to a final four. In no species are there ever less than four strands in the apical portion of the primary root.

Owing to the highly scattered nature of the xylem elements it is often impossible to ascertain the exact area wherein the inversion of orientation is effected.

In seedlings of the same species there is a great variation; sometimes only one lateral cotyledonary trace undergoes division, sometimes all three; the epicotyledonary traces when present may remain compact, or each may separate into two or three strands. In a general way it may be stated that the type of xylem in the seedlings is one where a splitting is seen in any of the cotyledonary traces into two or

three portions, together with a prolongation of epicotyledonary strands to different distances in the primary root.

In seedlings where the epicotyledonary traces are not continued into the primary root a similar splitting of the xylem of each cotyledon trace may occur.

The presence of twelve to twenty-two xylem strands in a comparatively narrow cylinder, where each strand is relatively large, renders the actual behaviour of each strand difficult to follow.

The reason for such profuse scattering of the proto-xylem system is perhaps to be found in the bulky nature of the parenchymatous system. In all cases the scattered condition attains its maximum in the collet area where the parenchymatous system is at the maximum, and it would appear probable that the mechanical support and supply of nutrition were the objects aimed at. The splitting is always more complicated in a wide parenchymatous seedling, such as D. Embryopteris, than in a narrow one, such as D. Ebenum, and the fact that the strands are thus distributed prior to the appearance of a vascular cambium is sufficient proof that the diffuse condition of the proto-xylem is not due to the pressure of new cambial products.

Direction of Lignification and Differentiation of the Vascular Elements.

If the embryo or young seedling be examined the differentiation of lignified elements can be determined. We may assume that lignification commences in the oldest element first and gradually appears in successively younger elements. *i.e.*, that the direction of differentiation of the elements is the same as that of lignification. In the embryo the beginning of lignification is seen in the xylem of the cotyledonary traces, and commencing at the cotyledonary node the lignified elements can be traced downwards into the primary root and upwards into the petiole of the cotyledons. The lignification at this stage is somewhat irregular, and appears to be a little

advanced in the median cotyledonary trace as compared with the laterals.

In the short axis of the embryo it is difficult to fix on the exact area at which lignification first appears. Examination of later stages shows the maximum lignification of the cotyledonary xylem at the collet area, and that the lignification subsequently spreads downwards into the primary root and upwards into the hypocotyl. The collet area is also the first to show a vascular cambium and the maximum parenchymatous system; it therefore appears to be the centre of activity of the seedling axis.

The fact that the lignification of the cotyledonary xylem reaches the maximum at the collet area may, however, still allow of the original starting point being at the cotyledonary node, and the enhanced lignification at the collet may be a secondary development associated with the requirements of the seedling subsequent to the purely embryonic stage. In the embryo the conducting systems are functioning in the conveyance of nutritive materials from the endosperm to the primary axis, and there does not therefore appear to be any necessity for lignification to commence at the collet area. There is the possibility that the direction of lignification may be purely responsive to the requirements of the seedlings, in which case no evidence can be obtained of the direction of differentiation of the original xylem elements.

The lignification is completed throughout the hypocotyl and primary root of the embryo within such a period, that prior to the apex of the primary root presenting itself at the micropyle a continuous series of lignified elements exist from root to cotyledons.

The epicotyledonary strands when present in the primary root show a definite direction of differentiation.

The phloem of each epicotyledonary strand begins at the epicotyl leaf and spreads downwards into the hypocotyl and root. This direction of differentiation is obviously the best,

since the function of the phloem strands is to conduct the materials prepared in the epicotyl leaves, together with the endosperm material absorbed through the epidermis of the young stem, to other parts of the seedling, viz., the hypocotyl and root.

The xylem of the epicotyledonary traces is, however, judging by the direction of lignification, differentiated in the opposite direction. This is obviously the best direction possible, as these tissues have to conduct the water from the root area to the epicotyl leaves, and since the cotyledons have become detached the sooner the xylem can be differentiated in the water-absorbing tissues the better.

The lignification of the epicotyledonary xylem usually reaches the cotyledonary node while the seedling is young and prior to the detachment of the cotyledons.

There is also another point in connection with the possible utility of the cotyledonary strands, which being disconnected from the cotyledons and endosperm seem likely to be in the way of any extra development of the epicotyledonary strands. The epicotyledonary traces remain separated from those of the cotyledons for a long time, but in D. Thwaitesii and probably in many others they become connected by the cambial products formed between the separate bundles. By this means the conducting power of the cotyledonary traces is tacked on to those of the epicotyledonary leaves and used in supplying the latter with the requisite food materials. This is therefore a good example of utilization of otherwise useless or abortive tissues during a phase of great urgency.

VI.—REPRODUCTIVE ORGANS.

The production of flowers in Ceylon species of Diospyros is usually associated with that of leaves, and is therefore subject to many variations. In many trees of D. Gardneri, D. Embryopteris, and D. sylvatica the flowers immediately follow the new leaves, and since the latter appear more or less regularly every year, an annual production of flowers

may be said to occur. Often, however, a leaf production may take place without a corresponding one of flowers, this being particularly noticeable in young trees having more than one period of leaf production a year. Again, flowers often appear on old woody twigs independent of leaf production, or recur in the same position year after year, sometimes in the axil of an old persistent leaf, and at other times in the old axil of a fallen leaf. In many trees of D. Ebenum and D. Toposia the majority of the flowers occur in the axils of new leaves, and therefore appear mainly at one time of the year, but such copious productions of flowers are invariably preceded and followed by periods of minor floral activity when the flowers appear without any definite relation to the leaves.

It is therefore obvious that no generalizations can be made beyond stating that the greater part of the flower system usually makes its appearance immediately after a copious production of leaves. The importance of realizing the irregular nature of leaf and flower production is great, and one cannot lay too much stress on the fact that in the forests of Ceylon the species of Diospyros have not one fixed time of the year for flower production. In the Sabaragamuwa districts there is not a month in the year when trees of D. insignis and D. hirsuta are absolutely flowerless, and the fact that trees of the same species growing alongside each other may possess either flower buds, mature flowers, ripe fruits, or no reproductive organs whatever during the same month, is sufficient to allow one to dispute any hypothesis based on the idea of a general seasonal periodicity.

It may be further stated that many Diospyros trees probably remain flowerless for many years at a time, and the appearance of sexual organs cannot be correlated with the prevailing seasons. This was the opinion of Thwaites and Trimen, and most forest officers still firmly believe that the majority of Ceylon Diospyros trees flower but seldom.

There are no records of careful observations made upon particular trees for many years in succession, and though the writer is prepared to admit the probability of the above contention, experience in the forests has led him to believe that the production of flowers in Ceylon Diospyros trees is by no means a rare occurrence. The great size of the trees, the inconspicuous nature of the flowers, and the uninhabitable districts in which many of our species occur, have led most people to believe that flower production is much rarer than it really is. We may, however, safely say that there is much irregularity in flower production, and the phenomenon can only be explained by a study of the individual equation of the plant we are dealing with.

Age of Flowering Trees.—In the absence of precise information on the rates of growth of tropical trees we can best state our ideas under this heading in terms of cauline dimensions. The majority of our dry zone species, particularly D. Embryopteris and D. ovalifolia, do not flower until the trees have attained considerable dimensions. Specimens of the former having a circumference of 3 feet and of the latter over 1 foot in girth are now growing at Peradeniya, but have not yet flowered. One specimen of D. quæsita, having a breast-height circumference of 47 cm. ($18\frac{1}{2}$ inches) and known to be over sixty years old, has not yet flowered at Peradeniya. Trees of D. Ebenum, D. affinis, and D. Gardneri are known to repeatedly flower at Peradeniya, and have a breast-height circumference varying from 38 to 50 cm. (15 to $19\frac{1}{2}$ inches).

On the other hand, trees of D. hirsuta and D. Thwaitesii in their native habitat flower when their stems have a diameter of 4 to 6 inches; D. pruriens may flower when the dimensions are still less, and trees of D. acuta and D. attenuata have been seen in flower when the diameter of their stems has not exceeded 25 mm. (1 inch). The following table is given with a view to elicit more precise

information in the future, and the dimensions quoted have been determined personally in the districts mentioned:—

Minimum Dimensions of Flowering Trees.

Name.	Locality.	Breast-height Diameter of Stem in Mm.
D. Embryopteris	Peradeniya	155
D. affinis	Bibile	130
D. oocarpa	Kalugala.	180
D. Ebenum	Pindeniya	125
D. montana	Madawachchi	75
D. quæsita	Karawita	250
D. crumenata	Hantane	260
D. Toposia	Gammaduwa	60
D. Gardneri	Hantane	120
D. hirsuta	Ratnapura	65
D. Moonii	Yagirilla	25
D. Thwaitesii	Hewessa	100
D. oppositifolia	Hiniduma	50
D. attenuata	Pasdun korale, near Hiniduma	25
D. sylvatica	Hantane	250
D. acuta	Pasdun korale, near Hiniduma	25
D. Melanoxylon	Bibile	110
D. pruriens	Kadawatta	60
D. insignis	Ratnapura	60
D. ovalifolia	Kanthalai	200

Position of Flowers.—The majority of the flowers, whether solitary or in the form of an inflorescence, appear in the axils of foliage leaves, and are therefore most usually found near the ends of the ultimate twigs. Many species, however, have their flowers disposed on old twigs or branches, this being characteristic for D. Moonii, D. ovalifolia, and D. insignis in particular.

When the flowers are monœcious the females usually appear in the axil of the youngest leaves and the males in the axil of lower leaves. In D. oppositifolia and D. acuta a female flower usually terminates each young shoot; other female flowers occur in the axils of young leaves, but the males occur either in the axil of old leaves, or on woody twigs independent of foliage leaves. The females are thus subject to more exposure, and being exposed to the wind on all sides are more likely to attract insects and to catch wind-borne pollen.

Nature of Flower System.—The nature of the flower system varies with the species and with the sex of the same species. The flowers may be solitary, pedunculate, or sessile, or in the form of an inflorescence having each member supported on a pedicel of varying length. When the peduncle and each lateral pedicel of a cymose inflorescence is very short the flowers form what may be conveniently described as a sessile cluster. The male and female flowers may each form inflorescences ; here both inflorescences may be in the form of sessile clusters, as in D. insignis, both inflorescences may have pedicellate flowers, as in D. Embryopteris, or the members of the female inflorescence may be sessile and the males shortly pedicellate, as occasionally occurs in D. Ebenum.

On the other hand, the females may occur solitary and the males as an inflorescence ; under this group we may have the female flower and each male flower markedly pedicellate, as in D. quæsita, or both sessile, as in D. Gardneri ; we may also have the female sessile, but males pedicellate, as in D. Melanoxylon, or the female pedicellate and the males sessile, as in D. oppositifolia.

Female Flowers.

In fourteen out of our twenty species the female flowers may occur solitary ; in nine of these, viz., D. affinis, D. pruriens, D. oppositifolia, D. quæsita, D. sylvatica, D. crumenata, D. Toposia, D. oocarpa, and D. montana, the flower is on a peduncle of varying length, whereas in the remaining five, D. ovalifolia, D. Melanoxylon, D. Gardneri, D. attenuata, and D. Ebenum, the female flowers are sessile.

In the remaining six species the female flowers form an inflorescence which in D. hirsuta, D. insignis, D. Moonii, D. Thwaitesii, and D. acuta is a sessile cluster of three to fifteen flowers ; but in D. Embryopteris the inflorescence is a cyme of three flowers, each of which is attached to the short peduncle by means of a short stout pedicel.

It must here be stated that the female flowers of D. acuta, D. sylvatica, and D. Ebenum may occur in the solitary or grouped condition on the same tree. It now remains for us to study the relationships between the parts of a solitary female flower and the members of a female inflorescence.

Development of the Female Flowers in D. Gardneri, D. Embryopteris, and others.—In D. Gardneri the pubescent flower bud arises in the axil of a new or old foliage leaf. The peduncle is very short and rarely exceeds 0·4 cm. in length, but very soon two small leaves appear at right angles to the antero-posterior axis. In addition to these a third leaf may appear between the normal foliage leaf and the anterior side of the flower, and this may be followed by a fourth on the opposite side between the axis and the posterior side of the flower. Under ordinary circumstances, and even if the flowers be cut away so as not to greatly disturb surrounding organs, no development takes place in either of the bracts numbered 1, 2, 3, and 4. If, however, we now study the development of the female inflorescence in D. Embryopteris, we find exactly the same sequence of events, but in addition a flower bud appears in the axil of each of the small leaves on the primary peduncle (pl. IX., figs. 7–10). Similarly with the female inflorescences of other species. It is further to be noted that when the female inflorescence forms a sessile cluster the appearance of each flower is always preceded by that of the small leaf, and in many of them a considerable amount of abortion occurs.

Often in D. Thwaitesii there is a solitary female flower surrounded at the base by an involucre of bracts, abortion having occurred in the axil of the lower bracts. We may therefore arrange the female flower systems in one series to show that the solitary flower arrangement is probably derived from the cymose inflorescence by abortion in the axil of the lower bracts. This is the most likely course of evolution, since the lateral flowers in the inflorescence of D. Embryopteris often drop before they reach maturity in consequence of the pressure exerted by the quickly growing median flower.

Male Flowers.

In every Ceylon species the male flowers occur in clusters of three or more individuals ; in D. attenuata and D. oppositifolia they may also occur solitary in the axil of the younger leaves. Sometimes the cluster of flowers is inconspicuous, as in D. attenuata, but at other times, particularly with D. sylvatica, D. quæsita, and D. Toposia, a single inflorescence may have a height of 50 mm.

The peduncle or the central flower of an inflorescence arises in the axil of a young leaf, which may be of the normal type or greatly reduced ; similarly with each lateral flower or its pedicel. When the individual flowers of a cluster are sessile there is often a great deal of abortion, and the remaining flowers therefore appear surrounded with very many bracts, so that a rudimentary involucre is formed.

The types of male inflorescences are three in number. In the first class we have the primary peduncle and the pedicel of each lateral flower so small as to be undistinguishable to the naked eye, and the inflorescence may therefore be described as a sessile cluster, as in D. ovalifolia, D. hirsuta, D. Moonii, D. insignis, D. Thwaitesii, D. oppositifolia, D. attenuata, D. acuta, and D. Gardneri. In the second class we have each flower disposed on a very short pedicel from 1 to 5 mm. in length, as in D. oocarpa and D. sylvatica. In the third class we have the remaining nine species, in each of which the flowers are supported on very long pedicels often considerably over 10 mm. in length.

Development of the Male Inflorescence.—It will be better to first detail the developmental phases of an inflorescence of the third type, and no better species can be chosen than D. Embryopteris. In the earliest stages the inflorescence appears as a globular apiculate axillary structure, supported on a short stout peduncle and covered by a varying number (two to five) of regularly arranged bracts. As the inflorescence gradually opens, the first pair of bracts are seen to be opposite or subopposite and disposed one on either side, at

right angles to the antero-posterior axis; these are the first to drop, and each possesses in its axil a semilunar pedicellate flower. Each lateral flower is in close contact with the median flower, which is always the largest and the oldest (pl. IX., figs. 1–4).

A second pair of bracts is seen in the early stages, arranged one on each side at right angles to the first pair, but at different levels; each of these likewise possesses a small pedicellate flower in its axil. At a much later stage, some time after the fall of the first two bracts, a fifth bract appears between the median flower and the third lateral flower, and in its axil a shortly pedicellate flower arises.

In point of time the median flower arising in the axil of a foliage leaf is not much in advance of the first pair of lateral flowers. The third flower does not, however, appear for some time, and the interval of time between its appearance and the next flower, with which it forms a subopposite pair, is still more prolonged. The appearance of the fifth lateral flower is considerably delayed, and often it does not appear until the majority of the bracts of the other flowers have dropped. We therefore see that the interval of time between the appearance of successive flowers of the same inflorescence increases gradually, and the flowers do not cease to appear until the oldest individuals have undergone considerable expansion and their subtending bracts have dropped.

We thus obtain finally a definite inflorescence having the terminal flower the oldest, but the youngest flower next to it, the development of each lateral flower being to the median centrifugal, but to one another centripetal. (See pl. IX., fig. 5.)

If we now compare the development of the male inflorescence of any other species, approximately the same phases are passed through. In some species the number of lateral flowers is small, as in D. pruriens, whereas other species, notably D. Toposia and D. sylvatica, have a much more complicated system of flowers, in consequence of each lateral

pedicel becoming the main peduncle of another cyme. (See pl. X., figs. 7–8.)

It is obvious from the descriptions given that the inflorescences of the male and female are similar in their phases of development, the only difference being one of degree, since the female more often than not consists of a single flower having a pair of bracts at right angles to the antero-posterior axis, or with two to four bracts along its peduncle. The solitary female flower with its concomitant structures is an exact representation of the early stages of the complex inflorescence of the male. It is quite probable that the whole of the Ceylon species of Diospyros can be traced back to a type of reproductive organs in which the flowers of an inflorescence were numerous and hermaphrodite.

Variation.—Though the solitary flower or inflorescence is fairly constant for the sex of the species, it is not by any means strictly so. The female flower, though occurring solitary in the majority of our species, is liable to be replaced by a simple dichasial cyme. This is particularly frequent in D. acuta, D. sylvatica, and D. Ebenum, and it is probably only a question of further observation to establish the same tendency on the part of the female flower in other species.

The variation on the male side is much more conspicuous. In D. oppositifolia, for instance, instead of a male inflorescence of many flowers, there may be a solitary male flower; in D. Toposia we may observe every variation from a single flower to a complex inflorescence of eighteen flowers.

This variation on the male side is not of any serious consequence to the plant, since the number of male flowers is always greatly in excess of the female. On an average there are about six times as many male flowers as female flowers in monœcious species, and probably a still greater proportion of males in those species which are not monœcious; hence, in the general characters of the inflorescence and individual flowers there is considerably more variation on the male than on the female side.

Sex.

According to Hiern the genus Diospyros is characterized by dicœcious flowers, and only rarely is a polygamous or moncœcious state to be observed. It is further stated that when such departures from the dicœcious condition do occur they do so only casually, and one is left to infer that the variation is one to be explained on individual grounds and is not of specific importance.

Including species imperfectly known, Hiern describes 170, and of these only 7 per cent. are recorded by himself or others as showing a departure from the dicœcious condition.

Accordingly, Hiern formed a classification for the whole of the Ebenaceæ, showing the genus Royena, L., with hermaphrodite or rarely subdicœcious flowers and the remaining genera, viz., Euclea, *Linn.*, Maba, *Forst.*, Diospyros, *L.*, and Tetraclis, *gen. nov.*, with dicœcious or rarely polygamous flowers.

Confining ourselves to the Ceylon representatives of Diospyros, we find that Thwaites and Trimen believed the genus to be characterized by dicœcious flowers, and that the flowers were only very rarely moncœcious. Thwaites noted the departure from the dicœcious condition in two of our species, and stated that in D. acuta the flowers were sometimes moncœcious, and that in D. hirsuta the female flowers are sometimes intermixed with the male.

The main source of error has probably been in that the material at hand has not been very abundant, or the examination has been made upon herbarium specimens or material which had been collected some time previously. In the so-called "male" flowers of D. Gardneri there is very little external character indicative of a fertile pistil in the fresh material, and it is only by continued observation that ripe fruits may be seen.

Herbarium specimens of known hermaphrodite and polygamous flowers of D. affinis, D. hirsuta, and others do not show any prominent external differences from known male

flowers of the same species, and it is only by actual observation of fresh material in the forest that the true sex has been determined. It has been the common experience of myself and many others to regard trees of D. sylvatica and D. Gardneri as males, until they have been felled, when in addition to flowers possessing fertile stamens, abundance of ripe fruits have been obtained on the same branch. In order to further emphasize this condition I may say that the whole of the anatomy and development of seedlings of D. sylvatica, to be published elsewhere, was first worked out from seeds obtained from a tree which has for many years been labelled as a "male," and from which material for sketching the "male" inflorescence has been derived.

From the following notes it will be seen that examination of fresh material in the forest has shown that there is a departure from the diœcious condition in ten out of our twenty species. Speaking generally, the sex appears to be very unstable, the diœcious, monœcious, polygamous, and hermaphrodite conditions having been found. The occurrence of hermaphrodite flowers resulting in a polygamous condition is so frequent that there is every reason to doubt their non-existence in any of the Ceylon species, providing sufficient material can be examined outside the herbarium.

It may be further stated that specimens of D. Thwaitesii have been repeatedly examined, which suggested that the sex of the flower might vary from time to time; this has been described for other plants.* Certain it is that the sex of the flower often exhibits every variation in the same inflorescence of D. sylvatica, and the many stages observed readily allow one to form a series having staminate flowers at one end and hermaphrodite at the other.

The types of flowers characteristic for the different Ceylon species may now be described under the following headings: (*a*) diœcious only, (*b*) monœcious only, (*c*) diœcious and polygamous, and (*d*) diœcious, monœcious, and polygamous.

* Willis, Gynodiœcism, &c. (3rd paper); Proc. Camb. Phil. Soc., 1893.

Diœcious only.—This condition prevails in D. Toposia, D. quæsita, D. pruriens, D. crumenata, D. ovalifolia, D. Melanoxylon, D. attenuata, D. montana, D. Moonii, and D. oocarpa.

In these species the female flowers may be solitary or form a simple or complex dichasium, having the staminodes of each flower with barren anthers. The males may form a cymose inflorescence, sessile or otherwise, in each flower of which the pistil is absent, rudimentary or represented by a bunch of hairs. It is highly probable that if more fresh material is examined at least the polygamous and very possible the monœcious condition will be observed. In many of the species included under this head the male flowers are always very numerous, often as many as fifteen to each inflorescence, and hence the possibility of variation and occurrence of polygamy. In some of the species, notably D. quæsita and D. Toposia, the rudimentary pistil of many male flowers is often of conspicuous size, and a transverse section reveals the presence of irregularly outlined cavities. Further, it is not unlikely that if the staminodes of the female flowers be examined fresh they will yield pollen grains. Very little material has been examined microscopically from this point of view.

The number of members in the staminal whorl and their orientation in the male and female flowers of the same species is sometimes widely different; for instance, in D. quæsita the female flower possesses five staminodes which alternate with the corolla lobes, whereas in the male flowers an indefinite number of stamens occur clustered together in the centre of the flower, and have no individual orientation to one another or to the members of other whorls. Similarly, great differences exist in the staminal whorl of D. pruriens.

In D. Melanoxylon the staminal whorl is very unstable in both sexes, there being ten, sixteen, or twenty stamens in the male, sometimes with the filaments free, at other times united in pairs, and twelve or more staminodes in the female flower having no fixed orientation to the four- to seven-lobed accessory whorls.

Monœcious only.—This occurs in D. oppositifolia and D. acuta.

In D. oppositifolia the female flower is usually solitary and at the end of a young twig. Occasionally a female flower occurs lower down in the axil of old or young leaves. When the flower terminates the young shoot it is usually on a peduncle from 5 to 20 mm. long; when in the axil of a leaf it is invariably sessile and mixed with male flowers. The staminodes are usually four in number, alternating with the corolla segments; or exceptionally eight in number, opposite and alternate with the corolla segments. In every case examined the anthers of the staminodes were barren. The male flowers occur in sessile or subsessile inflorescences in the axil of old leaves or on old twigs. Each flower possesses eight stamens and a rudimentary apical mass of long unicellular hairs in the position of the pistil of other flowers. The stamens are usually paired, the pairs usually alternating with the corolla segments. The resemblance between the orientation of the staminal whorl of the female flower and that of the stamens of the male flower is here very great, and as far as this whorl is concerned we may speak of the flowers as male or female, according to the fertile or barren condition of the anthers.

D. acuta, according to Thwaites, is occasionally monœcious; personally I have never been able to obtain any other condition, though I found it in abundance at Wewella, Weerakanda, Hewessa, and Pasdun korale. The male and female flowers occur in clusters in the axil of old or young leaves, the individuals of the same cluster being of the same sex. As in D. oppositifolia, the female flowers occur mainly in the axil of the younger leaves, the male flowers being below. In the number and orientation of the members of the staminal whorl there is a tendency to variability on the male side. In the male flowers there may be five, seven, or nine epipetalous stamens, usually separate but occasionally united in pairs, and when the latter condition obtains the inner

stamen of a pair is very small and contains very little, if any, pollen when mature.

On the other hand, the staminodes of each female flower are always five in number, epipetalous, and arranged so as to alternate with the corolla segments.

It is therefore to be noted that in the species which are monœcious only the staminodes are constant in position and number, the stamens may equal or double the staminodes in number, and a rudimentary pistil usually occurs in the centre of each male flower. As to whether the male flower can be derived from the female, or *vice versâ*, by sterilization of sporogenous tissue, nothing need be said in this part of the paper.

Diœcious and Polygamous.—This occurs in D. sylvatica, D. Gardneri, D. affinis, D. Embryopteris, and D. insignis.

Under this section we must differentiate between the polygamous condition due to replacement of a staminode by a stamen, as in D. Embryopteris, and that due to the pistil of a male flower exerting its potentiality, as in D. affinis, D. sylvatica, and D. Gardneri.

In D. Embryopteris we have the distinct male and female forms, and the species can be said to be diœcious. The female flowers have four staminodes* alternating with the corolla lobes and a central pistil having an eight-celled ovary. The male flowers have an indefinite number of stamens and a rudimentary pistil. It has, however, been noted by Hiern that the staminodes of the female flower may be replaced by perfect stamens, thus giving rise to a polygamous state. The male flowers of the same species likewise show an occasional fertile pistil, resulting in a polygamous condition on the same tree

In D. sylvatica, D. Gardneri, D. insignis, and D. affinis we have the diœcious and polygamous conditions well

* Hiern states (p. 258) that D. Embryopteris has one to twelve staminodes in the female flower.

demonstrated. The conditions are the same for each of these species, and a description of one will therefore be sufficient.

Selecting D. sylvatica, we find that in this species we have three kinds of trees, viz., (*a*) female trees, (*b*) male trees, and (*c*) polygamous trees.

The female trees have their flowers arranged either solitary or in simple cymes, each component having four or eight staminodes and a six- to eight-celled ovary. The calyx is usually accrescent and larger than that of the male.

The male trees have dense cymes, each often with fifteen flowers. Each male flower possesses an indefinite number of stamens and thin calyx segments.

The polygamous trees have the flowers arranged as in a male cyme, and among them three types of flowers can be distinguished. In the first section we have hermaphrodite flowers, each of which is characterized by large accessory whorls, twenty-two stamens, and a fertile pistil. The fruits from these flowers possess seeds which in the characters of the testa and embryo exactly agree with those from known female trees. In the second class we have flowers with large accessory whorls, twenty-two stamens, and an abortive pistil showing an ovary one- to six-celled. These never yield good fruits. In the third class we have flowers with small accessory whorls, twenty-two stamens, and an abortive pistil.

It is therefore clear that in the polygamous trees we can obtain every stage from purely staminate to hermaphrodite flowers.

It must not be supposed that the polygamous condition may occur on any tree. There are male trees which never produce anything but staminate flowers and female trees which never possess stamens, and these must be clearly distinguished from those trees showing the polygamous condition.

The difference between the indefinite staminal whorl of the male and polygamous flowers and that of the true female

is very great, and though it is easy to connect the flowers of the third class in the polygamous group with those of the true male, it is not so easy to connect the hermaphrodite flowers of the polygamous group with the ordinary female flowers.

We have again to realize that in the same species there is a wide variation in the number and orientation of the floral parts of male and female flowers.

Diœcious, Monœcious, and Polygamous.—This may occur in flowers of D. hirsuta, D. Thwaitesii, and D. Ebenum.

In these species a very complicated sex relationship exists. If we take as our example D. Thwaitesii, we find that three types of trees exist.

In the first place there are pure female trees. Here the flowers may occur solitary or in small sessile axillary clusters of two to seven flowers, each component having five staminodes disposed so as to alternate with the five lobes of the corolla and a four-celled ovary.

In the second class there are pure male trees having the flowers in axillary groups of four to fifteen. Each flower has ten stamens arranged in five pairs alternating with the corolla lobes, or several pairs and the remainder single, arranged irregularly or as five series. In these flowers the pistil is always rudimentary, and consists of nothing more than a central mass of brown hairs. It is in the third class of trees that complicated relations exist. In this class we have the true male and true female flowers occurring on the same tree, sometimes in separate axillary groups of the same branch, and at other times in the same axillary group. Thwaites noted that in D. hirsuta the female flowers were sometimes mixed with the male. We may therefore speak of the monœcious condition in these species. But in addition to the monœcious condition we may have on the same tree a truly polygamous group or groups of flowers exactly analogous to the polygamous flowers described for D. Gardneri, D. sylvatica, and others. The polygamous

condition is where each flower has ten or more stamens, each with a perfect anther and occasionally a central pistil which ripens into fruit.

It is obvious that a distinct correlation can be established in the number and position of the members of the flowers borne on trees of this class, and since the occurrence is so irregular and the stages established include the male, hermaphrodite, and female conditions, some light may be thrown on the evolution of sex in this genus.

In considering the relations between the members of the flowers on trees of the third class we may at once eliminate the calyx and corolla, since in all the flowers the variation is only one of size, the maximum and minimum dimensions being in the female and male flowers respectively.

The staminal whorl in the male flowers, whether these form a separate cluster or part of a monœcious or polygamous group, consists usually of ten stamens arranged as five pairs, alternating with the corolla segments. In some male flowers there may be only eight stamens arranged as three pairs and two separate individuals, and in others I have met with an irregular epipetalous group of stamens. In the female flowers, no matter where they occur, the staminal whorl is represented by five epipetalous staminodes disposed so as to be alternate with the corolla lobes. The position of the members of the staminal whorl in male and female flowers is approximately the same, and the five single staminodes of the female can be connected with the five groups of stamens usually existing in the male flowers. Since the staminode is really a stamen having a barren anther, we therefore see that the difference between the male and female flowers can be easily accounted for, assuming there has been abortion of sporogenous tissue.

In the gynœcium the number of loculi in the ovary and the number and position of the ovules and seeds is the same, whether the pistil is part of a hermaphrodite or female flower.

It is therefore possible to make a complete series from flowers on the same tree, having staminate flowers at one end, passing through hermaphrodite to female flowers.

In other trees of the same species the sex is either male or female and is fixed.

D. Ebenum is included under this heading, and though the dicœcious condition is the most common form for this species, yet observation of fresh material in the forest has revealed the frequent occurrence of the monœcious and polygamous state. The monœcious state consists of female flowers often ripening into good fruit on a pedicel in a male inflorescene. The monœcious condition in D. Ebenum is unlike that in D. oppositifolia or D. acuta, since the female flowers do not occur solitary but as sporadic members of a male cyme. On first examining such a monœcious inflorescence the thought uppermost in my mind was that here we were dealing with a male inflorescence, some members of which had reverted to the condition of a potential gynæcium, but this idea was abandoned in consequence of the fact that each of the female flowers when thus occurring possessed eight staminodes each with a barren anther, and an eight-celled ovary. We therefore have true female flowers occurring in the same cluster as the males.

The female flowers may occur in any part of the inflorescence, but the most usual position is that terminating the inflorescence and therefore occupying the central position. Since the central flower is the first formed we therefore obtain a time relation in the production of sex, the female flowers being produced first and the male flowers afterwards.

The production of female flowers in the axil of the youngest leaves, and that of the males in the older leaves in D. acuta and D. oppositifolia is a sequence to be correlated with this.

In consequence of the complex relationships in species described it is well to realize that the monœcious state in

D. Ebenum is due to the interpolation of a female flower in a male cyme. The female flower when thus occurring presents no differences from the female flower of diœcious trees, except in that it is pedicellate. In no case have I met with the monœcious form due to the replacement of a female flower by a male.

The occurrence of true male and female flowers in the same inflorescence is of importance, since the characters of the accessory and essential whorls in the male and female are often so widely different. It has been suggested by many observers that since the flowers, the habit, and foliage of what are regarded as the male and female trees of the same species often show great differences, we might be erroneously considering male and female trees of what are really separate species as being of the same species. Subsequent observations demonstrated the frequent occurrence of polygamy, and for a time these gave support to the above contention. Now, however, we have seen that the true male and true female flowers possessing different types of accessory and essential whorls can occur in the same inflorescence, and we can therefore adhere to the former ideas as to the true diœcious form of some species.

Characters of Accessory and Essential Whorls.

Calyx.—The calyx is always inferior and gamosepalous; sometimes glabrous or nearly so, as in D. sylvatica, at other times densely pubescent, as in D. Embryopteris and D. pruriens.

In the male flowers the calyx segments are relatively small and accrescent, whereas in the female and hermaphrodite flowers they attain considerable dimensions and the segments project outwards.

In the Ceylon species the calyx segments are usually very distinct, varying in number from two to seven; the common number of segments is four or five. In some species, however, the calyx segments cannot be distinguished, as in D.

oocarpa ; in D. Toposia the calyx of the male flower is closed in the bud, and bursts irregularly into two or more segments when the flower opens. The calyx segments are most strongly marked in D. Embryopteris, D. Ebenum, D. Gardneri, &c., but in many of the species belonging to this class the conspicuousness of the calyx segments becomes reduced during the development of the fruit.

The calyces of the female and hermaphrodite flowers can be divided into several classes, the first comprising those which even after fruiting remain small, thin, and horizontal, as in D. pruriens, D. montana, D. sylvatica, D. attenuata, D. oocarpa, and others, the second class comprising those which, though they have undergone considerable enlargement during the formation of the fruit, remain relatively thin and horizontal, as in D. Moonii and D. hirsuta, the third those which increase considerably in size and form a shallow or deep cup in which the ripe fruit is lodged, as in D. Gardneri, D. oppositifolia, D. affinis, D. quæsita, D. insignis, and many others.

During the formation of the fruit the calyces of the third class show different courses of development. The most usual is to form a very large intersegmental pouch and pointed apices, together with a feeble reflex margin ; this is best seen in D. quæsita ; in other species, notably D. Ebenum, the apices become strongly pointed and horizontal and the margin strongly reflexed ; in D. insignis and D. crumenata the enlarged woody calyx becomes strongly four-sided in consequence of the dying back of the apices of the segments and the very reflex nature of their margins.

Many of the calyces, though highly pubescent in the flower stage, become glabrous in the fruiting stage. The hairs, with one exception, are long unicellular outgrowths from single cells. In D. Ebenum, however, the base of the shallow calyx cup is covered with unicellular and pedicellate hairs, the latter having very much the appearance of globular multicellular glands supported on pedicels of

varying length. I have not met with these multicellular glands on the calyx of any other species, though they occur abundantly over the carpellary wall of D. Embryopteris (pl. XIX., figs. 10–11).

The calyx usually persists on the ripe fruits, but in many of those which form deep cups the fruits seem to become detached and the calyx is left on the twig.

The general characters of the calyx segments and the ferrugineous hairs with which they are very often coloured are, according to Hallier,* of systematic importance and comparable to similar structures in the Pittosporaceæ.

The same botanist† also calls attention to the fact that in Scytopetalum the segments of the small calyx cannot be distinguished, and suggests an affinity with the Ebenaceæ. We have seen that in D. oocarpa particularly, and also to a less marked extent in D. Toposia, the calyx segments are often undistinguishable.

Corolla.—The segments are united and usually, though by no means always, isomerous with those of the calyx. The colour is yellow, white, or greenish. The tube and segments are often covered with silky or brown hairs, sometimes on the outside only, at other times on both sides. The margin of the segments in species like D. hirsuta is very hairy. The segments are usually equal, and according to Hiern‡ are contorted sinistrorsely in æstivation as regarded from inside, except D. oocarpa, in which the æstivation is variously imbricated. The corolla is occasionally very conspicuous, as in D. Embryopteris and D. Ebenum, but most usually is small and unattractive, as in D. Toposia and D. attenuata. The segments may be relatively long, as in D. pruriens, or very short as in D. Toposia.

For convenience we will distinguish two types of corolla. The first type comprises all those in which the corolla

* Hallier, *l.c.*, p. 33. † Hallier, *l.c.*, p. 36. ‡ Hiern, *l.c.*, p. 60.

is widely open, as in D. Embryopteris and the urceolate flowers of D. sylvatica, the second all those in which the corolla tube communicates with the exterior by a very small aperture. The majority of the species have the corolla of male and female flowers of this type, and in many of them the aperture is exceedingly narrow and appears to be closed until a late stage in the development of the flower. The smallest apertures are to be seen in D. attenuata, D. quæsita, and D. Toposia.

The smallness of the aperture renders it impossible for any but the smallest insects to enter them, and this, together with the inconspicuous nature of the flowers in general, may yet be found to be correlated with the evolution of sex in this genus.

The sympetalous corolla with imbricated æstivation reminds one of the Styraceæ, Sapotaceæ, and Ilicineæ*. It is also true that the corolla segments are often deeply partitioned, and that such bear a resemblance to polypetalous orders.

Hallier† lays stress upon the fact that the corolla segments are alternate with the five small, narrow and acuminate calyx segments in Pittosporaceæ and the Ebenales. This cannot be seriously regarded as of great importance, though one cannot but admit that the accessory whorls of, say, Pittosporum Timorense, *Bl.*, have a strong resemblance in form, colour, and texture to those of the male flowers of Diospyros species.

Staminal Whorl.—The staminal whorl is in the form of an epipetalous, hypogynous, or perigynous ring of stamens or staminodes in the male and female flowers respectively; it is present in the flowers of every Ceylon species of Diospyros, and as an essential whorl is characteristic of the genus throughout the world.

The components of the staminal whorl have a much more constant orientation and number in the female than in the

* Hiern, *l.c.*, p. 62. † Hallier, *l.c.*, p. 33.

male flowers, and it is not always easy to correlate the members in the different sexes of the same species. The relation between the male and female staminal whorl is sometimes very simple, as in D. hirsuta, where there are five staminal organs in each male and female flower disposed so as to alternate with the corolla lobes. In the majority of Ceylon species, however, the staminodes of the female flowers are much fewer than the stamens in the male, a typical instance of which is seen in D. sylvatica, the male flowers of which have from thirteen to twenty stamens and the female flowers only four staminodes. The staminal whorl is of great interest, and since we have for the first time a complete collection of male and female flowers of every Ceylon species of Diospyros, a detailed account is here given.

The Staminal Whorl of the Male Flowers.—In every species of Ceylon Diospyros the male flower possesses many perfect stamens. These occur either as an epipetalous ring having a definite or indefinite orientation to the accessory whorls, or as a central hypogynous group; sometimes both conditions are observed in the same flower.

The filament is white or yellow and varies in length from 0·25 to 0·35 mm.; it is perfectly glabrous in some species, *e.g.*, D. acuta and D. affinis, and densely pubescent in others, *e.g.*, D. oppositifolia and D. Embryopteris.

The anther is usually brown in colour and when mature measures from 0·2 to 0·3 mm. in length; sometimes it is strongly apiculate in consequence of the presence of a large number of unicellular hairs which seem to have a duty to perform in the dissemination of pollen; at other times it is perfectly glabrous. Each anther is lanceolate-linear in shape, erect, two-celled, and dehisces by two longitudinal slits.

It is characteristic of the stamens in the majority of the male flowers to exhibit fusion; sometimes the filaments are united throughout their lengths, at other times only for a short distance. In the case of D. hirsuta there are five separate stamens alternating with the corolla lobes; in D.

Gardneri the numerous stamens are arranged in pairs, the inner stamen of each pair having a shorter filament united throughout to the filament of the outer stamen ; in D. Ebenum the stamens are united to form groups of three or four, the filament of the individuals of each group being united in the basal part, and therefore attached to the corolla as a single column ; in D. pruriens the fusion has gone to such an extent that a single column formed by the fusion of the filaments of twelve or more stamens exists, similar to what occurs in the Malvaceæ. The importance of these stages in the fusion of the stamens when numerous will be discussed later.

We will now describe the types of male staminal whorls met with in Ceylon species.

(*a*) The simplest type is that in which the stamens are few in number and disposed so as to be in definite orientation to the members of other whorls. This is seen in D. hirsuta and D. Moonii, where each male flower possesses five epipetalous stamens alternating with the corolla lobes.

(*b*) A slightly more complex type is where the number of stamens is in excess of the members of any other whorl and their orientation becomes variable. In D. oppositifolia there are eight stamens usually arranged as four pairs alternating with the four corolla lobes. The members of each pair are separate from one another throughout their length, and a variation occurs when the members of one or more pairs become relatively widely separated. In D. acuta there may be only five stamens alternating with the corolla lobes, or there may be seven or nine, in which case some of the number may be single and the remainder as pairs with fused filaments. In D. Gardneri the complexity is increased, since there may be from six to eight pairs of stamens definitely orientated to the corolla lobes, or a monadelphous ring of stamens may occur.

(*c*) The next type is where the number of stamens is very large and no orientation to other whorls can be distinguished. In D. Embryopteris the male flower may possess from

twenty to forty stamens arranged to form an epipetalous ring, a hypogynous group, or part epipetalous and the remainder hypogynous. The stamens are nearly equal in length and occasionally the filaments are fused at the base. In D. Toposia there are from eighteen to thirty-four stamens of unequal length usually forming a hypogynous central group. In D. Melanoxylon there may be from ten to twenty stamens usually paired and forming a hypogynous group terminating the receptacle. In one flower there were thirteen stamens arranged as five pairs, each having the inner stamen shorter than the outer one, one pair with individuals of equal length, and one long stamen separate from all others.

In another flower of the same species there were fifteen stamens arranged in two whorls, the outer with eight and the inner with seven members. In the outer whorl four were arranged as two adjacent pairs and the remaining four as separate successive stamens; the inner whorl consisted of two united at the filament and the remaining seven separate.

In all those cases where there is an outer and inner whorl the stamens of the inner whorl are always shorter than those of the outer, the difference in length being usually in the filament.

In the male flowers of D. Ebenum similar variations may be noted in the number and position of the stamens. The number varies from about sixteen to thirty-five, but in the majority of flowers examined they are arranged as eight groups, each group having two, three, or four anthers supported on filaments of varying length. These eight groups are usually epipetalous and arranged opposite to and alternate with the corolla lobes. If we take one group of four stamens, we find it to be composed of a basal pedicel 0·1 cm. long, and bearing at this level two lateral, fertile, sessile anthers; above this level a third anther disposed introrsely is given off, and on the continued filament above this level is the fourth anther, always the outermost and disposed introrsely. The total length of such a stamina

group is often over 5 mm. In one flower there were six groups each with four stamens ; and two groups each with two.

(*d*) In the last class we may include all those species the male flowers of which have numerous stamens united to form a central hypogynous column. This is typified in the staminal whorl of D. pruriens. According to Hiern* the stamens are thirteen or fourteen in number and always connate at the base and surround the hairy rudiment of the ovary. In examining fresh material in the forest the stamens of the male flowers were seen to form a central column, the filaments being completely united at the base. Towards the base seven separate stamens could be distinguished, each of which consisted of a short white curved filament and an anther disposed introrsely ; projecting above this outer ring is a yellowish white stout pedicel 3 mm. in length which terminates in five sessile introrse anthers, the pedicel presumably being composed of the united filaments belonging to the five stamens. The total length of this staminal system is 6 mm., and its members exhibit no great variations except in that one may be epipetalous. I have not been able to determine the same condition in the scanty herbarium material of D. pruriens.

It is obvious that in the staminal whorl of the male flowers there are very many characters which can be used in the study of the ontogeny and phylogeny of the genus Diospyros. In descriptions of many species the staminal whorl is not even mentioned, and a somewhat detailed description will therefore be given in this work.

In the regular orientation of a fixed number of stamens, as in D. acuta and D. oppositifolia, and in the paired arrangement of the stamens, as in D. Gardneri, there is a strong resemblance to the Sapotaceæ. Further, the occurrence of a fixed number of stamens and staminodes in the male and female flowers of species which can assume the hermaph-

* Hiern, *l.c.*, p. 43.

rodite and monœcious condition is suggestive of the genus Sideroxylon and others, where stamens and staminodes are known to occur in the same flower.

In the indefinite groups of stamens a resemblance to Styraceæ and many polypetalous orders, particularly with the Anonaceæ and Ternstrœmiaceæ is suggested.

On the other hand, the central column of united stamens (D. pruriens) and the extensive union of filaments in other species is suggestive of like features in the Malvaceæ and Geraniaceæ, and Hallier asserts,* though without giving good reasons, that the Ebenales have their origin closely connected with the Malvales, Geraniales, and Theales. That botanist also states† that the genus Scytopetalum, in that it shows numerous stamens inserted on the base of the corolla and on the flat axis of the flower, and in the arrangement of the anther when in bud, possesses characters which bring it near to the Ebenales.

It is important to realize that in the staminal whorl of the male flowers of only twenty species there are types of character which are only met with in natural orders now widely separated.

The Staminal Whorl of the Female Flowers.—The members of this whorl in the female flowers are but slightly known. They occur nearly always as an epipetalous series, and only rarely, as in occasional flowers of D. Toposia and others, in the hypogynous position.

The filament is very similar in colour, form, and dimensions to that in the male flower.

The anther is usually hastate in form, and is regarded universally as barren. It consists, as seen in transverse section, of regularly disposed parenchyma with a small strand of vascular tissue in the centre.

The filament is usually glabrous, but the anther in some species, notably D. hirsuta and D. Thwaitesii, is strongly apiculate in consequence of the presence of numerous long

* Hallier, *l.c.*, p. 85.

† Hallier, *l.c.*, p. 36.

unicellular hairs, as in the anthers of perfect stamens from the male flowers.

In point of number the staminodes are, compared to the stamens of the male, very few. Usually the number is the same as that of the corolla or calyx segments. The series alternate with the corolla lobes when the number of members of both these whorls is the same, as in the four staminodes of D. oppositifolia, D. sylvatica, and D. Embryopteris, and the five staminodes in D. acuta, D. Thwaitesii, and D. hirsuta.

When the staminodes are an exact multiple of the corolla segments they are disposed opposite to and alternate with them, as in the twelve staminodes of D. Melanoxylon, and the eight staminodes of D. Gardneri and D. Ebenum. When the number of the calyx and corolla segments varies the number of staminodes usually shows exactly the same numerical variations, as in D. insignis, D. attenuata, and D. affinis, where the flowers may have their parts in fours and fives, and even threes.

In D. Toposia there seems to be an erratic number of twelve to sixteen staminodes arranged either epipetalous or hypogynous.

Pistil.—The pistil is represented in the male flowers of polygamous trees by a central, hairy, apiculate, or flattened disc; in female flowers it is sub-globose or ovoid in shape, green, and glabrous or hairy; in D. Embryopteris and D. pruriens the carpellary wall is covered with a dense layer of multi- and uni-cellular hairs which persist in the fruit; the stigmas are green and sessile; the ovary is four-, eight-, or ten-celled; the ovules are pendulous from the top of each cell of the ovary.

The relation of the Staminal Whorl in Male and Female Flowers.—A staminode is similar in form and size to a stamen, and differs from it mainly in that its anther is barren. It may be possible to derive one from the other, and with this object in view I have drawn up a table showing the number and orientation of the members of the staminal whorls for each species.

Group A.—Species which may be Dicœcious, Monœcious, and Polygamous.

Abbreviations: c.s. = corolla segments; epi. = epipetalous; alt. = alternate; opp. = opposite; hyp. = hypogynous.

	Stamens of Male Flower.		Staminodes of Female Flower.	
	No.	Arrangement.	No.	Arrangement.
D. hirsuta	5	epi.; alt. with c.s.	5	epi.; alt. with c.s.
D. Thwaitesii	10 or variable	epi.; paired and alt. with c.s. as 5 series; or irregular	5	do.
D. Ebenum	16, 20, 32	epi.; connate groups to form series of 8 alt. and opp. to c.s.	8	epi.; alt. and opp. c.s.

Remarks.—Exact equality in number and position in one species; in each of the others the groups of stamens are equal to the separate staminodes in number and position.

Group B.—Species which are Monœcious only.

	Stamens of Male Flower.		Staminodes of Female Flower.	
	No.	Arrangement.	No.	Arrangement.
D. acuta	5, 7, 9	epi.; separate or paired	5	epi.; alt. with c.s.
D. oppositifolia	8	epi.; four pairs usually alt. with c.s., but variable	4 (rarely 8)	do.

Remarks.—Stamens exact multiple of staminodes, exact equality or slightly variable, not widely different.

Group C.—Species which may be Dicœcious or Polygamous.

	Stamens of Male Flower. No.	Arrangement.	Staminodes of Female Flower. No.	Arrangement.
D. Gardneri	12–16	separate or paired in a series of 8	8	epi.; alt. and opp. with c.s.
D. sylvatica	13–22	epi.; grouped to form series of 8 or 10	4	epi.; alt. and opp. with c.s.
D. Embryopteris	24, 30, 40, 64	epi.; grouped irregularly	4	epi.; alt. with c.s.
D. affinis	6–16	single or grouped ...	6–8	epi.
D. insignis	14–20	epi.; single or grouped	4–5	do.

Remarks.—Irregular. In some the stamens and staminodes are in equal numbered series, or former in multiple series of latter, or there may be an inconstant number and orientation of stamens and even staminodes.

Group D.—Species which are Dioecious.

	Stamens of Male Flower. No.	Arrangement.	Staminodes of Female Flower. No.	Arrangement.
D. attenuata	4–6	epi.	4–5	epi.; alt. with c.s.
D. Melanoxylon	8, 10, 16, 20	single, or connate to form series of 8	8, 10, or 12	epi. or hyp.
D. pruriens	12–14	hyp.	5	—
D. quæsita	16 or x	hyp.	5 or x	epi.; alt. with c.s.
D. crumenata	8–14	hyp. or epi.	8	epi.; alt. and opp. c.s.
D. Toposia	18–33	—	12–16	epi.
D. ovalifolia	13–20	single or grouped	4 or (1–7)	—
D. montana	16 or x	single or united to form a series of 8	4–12	—
D. oocarpa	9–14	epi. or hyp.	3	epi.
D. Moonii	5	—	5	—

Remarks.—Very irregular; more variable than any of the foregoing groups. In two or three species only is the number of staminodes constant. This group contains half the Ceylon species.

The most perfect agreement in number and position of members of the staminal whorl is in Group A, where the sex relationship is the most complicated, and there is least agreement in Group D, where the sex is diœcious only.

It would appear that the greater the departure from the diœcious condition, the more nearly do the male and female staminal whorls agree ; the diœcious condition is further from the hermaphrodite state than any of the Groups A, B, and C.

From the above table we can deduce certain generalizations which will probably throw some light on the exact ontogenetic relationships of the organs considered. The remarks on this subject are made purely in relation to the flowers of the Ceylon species examined, and it is possible that examination of other species in other countries may lead to quite contrary or to similar conclusions.

Since we have classified certain species into groups according to their sex relationships, it will be convenient to adhere to the above plan in describing the staminal whorl in each sex group.

We will commence with Group A, in which there are species having the monœcious, diœcious, and polygamous condition. The complicated sex relationships here existing show that it is possible to have on the same tree every stage between a perfect hermaphrodite flower and a staminate or pistillate flower. The hermaphrodite flower in giving rise to a staminate or pistillate flower must undergo abortion of the gynœcium and anthers respectively. In every pistillate flower an epipetalous ring of staminodes exists, and in every staminate flower a rudimentary pistil remains. Can it be that the unisexual flowers have been derived from the hermaphrodite, or *vice versâ* ? In one species of this group, viz., D. hirsuta, we see that in number, form, and orientation the stamens of each male flower exactly agree with the staminodes of the female flower. Such equality in the staminal whorl does not occur in any other Ceylon species of Diospyros. The complex sexual relationships may have

been derived from a hermaphrodite type by sterilization without reduction in number of parts.

If the unisexual type was the primitive, the flowers are now perhaps progressing towards the production of an uniform hermaphrodite type. When one considers how definitely monœcious or diœcious many other species are, and that sterilization of sporogenous tissue is frequently met with in the ontogeny and phylogeny of the higher plants, it seems more reasonable to regard the more specialized condition of unisexuality as the latest phase in development, and, in view of other facts, to believe that the hermaphrodite condition is the more primitive in this genus. The female inflorescences in many species appear to have undergone much abortion; this is probably true of the parts of the flower also. It is not meant to imply that the species showing this condition are necessarily members of the most primitive section of Diospyros. The statement is made purely in relation to the evolution of sex in Diospyros, a development which may or may not be correlated with that of the vegetative organs.

It would therefore seem an easy task to derive the present mixed sexual condition in D. hirsuta from a primitive hermaphrodite flower. In the production of female from hermaphrodite flowers the anthers, though persisting, become barren. It seems more reasonable to regard a staminode as being a stage in the abortion of a stamen, rather than one in the development of a stamen towards fertility.

If, however, we consider another species showing the same variation in sex, viz., D. Thwaitesii, the evolution from the hermaphrodite flower is more complicated. In this species the staminodes are, as in the female flowers of D. hirsuta, five in number and arranged on the corolla so as to alternate with their lobes. In the male flowers, however, the number of stamens always exceeds that of the staminodes of the female flower, there being usually ten, and in one case twelve fertile stamens present. It is interesting to note that when there are ten stamens present these are arranged

in pairs, each pair alternating with the corolla segments and being attached to the corolla as one or two filaments.

When there are less than ten stamens some are arranged in pairs and others singly, but always as a series of five alternating with the corolla lobes. It would thus appear that if we have to maintain the importance of abortion we must have the primitive hermaphrodite flower with numerous stamens arranged in pairs or otherwise. It would by no means necessitate a complex series of changes to derive the five-seried staminal whorl of the female flower from that of the male, the barrenness in the anthers of the staminodes being followed by a reduction of each pair to a single member ; the inner stamen is always small.

Now, let us take the case of D. Ebenum, the flowers of which may be polygamous, diœcious, or monœcious. We have seen that though the male inflorescence and female flowers usually occur on separate trees, examples have been found where a true female flower replaced a member of a male inflorescence. The staminal whorl of the female flowers is constant in number, form, and orientation. There are always eight epipetalous staminodes alternating with and opposite to the corolla segments. In the male flowers a variable number of stamens occur, but coalescence of the filament occurs so frequently that the resultant number of groups is relatively small. In one case there were sixteen stamens, either single or in groups of two and three, while in another flower thirty-two stamens occurred showing various degrees of coalescence, but in each of these the resultant groups were eight in number and arranged so as to alternate with the corolla segments. Hiern* mentions the occurrence of as many as thirty-two stamens on eight filaments.

This being the case, we have another example in which the origin of unisexuality can be easily understood, since the staminal whorl always forms a series of eight. The monœcious state would represent the intermediate between a

* Hiern, *l.c.*, p. 208.

hermaphrodite and dicœcious condition. It is important to realize that here we have a species which is mainly dicœcious, but where the staminal whorls of male and female flowers agree in number, if we regard a group in the male as equivalent to one member in the female.

In the species belonging to this group the production of a pistillate flower is attained by sterilization of the male sporogenous tissue (the anther still persisting) followed by a reduction of pairs or groups to single members. The original hermaphrodite flower still occurs on polygamous trees and always possesses stamens of different sizes, the innermost being the smallest.

The accessory whorls of the male and female flowers of this and in fact of all the other species are widely different, but since the differences are those of size and form they may be neglected in considering the evolution of unisexuality in Diospyros.

If we now consider the species in Group B, D. acuta and D. oppositifolia, which are only known in the monœcious condition, we find that they can be easily arranged in a series to show the similarity in the whorls of male and female flowers. In D. oppositifolia the female flowers usually possess four epipetalous staminodes alternating with the corolla segments. In one female flower there were eight separate staminodes arranged so as to be alternate with and opposite to the corolla segments, each being typical in form and possessing a completely barren anther. In the male flowers of this species there are always eight epipetalous stamens usually paired, with the inner member the shorter of the two, but each stamen is attached to the corolla by its own filaments. The pairs invariably alternate with the corolla segments, though this orientation is liable to variation. The variation in the male staminal whorl is where the members of one or more pairs are not exactly opposite one another, a deviation from the normal which tends to simulate the occasional eight separate staminodes of the female flower. It is therefore very easy to correlate the staminal whorl of the male and female flowers of D. oppositifolia with

one another and consequently to derive both from a common sex type.

In D. acuta the staminal whorl of the female flowers consists of five epipetalous members alternating with the corolla segments. The male flowers have, according to Hiern,* from four to five stamens, corresponding to the number of accessory whorl segments, and presumably alternating with those of the corolla. It would thus be quite as easy to derive each sex from a common hermaphrodite flower as with D. oppositifolia.

The male flowers of D. acuta, though usually possessing five epipetalous stamens alternating with the corolla segments, often have seven to nine epipetalous stamens, single or united in pairs and of very unequal length. If the sexes in this species have originated from a common hermaphrodite flower then the original type may have possessed numerous stamens, which in the evolution of the female flower have undergone abortion at a quicker rate than in the male. The very small stamens which occur when the total number is more than five per male flower are perhaps in their last stages, and may represent a phase passed through in the ontogeny of the female staminal whorl from the hermaphrodite type.

We have therefore seen that in considering flowers of species which are (*a*) diœcious, monœcious, and polygamous, and (*b*) monœcious only, the staminal whorls of the male and female flowers are at the present time in general agreement in number, form, and orientation, and the sexes in these species can be derived from a hermaphrodite type of flower having a relatively large number of stamens. In the remaining groups, which are either diœcious only or diœcious and polygamous, the relationships are more complicated.

If we take the Group C, which shows the diœcious and polygamous condition, we find a great variation in the staminal whorl of the different species. The simplest arrangement is perhaps in D. Gardneri. Each female flower

* Hiern, *l.c.*, p. 183.

of this species possesses eight epipetalous staminodes arranged opposite to and alternate with the corolla segments. In the male flowers the number of stamens is large, there being from twelve to sixteen in each flower. When sixteen in number they are usually as eight pairs, the members of each pair being united at the base of the filaments and having the inner stamen smaller than the outer. When only twelve stamens occur these are often arranged as four pairs and four single.

In each case, whether there are sixteen or twelve, they always form an epipetalous series of eight, each pair being either opposite to or alternate with the corolla segments. The inner stamens are always small, and by their abortion a series of eight would result. This condition, which prevails in many flowers, may represent the transition of the staminal whorl of the female flowers, in which case it would be easy to derive both sexes from a common hermaphrodite flower having a large number of stamens. Such a hermaphrodite flower does exist at the present time in those trees showing the polygamous condition. In the hermaphrodite flowers there may be as many as sixteen perfect stamens arranged as a monadelphous hypogynous ring, or arranged part epipetalous at the base of the corolla and part hypogynous. The parts of the pistil and also the seeds of polygamous flowers resemble those of true female flowers. If we assume that the primitive type of flower was hermaphrodite, then a very definite abortion in either of two directions must have taken place, some of the trees having, so to speak, allowed the pistil of every flower to entirely abort, while others reduced the number of stamens in each male flower and eventually suffered sterilization of the male sporogenous tissue. Other trees have undergone occasional sterilization of the pistil, resulting in the polygamous state so prevalent at the present time.

The next most simple case in this group is seen in D. sylvatica. In this species the female flower possesses four epipetalous staminodes disposed so as to alternate with the

corolla segments. The male flowers possess a very large number of stamens, there being rarely less than sixteen and very often over twenty-two in each flower. The stamens are nearly all in pairs, each having the inner stamen shorter than the outer and with the filaments of each pair united throughout the greater part of their length; sometimes three anthers are supported on the same united filament.

In some flowers I have found eight pairs arranged opposite to and alternate with the corolla segments, but in by far the greater number of flowers the pairs of anthers are in excess of twice the corolla segments. In one flower possessing ten pairs of stamens there was always a pair alternating with the corolla segments; the remaining six pairs were arranged as two pairs on each of two corolla segments and a separate pair on each of the other two corolla segments.

If we allow that in the production of the female flower sterilization and reduction in number has occurred, we can easily understand the derivation of the four-seried flower from one having staminal members alternate with and opposite to each corolla segment, as is now seen in male flowers possessing eight groups of stamens. Hence the evolution from the hermaphrodite type is rendered possible.

In D. Embryopteris we have a difficult case, since there is practically nothing to connect the four staminodes of each female whorl with the male ring of thirty or forty stamens. The indefinite stamens in each male flower are sometimes separate, at other times united in pairs, and may be epipetalous or hypogynous. In D. affinis the conditions are almost the same as in D. Embryopteris, since the male staminal whorl consists of sixteen or more members apparently disposed without any definite relation to the accessory whorls. The stamens occur in pairs or are single, and form an epipetalous ring or hypogynous group. Each female flower possesses from six to eight staminodes arranged on the corolla opposite to and alternate with its segments.

Hiern* gives the number of stamens in each male flower of D. affinis as six to sixteen, usually about nine, and some or all in pairs. It is thus clear that in D. Embryopteris and D. affinis the staminal whorls are widely different, and until some intermediate links have been observed the evolution of the sex must remain particularly problematical.

Turning to Group D. (diœcious only), in D. attenuata the members of the staminal whorl are few in number. Each female flower possesses four to five epipetalous staminodes which alternate with the corolla segments; whereas each male flower has a variable number, four to six, of epipetalous stamens, but their orientation is not constant. It is somewhat remarkable if no fixed orientation exists when the members of the male staminal whorl are so few in number. The male flowers are so very small, often less than 1 mm. diameter, that to determine the exact orientation is a difficult undertaking.

The flowers of D. Melanoxylon show a variability in the staminal whorl in both sexes. The female flower possesses accessory whorls in parts of five and six. In those I have examined there has usually been twelve staminodes, either hypogynous or epipetalous, but in positions opposite to and alternate with the corolla lobes. Hiern† states that the staminodes may be eight or ten in number. Each male flower possesses from eight to twelve and even sixteen stamens. When sixteen in number they are always in eight pairs, though according to Hiern‡ it is rare that one finds eight single stamens only. In one flower there were twenty stamens arranged as a hypogynous group. The variability in number of stamens and staminodes and their occurrence mainly in the hypogynous position renders it inadvisable to make any definite statement as to the derivation of one from another or from a common parent.

In the flowers of D. pruriens and D. quæsita the staminodes of each female flower are equal in number to and alternate with the corolla segments, whereas the male flowers possess a more or less hypogynous group of twelve or twenty

* Hiern, *l.c.*, p. 169. ‡ Hiern, *l.c.*, p. 159. † Hiern, *l.c.*, p. 160.

stamens. In D. crumenata the staminodes of each female flower are in number an exact multiple of the corolla segments and are disposed opposite to and alternating with them, whereas the male flower resembles D. quæsita and D. pruriens in the indefinite hypogynous character of the stamens.

There is one species—D. Toposia—in this group which shows an unstable staminal whorl in the female flowers, the number usually being greatly in excess of the members of other whorls, and presents no fixed orientation to them. Each female flower of D. Toposia may possess from twelve to sixteen staminodes, which form an epipetalous or partly hypogynous ring; the stamens of each male flower may be from ten to over thirty in number, of unequal length, forming a hypogynous group terminating the receptacle.

VII.—AFFINITY.

The phylogeny of the Ebenales has formed the subject of much discussion.

Hiern (p. 62) states that the Ebenaceæ shows the closest affinity to the Olacineæ, Styraceæ, Anonaceæ, Ternstrœmiaceæ, Sapotaceæ, and Ilicineæ, but also draws attention to the points of difference between these natural orders and the Ebenaceæ. He also states (p. 63) that other orders including Tiliaceæ, Magnoliaceæ, and the Euphorbiaceæ show affinity in a less degree to the Ebenaceæ.

Miers compares them with the Anonaceæ and suggests their grouping among the polypetalous section; Choisy points out their proximity to the Ternstrœmiaceæ.

Parmentier, in his monograph on the histology and morphology of the Ebenaceæ, does not commit himself to statements as to the phylogeny of the natural order.

Hallier, on the other hand, points out that there are many features in which the Ebenales resemble many other natural orders, and in this respect goes into much more detail than Hiern.

Under the circumstances I cannot do better than point out the main facts as supplemented in the present paper, and

leave the question of affinity until detailed information for the remaining species is at hand.

The fossil species described by Unger, Ettingshausen, Massalongo, and others, the present distribution through tropical regions of the eastern and western hemispheres, in sub-tropical South Africa and Madagascar, and the occurrence in temperate regions are suggestive of great age. The fossil forms, the conspicuous differences between existing species, especially between those in Ceylon, together with the probable early extinction by natural causes of many Ceylon species, suggests the likelihood that the Ebenaceæ had in the past a much wider distribution and a larger number of species than at the present day.

The great point of interest in connection with the Ceylon species is the fact that a good artificial key for working out the species can be constructed on separate characters, *e.g.*, the leaf, flower, or seedlings. The differences in leaf characters are very marked. It is impossible to confuse the tough large leaf of D. Moonii or D. acuta with the thin leaves of D. Thwaitesii and D. montana, or with the thin hairy leaves of D. pruriens. The pellucid character of the veins in leaves of D. Ebenum, D. Embryopteris, D. Toposia, and D. Gardneri separates these species from one another and from all other species, and questions of size and form provide sufficient differences for separating the remaining species. Then again we have seen that it is very convenient to group the species according to their sex characters.*

A good artificial key for the Ceylon representatives can be made on the characters of the seedlings alone, the classification being based on the number of traces per cotyledon, abortion or persistence of the median cotyledonary traces, characters of cotyledons, epicotyledonary leaves, and hypocotyl.

The secondary xylem is the most constant structure throughout the genus, and in the respective species shows differences only in percentage number of the elements.

* Sex in Diospyros, Brit. Assoc., Belfast, 1902.

[*To be continued in next number.*]

Ecological Notes on Turnera ulmifolia, *L.*, var. elegans, *Urban.*

BY

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Introductory—Descriptive—Heterostylism—Self-sterility. Insect Visitors—Seed Distribution by Ants.

TURNERA ulmifolia, *L.*, is a comprehensive species, including a large number of so-called varieties. In Ceylon two such forms exist—the varieties T. angustifolia and T. elegans. The latter is perhaps better known as a separate species under the name T. trioniflora, *Sims*. With the exception of these two forms, which occur scattered in several places on the coasts of the Indo-Malayan region, the family Turneraceæ is confined to America and Africa. Urban regards the presence of these two varieties in Asia as being accounted for by their escape from gardens; and there can be little doubt that this is the true explanation in the case of Ceylon.

The species has existed in Ceylon for a long time in a wild condition. Trimen* describes it as a common weed of road-sides and waste ground about Colombo and other places in the low-country, but makes no mention of the date of its introduction. The form commonly occurring wild is T. angustifolia, as I learn from Mr. Willis. T. trioniflora, *Sims* (elegans, *Urban*), is mentioned in Trimen's List of Plants growing in the Royal Botanic Gardens as having been introduced before 1845; it grows luxuriantly at Peradeniya.

* "Flora of Ceylon," vol. II., p. 239.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. II., Pt. I., January, 1904.]

Urban has made important observations upon the floral mechanisms of the Turneraceæ.* I have not had access to Urban's original monograph, and have relied principally upon the fairly full abstracts given in Just's Bot. Jahresb. for 1883. But for a complete transcription of the chapter in which this observer describes the result of his examination of living plants I am indebted to Miss M. A. Graves of Cambridge, to whom I desire to express here my very hearty thanks for her assistance.

Gilg† thus summarizes Urban's observations upon the method of pollination in the order :—The flowers of very many Turneraceæ open their petals, which are often brightly coloured, in the morning or sometimes not until midday; in the evening they become closed again and withered. During the day honey is very abundantly secreted by the flowers, and many insects are thus attracted. If, however, cross-pollination has not taken place by their aid, self-pollination occurs with great regularity, for when the petals close they fall together at the apex, and the anthers and stigmas are thus brought into close contact.

Urban‡ described forty-eight species of Turneraceæ as being undoubtedly, eight as probably dimorphic, and six as incompletely dimorphic. One species§ was in six forms homostyled, in six forms heterostyled. The total number of species examined was eighty-three.

The variety of T. ulmifolia known as T. angustifolia is stated to be homostyled, and is described at length. This description, which was taken from living plants, I shall here briefly summarize before passing on to my own

* Monograph of Turneraceæ, Berl. Bot. Jahrb., vol. II.
† Engler and Prantl. Nat. Pflanzenf., III., 6 a, p. 64.
‡ *Loc. cit.*

§ Since these notes were written I learn that this actually applies to the species T. ulmifolia. (The reviewer in Bot. Jahresb. gives, as far as I can discover, no hint of this being the case.) It appears therefore that the heterostylism of certain varieties of T. ulmifolia has already been described. but only from herbarium specimens. This being so, it appears unnecessary to alter the form of my remarks, whilst noting in this place the earlier record of dimorphism.

observations upon the variety T. elegans. Living specimens of T. angustifolia taken from the garden at Peradeniya entirely bear out Urban's statements.

According to Urban, then, T. ulmifolia is homostyled.* T. angustifolia is a narrow-leafed form of it. In the latter the peduncles are fused to bracts which bear glands near the base. The bracteoles are large and leafy and resemble an involucre of two leaves. The petals are golden yellow in colour, and when fully open lie almost in a plane ; their edges do not then overlap. The spread of the corolla is about 3·5 cm. The three styles stand up close together, and the brush-like stigmas spread out their branches into the form of a hemisphere. The filaments stand upright below, but above they spread outwards, so that the introrse anthers do not touch the stigmas. Honey tubes 4 mm. long are formed by fusion of the edges of the flattened base of the filaments with the receptacle. The openings of the tubes are protected from small insects by hairs on the bases of the petals.

In the case of failure of insect visitors, self-pollination is effected by withering of the corolla, which brings the anthers into contact with the stigmas. Good seed is produced by this method of pollination.

The only other form of Turnera examined by Urban in the living condition was the variety T. cuneiformis, which showed some marked deviations in its floral mechanism. In this variety the styles diverge above and bring the stigmas almost into the circle of anthers. The stigmatic rays are all upright ; their apices lie in an oval plane. All the anthers, except (usually) one, twist completely round during the opening of the bud, so that the pollen chambers open outwards. The exceptional, introrse, anther bends away from the stigmas like all the anthers of T. angustifolia, and this anther serves for self-pollination if the visits of insects fail.

* See previous note. I have evidently misunderstood Urban's words, which are as follows :—" Bei der homostylen Turnera ulmifolia (und zwar der schmalblatterigen Form, welche den Namen T. angustifolia hat)."

Descriptive.—Specimens of the form previously known here as T. trioniflora were sent to Kew this year and there determined to belong to the variety T. elegans of Urban. A good figure of this variety appeared in Curtis's Bot. Mag., vol. XXVI., No. 2,016, in which the long-styled form is accurately represented under the name Turnera trioniflora. The figure of T. angustifolia, vol. IV., No. 281, is also quite unmistakable.

The plants of T. elegans which I have examined are markedly dimorphic. The flowers are perigynous, and in both long- and short-styled forms the petals are inserted on the tubular receptacle nearly 2 mm. above the level of the top of the ovary. The stamens are inserted between the petals, but lower down just on a level with the insertion of the styles upon the ovary. At this point, that is to say, the edges of the band-like lower part of the filament become fused with the receptacle ; but the central part remains free, and a space is thus left which forms the honey tube or nectary. The opening of the nectary is thus outside the base of a stamen and between the bases of two petals. Its mouth is protected by fine hairs situated on the bases of the adjoining petals. The three free styles terminate in much branched brush-like stigmas.

The presence of two styles only was noted as a rather frequent abnormality. This condition appeared to be always due to a fusing together of two of the three normally free styles ; and in this way the semblance of a small fasciation was produced. The anomalous flowers seemed to be as frequently of one form as of the other, and made up nearly 1 per cent. of those which I was able to examine.

The anthers of the long-styled form and the stigmas of the short-styled lie relatively close above the opening of the nectary. The longer styles or stigmas stand higher up, but spread out so as to leave only a narrow space between themselves and the funnel-shaped corolla. All the anthers become completely extrorse by twisting during the later development of the bud.

T. elegans differs markedly from T. angustifolia in the following points :—(1) The plants are heterostyled, and, as will subsequently be seen, (2) self-sterile ; (3) the habit is more branched and spreading in the former plant ; (4) the branches are thinner and (5) more herbaceous ; (6) the leaves are oval and only half as long ; (7) the bracteoles are about 1 mm. wide, setaceous, and purple in colour ; (8) the calyx tube and honey tube are only half as long as those of T. angustifolia ; (9) the calyx is edged with purple ; (10) the corolla is of a pale cream colour, shading into yellow and with a dark purple spot at the base ; (11) the petals are nearly twice as wide as those of T. angustifolia and overlap when the corolla is fully expanded ; (12) all the anthers are extrorse ; (13) the fruits are more pointed at the apex, they are (14) more hairy, and (15) much smaller ; (16) the seeds number usually fewer than twelve, as against fifty or more in T. angustifolia, and they are (17) nearly twice as large.

In view of these differences, all of which appear practically constant, I would suggest the propriety of regarding this form as a distinct species from T. angustifolia (ulmifolia), and in this case a return might be made to the name T. trioniflora, *Sims*, 1820.

It is no doubt probable that Urban was induced to follow Linnæus in retaining T. elegans as a variety of T. ulmifolia by a study of intermediate "varieties," and indeed T. cuneiformis seems to show a transition in at least one respect, namely, the position of the anthers. Not having had the opportunity of examining other forms, I can only point out here the striking differences which exist between these so-called varieties.

In May and June of this year I began experiments in artificial pollination with T. elegans in the hope of being able to compare the offspring of legitimate and illegitimate pollination. Up to the present time, however, I have not succeeded in obtaining a single seed by the illegitimate method of fertilization. While engaged in this way my

attention was naturally attracted by the behaviour of bees and ants visiting the plants, and the results of my watching are embodied in the following notes. It appeared worth while also to record the facts of heterostylism and self-sterility. As might have been expected, my notes fully bear out Darwin's comprehensive work on other plants.

Heterostylism.—In the *long-styled* form the average length of the styles of twenty flowers was 12 mm. including the stigmas. The total length of the stigmas themselves was on the average 2·5 mm. The average length of the stamens from their point of first fusion with the receptacle to the extremity of the extrorse anther was 7·5 mm. In the *short-styled* form the average length of the styles from the same number of flowers was a little over 6 mm., the stigmas were 1·5 mm. in length, and their branches were finer and more numerous than in the long-styled form. The average length of the stamens was 10·8 mm. The average diameter of pollen grains from the long-styled flowers was 36 μ, from the short-styled 44 μ; *i.e.*, they are in the ratio of 9 to 11. The size of the unfertilized ovules was approximately the same in the two forms; their diameter was about ·4 mm.

All these measurements were made upon good-sized flowers from vigorous parts of the plant, and in these the variation from the sizes given was not great. Much smaller flowers occurred at the extremities of old flowering branches in both forms.

Contrary to the state of things described by Darwin* in the case of the cowslip (Primula veris), the long-styled form regularly produces a much greater quantity of seed than does the short-styled. Three well-grown bushes of each kind were examined in May. With free pollination practically every flower of the long-styled form produced a capsule. Two of the short-styled plants produced some 90 per cent. of capsules; the third, not 50 per cent. Moreover, the capsules produced by the long-styled plants were

* "Different Forms of Flowers," ed. II., 1880, p. 20.

obviously larger when ripe than those of the short-styled. As regards number of seeds : 139 capsules were taken at random from the three long-styled plants and 93 capsules from the short-styled. The former contained 1,298 good seeds, or an average of 9·4 per capsule ; the latter contained 481 seeds, being only 5·2 per capsule on the average.

From seed of the long-styled form legitimately pollinated by bees I raised eleven long-styled and ten short-styled plants, and from short-styled legitimately pollinated two long-styled and three short-styled plants, *i.e.*, in each case a nearly equal number of each form. These examined at the end of September showed an extraordinary difference in the production of capsules by the two forms. On the long-styled plants almost every flower had produced a fine large capsule; on plants of the short-styled form only a few miserable capsules could be found, and this was the case with plants grown from the seed of either form.

I give the actual figures for a plant of each form, the two plants being of very nearly the same size.

	L.		S.	
	Ov.	Ca.	Ov.	Ca.
1	9	9	12	1
2	8	8	9	—
3	8	8	8	1
4	9	8	9	3
5	6	6	4	—
6	6	6	9	2
7	6	6	7	1
8	6	5	6	—
9	4	3	9	2
10	5	5	5	—
11	4	4	7	1
12	5	5	4	—
13	3	3	4	—
14	—	—	2	—
15	—	—	2	—
Total	69	66	91	11

L. is the long-styled and S. the short-styled plant. Ov. denotes the total number of flowers which had fallen from each branch, leaving the ovary either shrivelled or swollen, and Ca. denotes the swollen ovaries. 1 is the main stem of the plant; 2, 3, &c., lateral branches counting from below upwards. It appears from the above that 95 per cent. of flowers of the long-styled form were in a condition to set seed, as compared with only 13 per cent. of the short-styled. Rain fell on twenty-seven days of September and on only seventeen in May; and although the rainfall for the two months was nearly equal (12·33 inches in May and 11·36 inches in September), yet the weather in September appeared distinctly less favourable for the flowers than that in May. And it is possible that this may partly account for the different result in the two months, for I have found the productiveness of other plants to vary greatly at Peradeniya according to the time of year at which the seeds were sown. Further, the plants examined in May were much older than those observed in September, which were only five months old.

Self-sterility.—Experiments in artificial pollination were begun with a view to comparing the offspring of legitimate and illegitimate fertilization. This object was not attained owing to the fact that the plants appear completely self-sterile, and that illegitimate pollination between separate plants was found to be equally ineffective. It has already been shown that the offspring of legitimate pollination consists of the two forms in about equal numbers, since if illegitimate pollination produces no seed the seed arising from insect pollination must be the result of legitimate fertilization. Brief details of the experiments which led to the conclusion that only legitimate pollination is effectual may be of interest.

The experiments were carried out in May and June. In every case the visits of insects were excluded by the use of parchment paper bags, which were wired on to the branches.

In the first place, thirteen flowering branches of the long-styled form and nine of the short-styled were completely

enclosed in large bags, which were not removed until some ten to twelve flowers had opened inside each. The flowers opened freely inside the bags and withered only a little later than those outside, as could easily be seen through the semi-transparent parchment paper. As a rule, one flower on each branch opened every morning, as is normally the case. Not a single capsule was formed, however, from any of these flowers, which numbered altogether over 200.

Next five flower buds of each form were opened, and the stamens removed and pollen applied in each case from a separate plant of the same form. No capsules were produced. As the manipulation appeared somewhat severe the stamens of the pollinated flowers were not removed in the next experiment. Sixteen flowers of the long-styled form were pollinated from separate plants of the same form, and fourteen short-styled flowers were similarly pollinated from separate short-styled plants. Here again not a single capsule was produced: altogether forty unsuccessful pollinations. As a control eight long-styled and seven short-styled flowers were pollinated legitimately, being otherwise treated in exactly the same way as the last set of flowers. Seven of the long-styled and three of the short-styled produced good capsules. It thus appears that the experimental conditions, especially the covering of the flowers, do not account for the entire failure of the illegitimately pollinated flowers to produce fruit. The numbers, although small, also further illustrate the greater fertility of the long-styled form when pollinated legitimately.

Insect Visitors.—The individual flowers last only a few hours. The flower buds complete their development rapidly during the night, but until 8 or 8.30 A.M. the corolla remains closely rolled up. Then, as soon as the sun begins to fall upon them, the corollas quickly expand. By 1 P.M. they are all completely withered if the sun has been bright during the interval. In dull weather the flowers never expand to quite their fullest extent.

During the morning, while the flowers were open, they were visited by bees in great numbers. Among these the two species Apis indica, *Fabr.*, and Melipona canifrons, *Smith*, constituted an overwhelming majority. The only other forms observed were a few examples of Halictus taprobane, and a single specimen of Allodape sp., a genus not previously recorded from Ceylon. The only other insects of any kind observed to actually visit the flowers were one specimen of an hemipterous insect, Riptortus linearis, and a solitary syrphid fly which was not captured.

On a dull morning three flowers of the short-styled form received in a quarter of an hour eight, seven, and seven visits respectively from Apis and Melipona. In full sunshine the visits were very much more frequent. The number of flowers open at one time on six plants covering an area of about four square yards amounted to over 300.

Apis appeared to be the most efficient worker. This bee often collected simultaneously honey and pollen from the long-styled form, whereas the smaller Melipona seemed unable to do so. In collecting honey from the short-styled form Apis usually, but not always, stood with its back to the stamens and stigmas; it invariably worked right round the flower, probing each of the five nectaries in turn. Pollen was collected from the short-styled form in a separate process, the bee alighting actually upon the anthers. Each of these processes was usually carried out by the same bee in a series of flowers of the same form. And, especially in the case of the short-styled form, the bee often visited a long series of flowers, discarding the other form and collecting pollen only from the long stamens. And this was the case when, as often happened, the two kinds of flowers grew side by side owing to the intermingling of the branches of separate plants. Honey, on the other hand, was often collected from either form indifferently. Melipona began its visits earlier than Apis, and was often to be seen crawling down into the flower whilst the corolla was still rolled up into a narrow tube just wide enough for entrance.

Both honey and pollen are produced in considerable abundance and appeared about equally attractive. The only other plants at Peradeniya which I have seen visited by bees with equal eagerness are Zea Mays—the male flowers—and Oreodoxa regia. The latter case was pointed out to me by Mr. Willis. It is noteworthy that all three are introduced plants.

*Seed Distribution by Ants.**—The seeds of Turnera elegans are 2 or 3 mm. in length and somewhat pear-shaped. The surface, although covered with an indented pattern, is very smooth and hard. Attached near the small end of the seed is a large shield-shaped aril which covers nearly half the surface. When the seeds are freshly ripe the aril is soft and fleshy, and under the microscope its cells were observed to contain much starch and oil. The fruit is a capsule, which when ripe opens by three apical teeth, which gradually widen into valves and allow the seeds to fall quietly out.

Certain species of ants, among others Phidole spathifera *Forel*, on coming across the seeds appeared almost invariably to pick them up and carry them away. I watched a member of this species carry a seed straight to the mouth of its nest, a distance of five yards. Watching the nest on another occasion, I saw more than thirty seeds carried in at a rate of quite one per minute. This was shortly after I had assisted by scattering numerous seeds under the plants. The seeds were always carried by the aril. But I also saw occasionally ripe seeds without the aril brought up out of the nest, carried away, and dropped at a little distance. These seeds were quite undamaged, but appeared dull on the surface as if they had been underground some time.

I placed a number of seeds close to the opening of the nest and these were usually carried into it at once by the finders. But there appeared to be some conflict of instincts, for

* *Cf.* Sernander, Den skandinaviska Vegetationens spridningsbiologi, Upsala, 1901.

occasionally seeds were carried away from the nest One of these was dropped about three feet away. A few minutes later it was picked up by another ant of the same family and carried into the nest. Another seed was carried away for three or four feet and then back and into the nest without having been dropped. Occasionally also seeds found at a distance from the nest were carried a little way and then dropped. Sometimes an ant coming from the nest would examine one of the seeds I had placed close to the opening and then hurry away without picking it up. But the great majority in all cases were safely carried into the nest.

The most frequent species of ant upon the plant itself was Camponotus mitis, *Smith*. This form seemed to be chiefly attracted by the extra-floral nectaries upon the bases of the leaves, and did not appear to take so much interest in the seeds, although occasionally carrying them away. One or two members of this species were usually to be found upon every branch of the plants. I was not able to discover whether they were "of use" in keeping off invaders. Other insects were certainly very rarely found upon the branches. On the other hand, Camponotus did not appear at all pugnacious when disturbed.

That the aril is the attractive part of the seed was well shown by the ravages caused by another ant—apparently an undescribed species of Sima—upon some seeds which I had kept in a paper bag in the laboratory. This species was too small to carry off the seeds, and accordingly I found the arils eaten into and reduced to powder and a great part carried away, the seeds themselves being uninjured. The arils of the ripest seeds were most eaten. Another small ant, whose name was not ascertained, carried off upwards of 200 seeds from a table in the laboratory during the interval of two hours at midday when I had left them unprotected.

It appears fairly certain from the above observations that a principal mode of distribution for the seeds of this plant is by the aid of harvesting ants. Ants carry away the seeds and sometimes drop them, and in this case they may easily

roll into crevices and so escape further notice on the part of the ants. Moreover, it appears that the seeds carried into the nest are not harmed ; but the aril only is devoured, whilst in some cases certainly the seed, minus the aril, is actually cast out of the nest.

The experiment was made of separating the seeds from the arils and putting both in the way of the ants (Phidole). Both seeds and arils were in this case carried into the nest, though the arils appeared to be somewhat the more attractive. This, however, may have been simply because they were more convenient to hold. It may seem strange at first sight that the seeds without arils should be carried into the nest, if the latter only are used as food. Yet it would argue a high degree of reason in the ants if they were to discriminate between the two, since doubtless traces of whatever was attractive in the aril—whether " taste " or " smell "—would linger about the seed.

In conclusion, I wish to express my thanks to Mr. E. E. Green, who very kindly determined the names of all the insects mentioned in the preceding pages. Also to the Director of the Royal Botanic Gardens, Kew, to whom I am indebted for the name of the variety of Turnera ulmifolia which is the subject of these notes.

December 3, 1903.

REVIEWS.*

The Origin of Species by Mutation.

[Die Mutations-theorie ; Hugo de Vries, vol. I., Leipzig, 1901.]

THIS book brings together the results of many years' labour devoted to subjects connected with the origin of species. The author brings forward a series of conclusions supplementary to Darwin's memorable works, and developed along a line which has diverged widely from that followed by the recent school of mathematical evolutionists. These experiments and the doctrines based upon them possess so unusual a degree of interest that it appears worth while to try to give a short account of them which will be intelligible to a Ceylon public. It is much to be hoped that before long an English translation will place the whole work within the reach of those who do not read the German language easily.

The second volume of this work, which has since appeared, deals mainly with experiments upon the crossing of various races of plants ; in the present article we are concerned only with the first volume.

Since Darwin established the importance of the struggle for existence, by reason of which weaker varieties die out and the stronger survive, the importance of a careful examination of the phenomena included by him under the head of variation has come to be recognized. In some writings upon this subject a confusion has arisen between the fact of the existence of varieties on the one hand and the process of variation to which they owe their origin on the other; in order to understand the problem of how species arise it is necessary to keep the two clearly distinct. As to the process by which varieties arise, two methods appear at first sight to be possible. One of these is by the gradual accumulation of individual differences, *i.e.*, such differences as occur normally among the several members of a family. This is known as the *continuous* method of origin of new forms, and takes place by the steady aggregation of differences occurring in the ordinary course of *normal variability*. Or, on the other hand, a new variety may appear *discontinuously*, at a single step ; the new form differing from its parent to a clearly recognizable extent, and showing no tendency in its offspring to "revert" to the parental type. An extreme case of this process is the appearance of "sports" and of the still more "abnormal" forms known as "monstrosities." De Vries applies the term *mutation* to this discontinuous method of origin of varieties or sub-species.

* Written for the Ceylon constituency of this journal, and dealing with advances in science of local interest.

In his account of the origin of species Darwin took varieties for granted ; he gave little or no account of the process of variation, but showed how by the survival of the fittest species may arise from varieties, no matter how slightly the latter differ from their congeners at any particular stage.

It was not until some time after the appearance of this theory that the distinction between continuous and discontinuous variation came to be clearly recognized. Wallace was the first to give it as his opinion that species arise only by the continuous method of development, refusing any assistance from sudden variations. And this view has remained for many years the prevailing one. Recently, however, several voices have been uplifted against it, and with increasing degrees of loudness. In 1889 Galton wrote as follows : "The theory of natural selection might dispense with a restriction for which it is difficult to see either the need or the justification, namely, that the course of evolution always proceeds by steps that are severally minute, and that become effective only through accumulation." And a few years later Bateson, in his "Materials for the Study of Variation," summed up his own conclusion in the following words: "The evidence of variation suggests, in brief, that the discontinuity of species results from the discontinuity of variation." In the present work De Vries goes still further, for he brings forward weighty arguments to prove that the selection of continuous variations does not lead to a production of specific differences. It would no doubt be rash to hastily accept such a conclusion ; nevertheless it must be admitted that a great deal of excellent evidence is adduced by De Vries in support of his opinion.

The problem of specific differences may be attacked by three distinct methods. The first or *comparative* method was exclusively used by the older systematists. Galton introduced the use of *statistics* in biological problems to English science. The third method, that of direct *experiment*, was effectively employed by hybridizers even before the time of Darwin ; but in recent years it had largely been discarded. De Vries makes valuable use of all three methods, but he rightly lays greatest stress upon the last.

"Die Mutations-theorie" begins with a critical examination of previous views, in the course of which the introductory questions already alluded to are discussed at considerable length. An important distinction is drawn between the elemental species of Jordan and the aggregate species of Linnæus. Linnean species are the somewhat comprehensive groups of plants which have been long accepted by botanists as the units of classification. Such species frequently include a number of minor forms, which differ from one another distinctly, though only to a relatively small extent, and which come true to their type when grown from seed. Jordan described more than two hundred such forms within the limits of the single Linnean species,

Draba verna. Linnean species arise, as Darwin taught, by the extermination of intermediate sub-species. The problem therefore is, how do Jordan's species arise? The answer previously given to this question was that they arose by natural selection acting upon continuous variation; and the principal evidence for this view was that analogous forms arise in cultivation owing to selection by man. Before giving his own view as to how species (*i.e.*, Jordan's species) arise, De Vries proceeds to demolish this opinion. The only new forms actually produced by man's selection, *e.g.*, improved races of cereals, of sugar beet, and other plants, are not analogous to new species, inasmuch as when selection ceases the improved condition of the characters selected dies away and there is regression to the parental type.

The varieties of the gardener, on the other hand, are analogous to Jordan's species; their tendency to regress is not to the original form, but to a type of their own. But garden varieties are not produced by selection. All that selection can do is to separate one of two or more forms already existing together and afterwards to improve it beyond its own type or modal value. The important process is the *isolation* of the new race.

What then is the meaning of individual differences, of continuous variability? De Vries points out that for no two plants are the conditions of life exactly alike; a considerable diversity among the plants themselves is therefore advantageous. Upon continuous variability depend local races, forms adapted to wetter and drier situations, highland and lowland races, and the like, but none of these are permanent. Beyond the effect of sexual reproduction, which combines the tendency to vary of two parents, De Vries believes that individual variability depends entirely upon nutrition, under which head may be included practically the whole environment of the plant—light, space, soil, moisture, and the like. Characters *acquired* in a similar way by previous generations are inherited, and the effect of conditions upon the developing seed while still contained in the parent plant may be considerable. The puzzling question of the inheritance or non-inheritance of acquired characters is thus disposed of: acquired characters are inherited; they are not of any importance in the origin of species.

Some account must now be given of the way in which, according to De Vries, species do arise. Broadly speaking, they arise by mutation: by a sudden step in which either a single character or a whole set of characters together become changed. In the former case a new variety in the strict sense of the word is the result; in the latter a new Jordan's species is produced. But mutation may be of several kinds. In the first place, an entirely new character or set of characters may make its appearance. This is the *progressive* method of formation of new species; and it is by a series of steps of this kind that De Vries

believes the main divisions of the vegetable kingdom to have been built up. In the case of such mutations the author believes that the new character first comes into existence in a latent condition, and it may be only after many generations that it makes its appearance visibly—the period of mutation is preceded by a "pre-mutation" period. A second method of species formation, entitled by De Vries the *degressive* method, is indicated when a change takes place in the partial "latency" of a character. A completely latent character is indeed unrecognizable as such. But characters may be partially latent, and in this case they exhibit themselves from time to time in rare individuals in the form of abnormalities or sports. An active character, on the other hand, is apparent in the great majority of individuals of a race. If a change from latency to activity occurs suddenly, this is a form of mutation. On the other hand, a character previously active may become latent; the character then appears to be lost and the mutation is said to be *retrogressive*. De Vries regards the great variety of allied species which occurs in many groups as being largely due to retrogressive mutation. It is also frequent in garden culture, where the appearance of a white variety of plant, previously only known to produce coloured flowers, may be a good example of a retrogressive change. Mutations may also be *atavistic*, the usual case being that an ancestral character which had become latent shows itself once more in the active condition. Finally, new forms may arise by the intercrossing of distinct species.

The greater part of the volume is occupied by an account of the experimental evidence upon which the conclusions summarized above are based. It is impossible to give here more than the barest idea of these observations. The main conclusions are based upon experiments carried out with plants of Œnothera Lamarckiana, which occurred in great numbers as "escapes" near Hilfversum, and which, according to De Vries's interpretation of the facts, were discovered in a period of mutation.

In the locality mentioned two forms of Œnothera, previously unrecorded, were found growing in company with their supposed parent; each of them on being tested came true to seed. Seed and roots of O. Lamarckiana were then taken and grown in the garden, and here a number of other new forms arose. In eight generations, starting from O. Lamarckiana in 1886, about 50,000 individuals were grown to a recognizable stage, and of these over 800 showed mutation, *i.e.*, 1·5 per cent., and this estimate is likely to be too low rather than too high.

The new forms numbered about 15, and most of them appeared repeatedly, but some were much more frequent than others. Many were recognizable as quite young seedlings, notably O. albida; others not until a considerably later period of growth. Having once appeared, the majority of new forms came true to seed. Sometimes among their

offspring there occurrred fresh mutations, but always in smaller numbers than in the case of the parent, O. Lamarckiana.

The characters of the new forms are given at length by de Vries. Tables showing the date and frequency of their appearance are provided, and analytical tables are given, by the aid of which the new forms can be distinguished, either as seedlings or from the habit or by examining the leaves or the floral organs. The new species are also compared with several previously known species of the genus Œnothera allied to O. Lamarckiana.

As a result of the observations detailed in this section of the book, De Vries comes to the following conclusions :—

(1) The new species arise suddenly, without transitional forms.

(2) They are usually fully constant from the first moment of their origin.

(3) The characters of the new forms agree in their nature with those which distinguish the older species allied to O. Lamarckiana, *e.g.*, O. biennis. Only one new form, namely, O. nanella, a dwarf type, is analogous with any usual kind of garden variety.

(4) A considerable number of like individuals arise at the same period.

(5) Although the new types vary normally and frequently transgress the limits dividing them from the parental type, yet their *appearance* has nothing to do with normal variability.

(6) Mutations occur indefinitely in any direction.

(7) The tendency to mutate recurs periodically.

Any direct observation of the origin of a species was formerly supposed to be out of the question. There is therefore much truth in De Vries's observation that the most important conclusion to be drawn from this section is the proof that this process is capable of experimental treatment. Of great importance also is the fact that towards the end of the experiments the ancestry of the mutating plants was exactly known for several generations. It is therefore most unfortunate that, as pointed out by Bateson and Saunders,* clear proof of the freedom of the original strain of plants from a cross with some other species of Œnothera is not forthcoming. The fact that plants tracing a pure descent through seven generations of O. Lamarckiana were still able to mutate in the same manner as earlier examples seems, however, to support the author's view ; and so to some extent do the results of crossing experiments detailed in the second volume. In the meantime we can only hope that the point will before long be settled by experiments with other strains of O. Lamarckiana crossed with allied species. But even if it can be shown that the original plants were of impure ancestry, the value of these observations and their bearing upon the

* Report to Evolution Committee of the Royal Society, 1902.

subject of discontinuity in the origin of species can scarcely be diminished.

The section dealing with Œnothera is followed by one in which are recorded experiments upon selection combined with increased nutrition. The result supports De Vries's contention that normal variability is a nutritive phenomenon, and that in most cases selection is simply the choice of the best nourished individuals. The author finds in several cases that high feeding and strict selection have a closely comparable effect. It would be a great advantage if experiments of this kind were to be repeated on a much larger scale and for a long series of generations.

Section IV. is concerned mainly with experimental studies in the origin of garden varieties. These largely substantiate the view that selection does not lead to the production of specific characters. De Vries introduces certain new conceptions, which require a brief mention on account of their great interest for practical gardeners and breeders. They consist in the idea of races existing intermediate between a species and a complete variety or race of it. Such *between-races* are of two kinds, which do not usually co-exist; moreover, either of them may occur even when the complete variety is quite unknown. In the case of a *half-race* a small percentage only of seedlings produce plants which show the racial character, and if seed is taken only from such plants this percentage does not notably increase. A *mid-race*, on the other hand, can be improved by selection, and normally either shows the racial character in about half its members or exhibits in the great majority of its members a combination of the character of the species with that of the race. For instance, an ordinary variegated plant is looked upon as showing a combination of green with the yellow character of a complete race—the *aurea* variety, which exists as such only in a few rare cases. On the other hand, many plants show a small proportion of variegated individuals at each sowing; and this indicates the presence of the corresponding half-race. The relative development of the two co-existing characters is in such cases highly variable.

It might be supposed possible to pass from the species to the half-race, thence to the mid-race, and so on to the complete race, simply by selection. De Vries shows that this is very rarely the case. The passage from a half- to a mid-race is a mutation (degressive), and is not more frequent than other mutations.

As a further illustration of what is meant by a between-race, mention may be made of the five-leaved race of purple clover (*Trifolium pratense*) obtained by De Vries. It would appear that the plants occasionally found growing wild and bearing a single four-lobed leaf belong usually to a half-race. De Vries was lucky enough to find two plants upon which several leaves showed the anomaly, and from these by an elaborate process of selection extending over several years, a race

was obtained, the majority of leaves of which had five lobes, whilst some had six or seven. Since, however, it appeared impossible to get rid by selection of a certain proportion of three-lobed leaves, or, on the other hand, to obtain leaves with more than seven lobes, De Vries regarded his experiment as showing the existence of a mid-race, and not of a constant race or true variety.

Several of the views enforced in the present volume have long been familiar to practical breeders and gardeners, to whom this confirmation of their established practice will be all the more welcome, because recently a majority of authorities upon the subject of variation have held contrary opinions. Still more must this work be welcome to those engaged in scientific investigations bearing upon the subject of species. And the general public interested in evolution may welcome it as introducing, on the whole, decidedly simpler ideas of method, in spite of the amount of novelty which accompanies them.

At the same time the originality of most of the work appears unimpeachable. As a connected argument, in which close reasoning and careful investigation are applied to the elucidation of a difficult biological problem, the book deserves comparison with that well-known model of these qualities, the Origin of Species. In scope it is more nearly comparable with that larger intended work, of which the Origin was only an abstract. The host of examples in which elemental species, between-races, and varieties are shown to exist and to be separable by selection is most striking. In no case has it been shown that such forms can be built up by the gradual selection of individual differences. Darwin was wont to say that as soon as the slightest tendency to vary in a particular direction has appeared, the breeder can by selection produce a race in which the character is strongly marked. De Vries now shows that in such cases the slight tendency indicates the appearance of a minus-variation of a definite new form, which only requires isolation for a few generations in order to appear fully and typically developed. Natural selection is active in "building up" species into genera, sub-species into species; it does not account for the differences between Jordan's species; and these are, in De Vries's opinion, true physiological species. Of the origin of such species mutation gives us a suitable explanation; it also explains the difficulty as to how characters of no use to a species or even actually disadvantageous may have arisen; a point which is quite inexplicable upon the rival view.

Many of De Vries's experiments have been carried out at what is for the subject lightning speed, and may require confirmation at a more wary pace. But it cannot be doubted that at the outset of a new century the writer has supplied a splendid starting-point for the progress of further studies in the origin of species, and that in the near future we may look for an even more marked advance.

R. H. L.

Useful Plants of South-Western Ceylon.

(A Descriptive Catalogue of the more useful Trees and Flowering Plants of the Western and Sabaragamuwa Provinces of Ceylon; F. Lewis. Reprinted from Journ. R.A.S., Ceylon Br., XVII., 1903, pp. 89-256 ; 4 maps.

COMMENCING with a brief description of the chief features of the country, its rainfall, and its division into climatic zones, the bulk of this useful little book is occupied by a description of 270 of the more important useful flowering plants—especially trees—of these Provinces. Though the district actually dealt with only forms one-eighth of the Island, it includes such variety of climates and elevations that most of the useful native plants of Ceylon are dealt with in the book.

In the absence of any key to the plants described, the ordinary reader, except in so far as he may depend upon the native names, will require some such aid as that afforded by Trimen's Flora or some botanical work dealing with the natural orders of flowering plants. The species dealt with being once identified, Mr. Lewis's book provides a very useful summary of information as to its native names, uses, &c. In particular, the work affords a mine of information as to the value, quality, and uses of the various timbers, and should be in the hands of every one using timber in any way in Ceylon, as well as of all who are interested in the wild flora and the economic products of the Island.

J. C. W.

The Timbers of India and Ceylon.

(A Manual of Indian Timbers, J. S. Gamble. Second Edition, London, 1902.)

A NEW edition of this, the standard work on Indian timbers, has lately appeared. The Ceylon timbers are included in this edition, and the work is indispensable to all concerned with timber, containing as it does all known reliable information about the various timber trees, their distribution and uses, the weight, strength, and durability of the timbers, and other points.

J. C. W.

The Botany of the Patanas.

(The Botany of the Ceylon Patanas, I., by H. H. W. Pearson, Journ. Linn. Soc., XXXIV., p. 300, 1899 ; II., by J. Parkin and H. H. W. Pearson, Journ. Linn. Soc., XXXV., p. 430, 1903.)

THE field investigations described in these papers were carried out in Ceylon by Prof. Pearson in 1897, and the subsequent microscopic studies were made by Mr. Parkin. The object in view was "to

ascertain (1) the probable causes which have led to the development of these remarkable savannah-like expanses in an otherwise forest-covered country; and (2) to what extent the vegetation of the patanas shows adaptations to the peculiar ecological factors under the influence of which it has been selected."

The great bulk of the patanas occur in the Province of Uva at elevations from 2,000 to 5,000 feet, but they also cross the central ridge of the mountains and occur in small areas in the wet summit levels, *e.g.*, at Nuwara Eliya and Horton Plains, and on parts of the western slopes of the mountains. A very remarkable feature is the sharpness of the boundary between forest and patana—two strides will often suffice to pass from one to the other. A critical discussion is given of the various theories that have been put forward as to the origin of the patanas. Evidence is adduced to show that probably the Uva patanas were once covered with a savannah-forest like that still existing in the "Park Country" to the east. The constantly recurring fires started by the graziers, consuming the grasses every year, would then gradually reduce the forest area (as is still happening), and lay bare the soil to the action of the heavy rain. The trees would thus in time be reduced to a few hard-wooded resistent species, such as the kahata or patana oak (Careya arborea), and the soil become shallower and poorer, till it reached the condition seen on the hills north of Bandarawela. Above 4,500 feet, *e.g.*, at Hakgala and Nuwara Eliya, the climate is wetter; the patanas, annually fired, have gradually spread into this wet region, but here, as in similar places in other countries, climatic and other conditions have led to the formation of a sour black soil, largely composed of humus.

The plants of the patanas are exposed to somewhat extreme conditions favouring evaporation of water, and show in general the structural characters of other dry-country plants (*e.g.*, thick or hairy leaves, protective leaf movements, &c.), though by no means to the degree that might be expected, even in such places as the exposed ridges near Bandarawela. Surprising as it may seem, these "xerophytic" characters are as well marked in the plants of the "wet" patanas above 5,000 feet as in those of the "dry" patanas. This result is probably to be ascribed to the effects of the coldness of the soil and the presence of humus acids in checking absorption of water. An interesting parallel is seen in the way in which Australian trees, from very dry climates, readily acclimatize themselves in the higher districts of Ceylon.

Interesting details are given of the many structural and other peculiarities of the patana plants, and a list of the 289 species of flowering plants and ferns found on the patanas. The whole forms a valuable contribution to the botany of Ceylon, and a good foundation for further work, in which good service may be done by local botanists. There is yet a vast amount of investigation required to render

complete our knowledge of the up-country flora ; more especially we need detailed study of the life-histories of the individual plants, and a mapping of the vegetation into zones and societies.

J. C. W.

The Growth in Thickness of Palms.

(M. Barsickow : Ueber das Sekundäre Dickenwachstum der Palmen in den Tropen. Verh. Phys. Med. Ges., Würzburg, XXXIV., 1901.)

A CONTINUATION of the work of Eichler and of Kraus, giving detailed accounts, with measurements, of the growth in thickness of four Javanese palms. The growth is shown to be due to increase in size of the parenchyma cells of the wood of the vascular bundles.

J. C. W.

Seed-dispersal in Thuarea sarmentosa.

(Die Schwimmvorrichtung der Früchte von Thuarea sarmentosa. M. Nieuwenhuis-Uexküll ; Ann. Jard. Bot. Buitenzorg, Ser. 2, vol. III., p. 114, 1902.)

Thuarea sarmentosa, a common creeping grass of tropical sandy beaches in the Old World, is carried from place to place by ocean currents (*cf.* vol. I., pp. 108, 146.) The flowering shoots stand erect, but afterwards curve over and push the fruits under the sand to ripen. The basal part of the spikelet is lobed, and enlarges to form an air-holding chamber round the fruit, so that it floats away when washed out of the sand.

J. C. W.

Formation of Shoots in Torenia asiatica.

(Ueber regenerative Sprossbildung auf den Blättern von Torenia asiatica, L.; H. Winkler, in Ber. d. Bot. Ges. XXI., 1903, p. 96.)

This favourite border plant, the kotala-wel of the Sinhalese, is frequent in wet places in Ceylon. If single leaves are planted, they rapidly form roots, and soon shoots develop all over them, a few ultimately growing into new plants.

J. C. W.

Notes on Derris uliginosa.

(The Anatomy of the Stem, by P. E. F. Perrédès ; The Chemistry of the Stem, by F. B. Power. Publications 33, 34 of the Wellcome Chemical Research Laboratories, London, 1902.)

Derris uliginosa, Benth., the kala-wel of the Sinhalese, is a woody climber belonging to the Leguminosæ, and common near the coast of Ceylon, especially in the dry region. It also occurs from Africa to Polynesia. The roots, according to Trimen, are employed in Ceylon

as a fish poison. In the present papers the stem only is dealt with; no evidence of the presence of any alkaloid was obtained, and the poisonous action of the bark is attributed to some constituent of that portion of the resin it contains which is soluble in chloroform.

J. C. W.

The Seeds of Brucea sumatrana.

(Chemical Examination of Ko-sam Seeds (*Brucea sumatrana*, Roxb.), by F. B. Power and F. H. Lees. Wellcome Chem. Res. Laboratories, 1903.

THIS little shrub is a common weed near Kandy and elsewhere, introduced from the Malay Archipelago. Lately a great amount of interest has been aroused in it as a remedy for dysentery, a purpose for which its seeds have long been used by the Javanese. The nature of the active principle has been supposed to be quassin, but this the authors show is not the case; they isolated two bitter principles hitherto unknown, and requiring further research.

J. C. W.

NOTES.

Personal Notes.

SCIENTIFIC visitors of the last eighteen months include Dr. H. Uzel of Koniggratz, who resided at Peradeniya from November, 1901, to July, 1902, and was engaged in entomological research ; Dr. Nils Svedelius of Stockholm (September, 1902, to August, 1903), who made extensive investigations of the seaweeds of Ceylon, chiefly at Galle ; Dr. F. E. Fritsch of London (August to November, 1903), who investigated the fresh water algæ, the plankton of the rivers and lagoons, and other points ; and several other workers for shorter periods. Numerous officials of similar departments in other countries also visited Peradeniya to study the working of the Department and to investigate local agriculture ; among them may be mentioned Mr. R. Dupont, the Curator of the Seychelles Botanic Gardens ; Mr. W. J. Johnson, Curator of the Gold Coast Botanic Gardens ; Mr. S. T. Dunn, Superintendent of the Botanical Department, Hongkong ; Dr. P. Preuss, Director of the Botanical Department, Kamerun ; Mr. B. C. Basu, Assistant to the Director of Land Records and Agriculture, Assam ; and others.

Mr. Herbert Wright was appointed in 1902 Controller of the Experiment Station, Peradeniya, and was succeeded as Scientific Assistant by Mr. R. H. Lock, B.A., Frank Smart Student in Botany of Gonville and Caius College, Cambridge.

Mr. J. C. Willis was absent on leave from July, 1902, to May, 1903, and spent part of the time in a tour through the United States and Cuba for the study of Agricultural and Botanical departments and their organization, &c. Articles dealing with these subjects will probably appear in later numbers of this journal.

Publications.

THE following numbers of the "Circulars and Agricultural Journal" have been published since the last notice :—

Vol. II., No. 1.—Annual Report of the Government Mycologist and Assistant Director, 1901. By J. B. Carruthers.

2.—Further Observations on Helopeltis. By E. E. Green.

3.—The Tea Tortrix (*Capua coffearia*, Nietner). By E. E. Green.

4.—A Report by the Controller, Experiment Station, Peradeniya. By H. Wright.

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Volume I. is now complete, and is published at Rs. 15 or £1, unbound. A few copies of Parts I. (Ceylon Botanic Gardens, &c.), III., and IV. (Podostemaceæ, &c.) can still be had. The following reprints are also for sale at the prices marked :—

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ANNALS

OF THE

ROYAL BOTANIC GARDENS, PERADENIYA.

EDITED BY

J. C. WILLIS, M.A., F.L.S.

DIRECTOR.

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The Genus Diospyros in Ceylon: its Morphology, Anatomy, and Taxonomy.

BY

HERBERT WRIGHT.

(With Plates I.–XX.)

Part II.

THE present contribution is the concluding portion of my paper, the first part of which was published in January, 1904. For local convenience the species are described in the same order as previously adopted in Trimen's Flora of Ceylon. A reference to Hiern's monograph for each species is also quoted. The synonyms for each species are not given since reference can always be made to those quoted in Hiern's comprehensive monograph on the Ebenaceæ.

In Part I. I explained that the flower systems were previously imperfectly known, and the descriptions given by Trimen and Hiern are frequently inadequate on account of the limited supply of fresh material which those botanists had at their command. In Trimen's Flora the staminal whorls of the male and female flowers, and often the accessory whorls, are not separately described.

In many species the flowers or fruits are not described in Trimen's Flora, but in several of these cases descriptions are obtainable from Hiern.

The male and female flowers, timbers, fruits, seeds, and seedlings have now been obtained for every Ceylon species except D. Moonii, and many of them are described here for the first time from material obtained in this Island.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. II., Pt. II., August, 1904.]

The object has been to work out all details of our recognized species rather than to subdivide into varieties. Hence the question of the possibility of two species in D. montana, *Roxb.*, D. Embryopteris, *Pers.*, and D. Ebenum, *Koen.*, is only briefly dealt with. I am, however, unable to agree with the grouping of D. Thwaitesii, *Bedd.*, D. Moonii, *Thw.*, and D. hirsuta, *L.*, under one species—D. hirsuta, *Linn.*, as adopted in Hiern's monograph, and have, therefore, for reasons obvious in the descriptions of these species, adopted the separate classification used by Trimen.*

D. ovalifolia, R. Wight, Ic. t. 1,227 (1850).

Kunumella, Habara, S. ; Vedukkanari, T.

Thw. Enum. 181 (1864). C. P. 1825 (2,533). Fl. B. Ind. III., 557. Wight, Ic. t. 1,227 (1850). Hiern, Mon. Eben. 237.

A moderate-sized tree, dicecious ; bark with brown and pale alternating streaks ; becomes partly deciduous in the dry season in the Northern Province ; flowers in September and fruits in March. Leaves 35–130 mm. long, 6–50 mm. wide, alternate, accrescent and crowded, oval or lanceolate-oblong, obtuse or rounded at apex, narrowed at base, glabrous, thinly coriaceous, paler beneath with prominent venation ; *petiole* 3–7 mm. long.

Male inflorescence consists of sessile clusters of 3–7 flowers mainly on woody twigs ; bracts form a basal involucre. (See pl. XV., fig. 1.)

Flowers yellow, 5–10 mm. long ; they appear from September to December.

Calyx green, slightly hairy, and openly campanulate : segments 4–5, apex rounded.

Corolla yellow, urceolate, glabrous or nearly so, 5–8 mm. long ; segments 4–5, obtuse apex, recurved when mature.

Stamens 13–20, paired, surrounding central rudimentary disc ; *filaments* unequal, about one-sixth the length of anthers ; *anthers* brown and glabrous.

* I have, since writing the above, received a communication from W. P. Hiern, Esq., in which that gentleman agrees with the separate classification here adopted.

Pistil rudimentary, apiculate, hairy.

Female flowers solitary or as sessile clusters of 3–9 flowers in axils of leaves or on woody twigs; buds pubescent, globular, surrounded by two or three small deciduous bracts. (See pl. XV., fig. 2.)

Calyx segments 4–5, brown or green, pubescent, 3 mm. long, rounded or bluntly acute at apex.

Corolla yellow, conical in bud, segments 4–5, shorter than tube.

Staminodes 1–7, usually 4, sometimes absent, hypogynous or at base of corolla.

Pistil green, pubescent; stigmas 2–4, green, reniform; ovary pubescent, conical, 4-celled (see pl. XV., figs. 4 and 5)

Fruit globose, 2 cm. diameter, solitary, subsessile, 1–3-4,—usually 1-seeded, glabrous; fruiting calyx enlarged, thickened, reflexed. Fruits ripe in March.

Seeds hard, globose when solitary, wedge-shaped when numerous; testa brown and superficially striated, 7 mm. diameter, 9 mm. long; endosperm abundant, equable; embryo white, 5 mm. long. (See pl. XV., fig. 3.)

Seedlings epigeal; cotyledons detached early, testa does not split (*cf.* D. pruriens); *cotyledons* ovate, rounded base and apex, 4–6 mm. long; *hypocotyl* white or yellow, thin, 50–60 mm. long, 2 mm. diameter; *epicotyledonary* stem 8 mm. long; first epicotyledonary leaves form an opposite pair, ovate, hairy, 8 mm. long, 4 mm. wide; *traces* 2 per cotyledon which are not split to any great extent at the node and give a four-cornered appearance to the vascular cylinder in the hypocotyl, thus resembling D. montana and D. Ebenum; epicotyledonary traces one per leaf, conspicuous in the ungerminated embryo, particularly the phloem. In the apex of the primary root there are only eight strands, which may be the result of the splitting of four cotyledonary or may consist of two epicotyledonary and six cotyledonary strands.

Timber brown or dirty white or faint red in colour, inferior, sapwood and heartwood of very old trees possessing

a high per cent. of tracheal elements and small quantity of gum-resin. The heartwood is usually small and considerably decayed. The contents of the elements are scarce compared with the red or black woods of other species. Many specimens show thinly streaked heartwood, the black lines of which help to form a pretty pattern (*cf.* D. quæsita). (See pl. I., fig. 6.)

Uses.—Only the timber is used.

Distribution.—Common in dry region and intermediate zone, rare in moist region. Trincomalee, Anuradhapura, Kalugalla, Vavuniya, Madawachchi. Also in Madras and Anamalai hills.

D. montana, *Roxb.*, Cor. Pl., p. 37, t. 48 (1795).

Mulkarunkali, Katukanni, Vakkana, T.

Thw. Enum. 423. C. P. 1,909 (3,774). Hiern, Mon. Eben. 220. Fl. B. Ind. III., 555. Wight, Ic. t. 1,125.

A moderate-sized or small tree, diœcious, partially deciduous in the Northern Province; bark yellowish or silvery grey, smooth, shiny, thin, being 4–6 mm. in thickness, yellow when freshly cut; sharp spines on main stem, branches, and twigs, stumps of spines often characteristic of old trunk; flowers in September; fruits ripe in March–September; tree flowers when only 75 mm. diameter. Leaves 25–100 mm. long, 15–50 mm. wide, alternate, oval, oblong or lanceolate-oblong, obtuse or rounded apex, rounded or cordate at base, finely pubescent when young, glabrous when old, thin, yellowish-green, venation not pronounced; *petiole* 2–12 mm. long, finely pubescent. (See pl. XVI., fig. 7.)

The spiny character of the stem structures is said to be found only on one variety of this species, but it has been noticed on every plant reared at Peradeniya, even when only two years old.

Male inflorescence; Cymes 3-flowered or panicled in axils of small caducous bracts or young persistent foliage leaves. Main peduncle of inflorescence thin, green, 2–6 mm. long. Each lateral flower arises in the axil of a small narrow

bract 2 mm. in length, and is supported on a thin pedicel 2–5 mm. long. Primary and secondary pedicels show great variation in length. Flower-bud 4 mm. long, conical, apical, scentless; mature flower 8 mm. long and somewhat bell-shaped when segments recurved. (See pl. XVI., fig. 9.)

Calyx segments 4, rounded or deltoid, thin, pubescent, small.

Corolla, wide throated, segments 4, twisted at apex, urceolate, white or yellow.

Stamens numerous or 16, in equal or unequal pairs, often united to form 8 pairs; *anthers* brown, glabrous, apiculate, 2–4 mm. long; *filaments* white, glabrous, absent or 1 mm. long.

Ovary is a flattened rudimentary disc often of considerable size, which may yet be observed to develop into a ripe fruit; the polygamous condition will probably be found if a sufficient number of trees are examined.

The female flowers are usually solitary on woody twig or in axil of leaf (see pl. XVI., fig. 10); peduncle 4–12 mm. long, glabrous or pubescent; bracts small, caducous.

Calyx green, hairy, 10 mm. diameter; segments 4, 2–5 mm. long, rounded apex.

Corolla white or yellow, wide-throated, 11 mm. long, glabrous; segments 4, rotate.

Staminodes small, 4–12, usually 4.

Pistil green, glabrous or nearly so; styles 4, bifid at apex, glabrous; ovary glabrous, 8-celled.

Fruit globose-apiculate, 12–20 mm. diameter, 16 mm. high, glabrous and shiny, cherry-red to brown in colour; fruiting calyx thin, glabrous, accrescent or nearly horizontal, slightly enlarged, with segments 6–8 mm. long. (See pl. XVI., fig. 7.)

Seeds 2–6–8 per fruit, semilunar, wedge-shaped, brown, smooth, 8 mm. long, 4–5 mm. wide, 3 mm. thick; endosperm equable, copious; embryo white, small, 8–10 mm. long. (See pl. XVI., fig. 8.)

Seedlings epigeal; *cotyledons* persistent, ovate, tapering towards apex, green, glabrous, 30 × 15 mm.; petiole of

cotyledon flat, 2 × 2 mm. ; *hypocotyl* green, cylindrical, faintly pubescent, 60 mm. long, 2 mm. diameter. The *epicotyledonary* system shows delayed development ; leaves alternate, the first leaf occurs 3–8 mm. above the cotyledonary node, at right angles to the plane of the cotyledons, 30 mm. long × 9 mm. wide, green ; the subsequent leaves arise in a spiral, and in size and form are similar to the first (*cf.* D. Ebenum and D. Gardneri for development).

Two *traces* per cotyledon ; one trace to each epicotyledonary leaf ; feeble splitting of cotyledonary xylem, epicotyledonary traces die out in hypocotyl.

Timber.—When freshly cut the wood is of a dirty white colour, but on exposure assumes a reddish tint. Black heartwood usually small, central part generally rotten. Some specimens show large heartwood not jet black, but often streaked (*cf.* D. affinis and D. oocarpa), and when such samples are sound the timber is equal to calamander in beauty. One specimen 30 cm. diameter, possessed a large heartwood consisting of a small black centre and a peripheral portion beautifully variegated in tints of brown and black. Most samples are inferior to ordinary ebony ; the timber possesses a high per cent. number of parenchymatous and tracheal elements. (See pl. V., fig. 19.)

Uses.—Only the timber is used.

Distribution.—Common in dry zones, especially along the roadsides to Trincomalee and Mannar ; characteristic of poor low-lying xerophytic forests. Jaffna, Matale, Trincomalee, Vavuniya, Puttalam, Mannar, Anuradhapura, Habarana, Kanthalai, Madawachchi. Also in India, Malaya, Burma, and Tropical Australia.

Diospyros Embryopteris, *Pers.*, Syn. 11, p 624, n. 6 (1807).

Timbiri, S. ; Panichchai, T.

Thw. Enum. 178. C. P. 1,915. Fl. B. Ind. III, 556. Wight, Ic. t. 843, 844. Bedd. Fl. Sylv. t. 69. Bentl. and Trim. Med. Pl. t. 168. Hiern, Mon. Eben. 257.

A large tree, evergreen, diœcious, and polygamous ; trunk fluted when old, black, thick, and scaly, red when freshly cut; branches spreading, forming dense wide head, which in young trees is often conical in outline ; flowers March–July; ripe fruit, September–February.

Leaves 120–200 mm. long, 25–55 mm. wide, alternate, oblong or lanceolate-oblong, acute-lanceolate, acuminate or obtuse at apex, rounded or narrowed at base, glabrous except slight puberulence on petiole, thick and coriaceous, pale green colour, pellucid venation, veins prominent in dried leaves ; *petiole* thick, rigid, slightly pubescent, 5–13 mm. long.

The flowers of some male trees often show a central pistil possessing definite loculi, and which often assumes a very large size. Mature seeds from a polygamous tree have not yet been obtained.

Male inflorescence arises as a globular apiculate axillary structure, strongly pubescent, supported on short stout peduncles and surrounded by regularly arranged bracts, 3–7 flowers (see pl. IX., figs. 1–5) ; peduncle yellowish-white to green, 20 mm. long, 2 mm. diameter, covered with fine coating of silvery unicellular hairs ; pedicel of each lateral flower 4 mm. long ; bracts large, one to each flower, greenish-white, frilled or straight margin, broad base, acuminate apex, both sides pubescent, early deciduous, length 8–10 mm. ; bracteoles small, two on each pedicel arranged one on each side as an opposite pair at right angles to antero-posterior axis ; brownish-black, caducous, acuminate apex, 2 mm. long ; scar inconspicuous. *Flowers* 6 mm. long and ovoid in bud, when open 10–15 mm. long.

Calyx segments 4–5, accrescent, rounded or acuminate apex, 3–5 mm. long, greenish, covered with silky unicellular hairs on both sides, cup-shaped in mature flower.

Corolla segments 4–5, canary-yellow in colour, ovoid, 3 mm. long, rounded apices, inbricated sinistrorsely in bud; segments in open flower are erect or strongly curved outwards and downwards ; total length of corolla 8–13 mm., diameter

of open flower 10 mm.; corolla throat is wide and covered with silky unicellular hairs on both surfaces.

Stamens 24–30–40–64 (very unequal numbers), form epipetalous ring around abortive pistil or occupy central position; very unequal in length, often united throughout greater part of filament; usually in pairs, average length 8 mm.; *anthers* free, equal in length, reddish-brown rectangular outline when mature, glabrous, attenuate apex; *filaments* united, white, short, and covered on all surfaces with long unicellular hairs; *pollen* grains circular, even outline, brownish-yellow, finely granular contents.

Pistil usually occurs as a flattened circular central apiculate disc, or as a bunch of hairs positioned on the receptacle; in several cases the pistil assumes large dimensions with ovary many-celled.

Female inflorescence arises as globular structure in axil of normal foliage leaf, 1–5 flowers, subsessile or cymose; peduncle 10 mm. long, 4 mm. diameter, covered with yellowish-white hairs which rapidly turn to brownish-red; bracts usually 4, 10 mm. long, brown, bluntly acuminate apex covered with unicellular hairs; lower two form an opposite pair at right angles to antero-posterior axis, upper two are larger, and arranged one on each side at right angles to the first pair, but at different levels.

Flowers occur one in the axil of each bract, but the upper pair usually drop; very frequently the lower pair do the same, thus reducing the inflorescence to a peduncle showing four leaf scars along its length and terminated by the oldest and fruiting flower (*cf.* D. Gardneri). (See pl. IX., figs. 7–11.)

Flowers larger than in male and largest in Ceylon Diospyros group, measuring 20 mm. high, 30 mm. diameter when mature.

Calyx 3–4–5-lobed, accrescent in young flower, but becomes horizontal shortly after fertilization, and finally the marginsare recurved; segments ovate, tapering towards apex,

15 mm. long, 15 mm. wide at base, glabrescent or covered with long black unicellular hairs.

Corolla wide-throated, 3–4–5-lobed, yellow; segments broad, 18 mm. long, 10 mm. wide, apices recurved, apex rounded or sub-acute.

Staminodes 4, alternating with corolla segments, adnate to corolla tube, short, hairy; sometimes 1–12 in number, and may possess fertile anthers. (See pl. IX., fig. 12.)

Pistil globular-apiculate in bud, yellowish-green, and covered with multicellular glands borne on many-celled pedicels, forming a dense layer 1 mm. thick in bud; styles 4, hairy; stigmas lobed and undulated; ovary 8-celled, loculi in four pairs alternating with calyx segments, sometimes 6-celled in pentamerous and trimerous flowers; fruiting calyx deeply 4-lobed, enlarged, strongly reflexed margin, woody, hairy or glabrous; fruit usually solitary, subsessile or pedunculate, globular or ovoid, very large, 45 mm. high. The remnants of the multicellular glands, many of which are dead and changed to a brown or red colour, give the fruit a "rusty mealy" appearance; carpellary wall pulpy and rich in gum and tannin (*cf.* D. crumenata; D. quæsita). (See pl. IX., fig. 6.)

Seeds 4–8 per fruit, large, 15 mm. wide, 8 mm. thick, 25 mm. long; brown testa, elliptical-wedge shape; endosperm copious, white, equable; embryo white, large. (See pl. XVIII., fig. 7.)

Seedlings epigeal, *cotyledons* detached early in embryo and measure 16 × 9 mm., pale yellow, never green or assimilatory; hypocotyl 30–40 mm. long, yellow to green turning black; *epicotyledonary* system shows enhanced development; epicotyledonary stem 35–40 mm. long, 2 mm. diameter, red, pubescent; first epicotyledonary leaves form a subopposite or opposite pair and persist alone for some time and carry on the assimilatory work allotted to cotyledons; *traces* 3 per cotyledon, considerably split, continued into root.

Timber usually white with occasional black strands; sapwood always white when freshly felled, but on exposure turns faintly brown; black heartwood is very small even in

centre of very old trees; black strands occur irregularly in parts of the sapwood usually in association with wounds. This species attains a very large size in the wet and dry zones. The coloured contents of the elements are rarely abundant and the tree is therefore seldom felled with a view to obtaining ebony therefrom. Seasonal rings of growth are poor and irregular, but visible to the naked eye (see pl. V., fig. 20). Some specimens possess 85·1 per cent. of fibres; nevertheless the timber is very inferior to ebony, and is even less durable than red woods of other species.

Varieties.—Var. *atrata*, Thw. *l.c.* C. P. 2,731.

Leaves thinly coriaceous; buds, peduncles, and calyx densely covered with brown hairs.

Var. *nervosa*, Thw. *l.c.* C. P. 1,910.

Leaves very coriaceous, veins prominent on both sides, rounded at base; buds, peduncles, and calyx covered with black hairs; calyx segments enlarged, erect, and about as long as fruit.

Uses.—The fruit possesses a large quantity of gum and tannin, and the juice is used as a tan for fishing nets and for the planks of boats. The fruit and the bark both possess astringent properties and are used medicinally. The leaves are sometimes eaten as a vegetable. The timber is occasionally used for masts and yards for small boats.

Distribution.—Common in dry countries, especially along banks of streams, tanks, &c., invariably associated with Terminalia glabra in these localities; also occurs in the moist regions, particularly along streams, and associated with D. Moonii, *Thw.* Galle, Rayigam korale, Ratnapura, Ambalawa, Bibile, Viriniya, Bintenna, Hinidum, Vavuniya, Jaffna, Madawachchi, Hantane, Gangaruwa, Kadugannawa. Also in India and Malaya.

Diospyros Toposia, Hamilt. in Trans. Linn. Soc., Vol. XV., p. 115 (1827).

Kahakala, Kaluwella, S.; Vellei Thoverii, T.

Thw. Enum. 179. C. P. 1,911. Fl. B. Ind. III., 556. Hiern, Mon. Eben. 263.

A large or moderate-sized tree, dicœcious, evergreen; branches glabrous, forming dense round head (*cf.* D. Embryopteris); bark thick, black, or dark grayish-brown. *Leaves* alternate, 75–300 mm. long, 25–80 mm. wide, acuminate apex, narrowed or rounded at base, glabrous, coriaceous, venation close, pellucid (*cf.* D. Ebenum), prominent when dry; midrib depressed on upper surface, green, paler on under surface; *petiole* stout, grooved, 5–12 mm. long, glabrous.

Flowers January–April–November; fruits ripe August–December.

Male inflorescence arises in axil of new or old normal foliage leaf or caducous bract. In the simplest case the cyme is 3-flowered, each lateral flower arising in the axil of a bract. The pedicel of each lateral flower bears a small bracteole (at an angle of 90° from the bract at the base of pedicel), which appears late and is positioned immediately beneath the calyx; bracts at base of peduncle green, pubescent, long tapering apex, prominent midrib, 7 mm. long and 2 mm. wide; bract at base of pedicel of each lateral flower is hood-shaped, has shortly tapering and acute apex, ventral surface pubescent, 2 mm. long and 2 mm. wide; bracteole on pedicel of each lateral flower is hood-shaped, ventral surface covered with short brown hairs, 1·5 mm. long, 1 mm. wide; primary peduncle green, covered with caducous or persistent brown hairs, 8–12 mm. long; lateral pedicels green, hairy, about 5 mm. long, and extending higher than median flower. (See pl. X., figs. 7 and 8.)

In a more complex inflorescence the lateral flowers arising on the long peduncle repeat the dichotomous structure detailed above; in cultivated specimens inflorescence 3–12-flowered.

Flowers yellow, globose-ovoid in bud, and measuring 8 mm. long, 5 mm. diameter; open flowers measure 11 mm. in length and 6 mm. in diameter, fragrant.

Calyx 2–3-lobed at apex, at first closed and may remain so, though ripe pollen grains formed within; segments thick, greenish-yellow, ventral surface pubescent.

Corolla yellow, urceolate, throat very narrow (*cf.* D. Embryopteris), and appears to be frequently closed; base 6 mm. diameter, apex 3 mm. diameter; segments 4, middle line pubescent on ventral surface, 0·8–1·5 mm. thick.

Stamens numerous and irregular, 18–24–33, yellowish-white, unequal length, hypogynous group or terminating receptacle; *anthers* 2 mm. long, not strongly apiculate, sometimes sessile, glabrous; *filaments* 2 mm. in length, white, glabrous, sometimes absent; *pollen* isodiametric, even outline, 2 mm. diameter, show one thin part in wall.

Pistil rudimentary disc or absent.

Female flowers solitary or cymose, occurring only on the lower part of young shoots in the axil of a bract or foliage leaf; bracts green to brown, caducous, small; pedicel green, covered with short adpressed hairs, 6–10 mm. long, 2 mm. diameter, widening towards flower.

A ringed scar is noticeable on the pedicel of each flower when solitary, which is probably the area of attachment of at least two bracts at an early stage, thus suggesting a cymose inflorescence with abortive lateral flowers. Such an inflorescence is shown in pl. X., fig. 9.

Flowers globose-apiculate in bud, with broad base, green, hairy, 5 mm. long; remain closed for a long time as in the male.

Calyx 4-lobed, segments deeply divided, tapering acute apex, green, both surfaces pubescent, dorsal surface silvery in appearance.

Corolla yellowish-white, tubular, urceolate; segments 4, short, and triangular-shaped, with acute apices.

Staminodes 12–16, usually as an epipetalous ring, short, white; anthers broad.

Pistil green, tetrahedral in bud and densely pubescent: style 0, stigmas 3–4, short: ovary 4–5–6-celled.

Fruit oblong or subglobose with wide base and flattened top, green, glandular, and covered with short thick-walled unicellular hairs, 40–60 mm. high, 30–40 mm. diameter : fruiting calyx enlarged, total diameter 25 mm., flat ; segments 10 mm. long, upper surface brown or green, rounded or oblong. (See pl. X., fig. 10.)

At Hiniduma there appears to be a variety having a globose-apiculate fruit about the size of ripe fruits in D. Ebenum or D. affinis.

Seeds 2–4 per fruit, oval or elliptical, or wedge-shaped ; smooth brown testa, 25 mm. long, 10 mm. wide ; endosperm copious, equable. Embryo white.

Seedlings epigeal, cotyledons detached early, epicotyledonary system not well developed, and in seedlings 50 mm. long. very minute ; *hypocotyl* white, thick, rather short, 40–50 mm. long, suggesting affinity with D. insignis and D. dodecandra. *Epicotyledonary* stem very long, 60–70 mm., longer than in any other species of Diospyros, suggesting D. insignis, except that it has no young leaves in the lower part ; first epicotyledonary leaves form an opposite pair, but at different levels ; 3 *traces* per cotyledon, 1 trace per epicotyledonary leaf ; cotyledonary xylem splits to form 10–15 groups ; epicotyledonary traces not well developed, and their courses are difficult to follow. (See pl. XVII., fig. 4.)

Timber red when freshly felled, deepening to reddish-brown on exposure. Black heartwood rarely of great size, usually numerous black strands irregularly distributed through the brown wood. This species is only rarely felled for the ebony it contains. (See pl. III., fig. 12.)

The tracheal elements contain abundance of a gummy deposit, yellow to brown in colour ; contents in parenchyma are brown and granular. The per cent. number of tracheal elements is low and that of the fibres high : the differentiation of all the secondary elements is relatively constant.

Rings of growth are often conspicuous to naked eye.

Uses.—The ripe fruits are steeped in water and afterwards eaten by some natives. The timber of freshly felled trees

often yields large quantities of a gummy extract reputed to be efficacious for toothache.

Distribution.—Moist region only, 2,000 to 4,000 ft.; abundant along precipitous banks and rocky damp gullies as in Adam's Peak Wilderness and North-East Matale. Sinha Raja Forest, Hantane, Rakwana, Balangoda, Hewesse, Hinidum, Ambalawa, Gangaruwa, Kadugannawa, Pindeniya, Gammaduwa, Pitigala, Pettiagalakanda. Also in Eastern Bengal, Silhet, Khasia.

Diospyros Ebenum, Koenig in Physiogr. Salsk. Handl. I, p. 176 (1776).

Kaluwara, S ; Karunkali, T.

Linn. f. Suppl. Pl. 440 (1781). Retz. Obs. Bot. V, 31. Thw. Enum. 180. C. P. 1,912. Hiern, Mon. Eben. 208. Roxb. Fl. Ind. II., 529. Alph. DC. Prodr. VIII., p. 234 (1844). Bedd. Fl. Sylv. Madr. t. 65 (1870). Wight, Ic. t. 188 (1840).

A large evergreen tree, dicœcious, polygamous, and occasionally moncœcious, trunk erect and foliage dense ; bark thick, dark grey or black, occasionally scaly, finely grooved in branches and twigs, red when cut.

Leaves alternate, numerous, spreading dichotomously, very variable, 50–130 mm. long, 20–60 mm. wide, oblong-oval or oblong-lanceolate, acuminate, rounded or obtuse apex, usually narrowed at base, glabrous, thinly coriaceous, bright green and shining above, paler beneath, venation strongly reticulate and pellucid, and meshes wider than in D. Toposia. *Petiole* 4–8 mm. long, green, glabrous.

This species could be arranged to include several varieties according to variation in size, venation, and form of the mature leaves.

The moncœcious state is rarely met with. I have seen it in the forests near Dambalagala Trigonometrical Station, Central Province, at an elevation of 1,900 feet, on rocky damp slopes. At this place one tree possessed the ordinary male flowers with indefinite connate stamens and rudimentary pistil, and female flowers each with 8 barren staminodes, typical calyx, and gynæcium. (See pl. XIII., fig. 5.)

The polygamous condition is much more common, and in some districts I have often experienced difficulty in finding a true male tree. When at Vavuniya with Mr. H. P. C. Armitage in April, 1902, every tree examined in the neighbouring village compounds possessed male and hermaphrodite flowers, and the extent to which polygamy existed reminded one of D. Gardneri, D. sylvatica, and D. affinis. (See pl. XII., fig. 4.)

The flower systems on the polygamous trees are dichasial cymes, and more often than not the median flower is hermaphrodite; sometimes the whole inflorescence consists of male flowers only. Hermaphrodite flowers are particularly abundant where there has been excessive production of flowers in a local area; perhaps this can be correlated, physiologically, with causes similar to those which determine the frequency as median or top flower of other cymes; certain it is that female flowers occur in areas where vegetative or floral construction is at the maximum.

Male inflorescence consists of a dichasial cyme of 3–15 flowers (*cf.* D. Toposia), sessile or subsessile on lower part of young shoots in axil of caducous bract of foliage leaf; bracts small, caducous, tapering apex, green, 2 mm. long. (See pl. XIII., fig. 1.)

Flowers.—The buds are linear, tapering, 10 mm. long and 2 mm. diameter.

Calyx funnel-shaped, green, 4 mm. long; segments 4, accrescent, green, speckled with white, rounded apex, short, nearly glabrous ventrally, hairy on dorsal surface, margins ciliate.

Corolla tubular, yellow, throat constricted, total length 11 mm.; segments 4 (rarely 3), glabrous, narrow, thick, rounded apex, rotate, 6 mm. long.

Stamens numerous, 20–30, usually 16, arranged in 8 epipetalous connate groups of 2's or 3's disposed opposite and alternate to corolla segments; one group of 4 consisted of a yellow pedicel 1 mm. long bearing 2 lateral sessile fertile anthers each 2 mm. long, immediately above this

point was a third anther disposed introrsely on a short filament, and above this, terminating the connate group, was the outermost and fourth anther, introrse, on a filament 2 mm. long.

One flower contained six groups of 4, and two groups of 2 stamens; the fusion of the filaments suggests a relationship to D. pruriens and D. Embryopteris; *anthers* white or brown, glabrous, apiculate; *filaments* glabrous, except near anther. (See pl. XIII., fig. 6.)

Pistil rudimentary, green flattened hairy disc.

Female flowers (see pl. XIII., figs. 2 and 3) are solitary, subsessile, in axil of foliage leaf or caducous bract; bracts 2, green, pubescent, forming on the short peduncle an opposite pair at right angles to antero-posterior axis.

Calyx green, cup-shaped, 3 mm. deep, with horizontal or descending segments; segments 3–4, 9 mm. long, acute apex, glabrous or nearly so.

Corolla yellowish-white, total length 15 mm., throat wide; segments 3–4, rotate, broad, 9 mm. long, rounded apex, recurved when mature.

Staminodes 8, flattened, epipetalous, opposite and alternate to corolla segments; *anthers* 1–5 mm. long, yellow or white deltoid, apiculate, hairy apex; *filaments* white, glabrous, broad base, 2 mm. long.

Pistil with green or yellow style; stigmas 4–5-lobed; ovary green, glabrous, 8-celled.

Fruit depressed, globose or subglobose, apiculate, glabrous, green; fruiting calyx forms an enlarged shallow woody cup lined with pedicellate glandular and also unicellular hairs; the margin becomes recurved and segments project outwards and downwards. (See pl. XIII., figs. 7 and 8.)

Seeds 2–8 in each fruit, flattened or wedge-elliptical in shape, 14 mm. long, 6 mm. wide, 3 mm. thick; testa brown or black; endosperm hard, copious, equable; embryo white, 5–6 mm. long. (See pl. XVIII., fig. 8.)

Seedlings epigeal, cotyledons persistent, epicotyledonary system delayed developmentally; *cotyledons* sessile or

subsessile, green, glabrous, ovate, tapering apex, broad base, size 26–38 mm. long, and 12–19 mm. wide, palisade tissue developed early; *hypocotyl* creamy-white, turning black, 50–60 mm. long. *Epicotyledonary* stem does not appear for several weeks or months after full exposure of cotyledons; when bearing three leaves it is about 15 mm. long.

The lowest epicotyledonary leaf is always very small, ovate, with broad apex; this serves to distinguish the young seedling from those of D. montana. The first pair of epicotyledonary leaves are at different levels but in the same plane, cutting that of the cotyledons at right angles; *traces* 2 per cotyledon, cotyledonary xylem may or may not become diffused; 1 trace per epicotyledonary leaf, which is not continued into the root.

Timber.—The wood from this species supplies the greater part of Ceylon ebony; that sold as bastard ebony may come from this species or from D. oocarpa, D. affinis, &c. D. Melanoxylon affords an equally good black heartwood. The ebony in the stem may increase from below upwards or may repeatedly increase and decrease in volume along the length of individual trees. Ebony has been noticed in saplings and in very small two year old twigs and even in roots.

The timber is jet black or streaked, very hard and heavy, and takes a good polish; the density is very high, and according to Hiern the seasoned wood weighs 81 lb. per cubic foot, and the unseasoned 90 to 100 lb. During the last five years no less than 2,635 tons have been sold in Colombo, realizing over £22,000.

The central black wood is usually obtained by cutting away the white sapwood. If the tree is allowed to lie on the ground for many months the white wood is removed by ants; occasionally wood borers eat into the hard black wood. As to yield of black heartwood per tree, Mr. Broun states that fifteen trees, varying in girth from 6 to 12 feet, gave a gross volume of 1,208 cubic feet, out of which only 282 cubic feet

consisted of ebony. The largest log seen by Mr. Broun measured 7 feet in circumference after the sapwood was removed. The proportion of black heartwood is said to increase on poor soils.

Rings of growth are inconspicuous, though in the sapwood a zoned structure of light and dark bands is presented. The area between any two narrow dark bands varies from 0·2–8 mm. radially. The dark band possesses fibres with thick walls and reduced radial diameters ; the wood parenchyma traverses these bands of thick-walled fibres without reduction in size ; the tracheal elements are equally abundant in the dark and light zones. (See pl. IV., fig. 16.)

There are not sufficient reliable data concerning the rates of growth of these trees. One tree at Peradeniya measured 147 mm. in circumference on 13th August, 1900 ; on 1st March, 1904, it measured 180 mm.; seedlings two years old may be 900–1,200 mm. high, and about 15 mm. diameter when grown in the open. Mr. Broun states that after passing 3 feet in girth they are very slow growing, and that probably a tree reaches a girth of 18 inches (4·57 metres) at 25 years, 26 inches at 75 years, 54 inches at 135 years, and 6 feet at the age of 200 years.

The anatomy and chemistry has been dealt with in the preceding part. (See pl. XIX., figs. 1–5.)

Uses.—The timber is used in China for making chopsticks, pipes, and carved stands ; in Europe for turnery, cabinet work, piano keys, rulers, walking sticks, brushes, and general furniture.

The gummy astringent fruits are often eaten for their medicinal and feeding properties.

Distribution.—Chiefly in forests of dry and intermediate zones. In the moist zone it is rare and sporadic, extending up to 4,000 feet ; it is abundant in the Northern Province, especially north-east ; among many other places the following may be mentioned : Colombo, Pasdun korale, Hinidúma, Hantane, Deltota, Matale, Kandy, Hewesse, Dambalagala, Pindeniya, Gangaruwa, Kaduganna wa,

Ambalawa, Passara, Bibile, Viriniya, Bintenna, Vavuniya, Trincomalee, Anuradhapura. Also in South India and Malaya.

Diospyros pruriens, Dalz. in Kew Journ. Bot., Vol. IV., p. 110, n. 2 (1852).

Bu-Kaluwara, S. (see below, p. 153.)

Thw. Enum. 423. C. P. 2,836. Hiern, Mon. Eben. 185. Fl. B. Ind. III., 553. Bedd. Ic. Pl. Ind. Or. t. 129.

A small drooping or erect tree with trunk rarely exceeding 1 foot circumference, evergreen, diœcious; branches and young twigs densely coated with long stiff brown hairs, 3–5 mm. in length; bark black, rather smooth, with narrow short ridges running longitudinally, reddish-brown when cut. Leaves not abundant, alternate, 50–100 mm. long, 15–45 mm. wide; obtusely acuminate apex, rounded or subcordate base, densely covered under surface with long yellowish-brown stiff hairs, especially on the veins, midrib, and margin, upper surface glabrous except along midrib, thin, not coriaceous, pale green below, venation widely reticulate and faintly pellucid, lateral veins not strong; *petiole* 2–5 mm. long, reddish-brown, covered with long stiff hairs. (See pl. XIII., fig 9.)

The male inflorescence arises in the axil of a foliage leaf, and consists of a raceme of 3–4 pedicellate flowers, the oldest being at the base and youngest at the top; primary peduncle is reddish-brown, covered with long stiff hairs, 10 mm. long, 1 mm. diameter, widening towards flowers; bracts subtending pedicel of each flower reddish-brown, rounded, very hairy on lower surface, caducous, 3 mm. long.

Flowers yellow, measuring 13–25 mm. in length. (See pl. XIII., fig. 9.)

Calyx green, 8 mm. long, 5 mm. diameter at base; segments 4, thin and papery, accrescent, linear-oblong, narrow at base, tapering acuminate apex, neutral surface covered with long yellowish-white hairs 5 mm. in length.

Corolla yellowish-white, 13–25 mm. long, 24 mm. top diameter when flower open, throat tubular, narrow inner surface hairy, ventral surface covered with long white hairs, 2·5 mm. diameter, but shows conspicuous basal swelling, segmental portion being much longer than tube ; segments 4, rotate with basal part overlapping considerably, tapering acute apex, reddish-brown tint when mature, 13 mm. long, 6 mm. wide at base.

Stamens 12–14, forming hypogynous connate group terminating receptacle or surrounding hairy rudiment of ovary ; in one case the connate base of andrœcium bore 7 separate stamens, each of which had a short white curved filament and gray anther opening introrsely by longitudinal slits, and measuring 1·5 mm. long; projecting above this was a yellowish-white pedicel 3 mm. long, which terminated in 5 sessile introrse anthers. The total length of this staminal system varies from 5–8 mm., and is the only one of its kind met with in Ceylon species. (See pl. XIII., fig. 10.)

Pistil absent or represented by rudimentary disc.

Female flowers yellow, solitary in upper axils of foliage leaves. Peduncle 16 mm. long, 12 mm. wide, covered with long stiff hairs, and often curved so as to place the flower with stigma pointed downwards.

Calyx green, accrescent in flower ; segments 4–5, oblong, tapering acute apex, 8 mm. long, 3 mm. wide at base, ventral surface covered with long white hairs, dorsal surface rather shiny and subglabrous.

Corolla yellow, tubular, constricted towards middle, 10–28 mm. long ; segments 4–5.

Staminodes 5 or more, epipetalous, linear ; anthers and filament glabrous.

Pistil greenish-yellow, densely coated with long white hairs, styles 2, separate, 4 mm. long, stigmas 4, yellow ; ovary depressed, globose, 4-celled, 5 mm. diameter.

Fruit solitary, globose, strongly apiculate, 20 mm. diameter, 25 mm. high, greenish-yellow, covered with long white hairs said to sting, wall thin and shrinks considerably

a few hours after fruits collected; fruiting calyx only slightly enlarged, segments inclined or nearly horizonal, thin, no cup formed, 11 mm. length, 4 mm. wide at base. (See pl. XIII., fig. 11.)

Seeds 1–4 per fruit, elliptical-wedge to globose-ovoid in shape; testa reddish-brown, smooth, 16 mm. long, 10 mm. wide, 10 mm. thick; endosperm equable and under great pressure in young fruits; embryo white, 6–10 mm. long. (See pl. XIII., fig. 12.)

Seedlings epigeal, cotyledons detached early, epicotyledonary leaves enhanced developmentally, testa does not split (*cf.* D. ovalifolia); *cotyledons* white, glabrous, square base, rounded apex, prior to detachment measure 11 mm. long, 8 mm. wide; *hypocotyl* reddish and densely covered with long white hairs (very characteristic), 70–80 mm. long, 5 mm. diameter; *epicotyledonary stem* red, 10 mm. long, first two epicotyledonary leaves form opposite pair; *traces* 3 per cotyledon, xylem of median trace equal or stronger than either lateral, diffused in lower part of hypocotyl; epicotyledonary traces 1 per leaf, weak, continued into root, but not into apical parts. (See pl. XVIII., figs. 1–5.)

Timber never black, but white tinged with yellow when freshly cut, on exposure turns red; heavy, compact; elements partially filled with reddish-brown deposit, low per cent. number of tracheal elements, and 78·30 to 80·99 per cent. fibres. The small size of trees of this species renders the extraction of the coloured wood, when present, unprofitable. (See pl. I., fig. 1.) The hairs on the twigs and fruits are said to possess stinging properties. F. Lewis, Esq., suggested the appropriate native name for this species.

Distribution limited to our wet zone, Southern Province and South-Western Province, up to 2,000 feet. This is one of our very rare species. Thwaites collected the vegetative organs only. Trimen did not see either flowers or fruits of this species. In the forests of Gilimale, Sinha Raja, Marakelle, Idikada-Mukalana, and Koskandahena the plant occurs as a sparsely foliated bushy tree, 900–1,500 mm.

high, and often a single plant is of a size convenient for a herbarium specimen. Owing to the kindness and assistance of F. Lewis, Esq., Assistant Conservator of Forests, I was able to make a tour through the Peak Wilderness, where this species proved to be very abundant in local areas. In the vicinity of Magala, Kadawatta, and Eratna, on rocky sandy soils andalong precipitous streams, this species attains a height of 6,000-9,000 mm. (20-30 feet) and a circumference of about 300 mm. (1 foot). It has also been found in the Marakelle forest, Kuruwiti korale (Lewis). Also occurs in Bombay and Mysore.

Diospyros attenuata, Thw. Enum. Cey. Pl., p. 182, n. 18 (1860).

Kadumberiya, S.

Thw. Enum. 182 (1860). Fl. B. Ind. III., 561. C. P. 3,478. Bedd. Ic. Fl. Ind. Or. t. 139. Hiern, Mon. Eben. 182.

A small tree rarely exceeding $1\frac{1}{2}$ feet in circumference and 20 feet in height, bearing flowers when trunk one inch (25 mm.) diameter ; forms a mat of roots at the base ; evergreen, dicœcious ; young shoots sparingly puberulous, quickly glabrescent ; bark black, not scaly, red when freshly cut ; branches and foliage present a weeping habit, branches given off low down.

Leaves (*cf.* D. Thwaitesii) alternate, 50–115 mm. long, 12–30 mm. wide, narrowly ovate or oblong-lanceolate, acuminate apex, narrowed or acute at base, young leaves glabrous except on under side of midrib, thin, reddish when young, green when mature, venation reticulate, feebly pellucid in young leaf, but opaque in old leaves, lateral veins fine but more conspicuous in old leaves ; *petiole* green, glabrous, 2–4 mm. long. (See plate XI., fig. 15.)

Flowers and ripe fruits September to December.

Male inflorescence consists of a sessile cluster of 3–25 very small narrow flowers borne in axil of leaf or on old twigs ; the same plant may bear flowers in successive years. Each flower is in the axil of a very small bract covered externally

with black hairs ; only rarely are the flowers solitary. (See pl. XI., figs. 10 and 11.)

Flowers long and narrow in bud measuring 9 mm. long and 1·5 mm. diameter, smallest flower among Ceylon species of Diospyros, dirty yellow in colour, usually turned downwards, and easily detached.

Calyx small, dark brown, pubescent, 2 mm. long; segments 4–5, deltoid, acuminate apex, 0·9 mm. long, densely coated with dark hairs.

Corolla small, dirty white, diameter of open flower 5 mm., diameter at base 2 mm., covered externally with dark adpressed hairs ; segments 4–5, acuminate, rotate, sub-glabrous inside, 2 mm. long.

Stamens epipetalous, 4–6, unequal in length, glabrous (4–5 in one row, Hiern) ; *anthers* yellow, 1·6 mm. long, tapering apex, occasionally apiculate ; *filaments* white, 0·3–1·2 mm. long ; *pollen* greenish-yellow, thin smooth wall, circular, coarsely granular contents.

Pistil rudimentary or as central flat hairy disc.

Female flowers sessile and solitary in leaf axil ; in bud four-sided, pyramidical, 7 mm. long, dirty yellow in colour; when open measures 10 mm. in length, average diameter 5 mm. (See pl. XI., fig. 14.)

Calyx segments 3–4–5, accrescent, brown, feeble inter-segmental groove and reflexed margin, deeply divided, deltoid, thinly covered with black stiff hairs, 6 mm. long.

Corolla dirty yellow when fresh, red when about to drop; projects 3–4 mm. above calyx ; segments 3–4–5, rotate, with under surface of exposed halves densely pubescent, tapering acute apex, 4 mm. long.

Staminodes 4–5, epipetalous, alternate with corolla segments ; *anthers* yellowish-brown, barren, glabrous, 1·2 mm. long ; *filaments* yellowish-white, glabrous, 2 mm. long.

Pistil yellow and covered with stiff black accrescent hairs; 6 mm. long in mature flower ; style short, stigmas 2, black, short, each about 1·1 mm. long ; ovary pear-shaped, densely pubescent, 4-celled, 3 mm. in length.

Fruit ovoid-apiculate having a basal diameter of 22 mm., narrowing sharply in the upper part, then tapering gradually to an acute apex ; total length 35 mm. ; wall light green in colour, hairs short and sparse ; calyx of fruit enlarged to total diameter of only 16 mm., not accrescent, deeply lobed, thin, green, hairy. (See pl. XI., fig. 13.)

Seeds 2–3–4 per fruit ; 25 mm. long, 10 mm. wide, 5 mm. thick ; elliptical-wedge or semilunar shape ; testa umber brown, smooth ; endosperm copious, equable. (See pl. XI., fig. 12.)

Seedlings epigeal, cotyledons detached early, epicotyledonary leaves enhanced developmentally. *Cotyledons* pale colour, ovate ; *hypocotyl* white turning black, 75–80 mm. long, 3 mm. diameter ; *epicotyledonary* stem 20–25 mm. long ; first epicotyledonary leaves form an opposite pair, leaves being broadly ovate with tapering apex, rounded base, venation reticulate and feebly pellucid, length 40–45 mm., and width 25–30 mm. ; *traces* 3 per cotyledon, xylem diffuse, epicotyledonary traces 1 per leaf.

Timber red with small black decaying heartwood, heavy, very compact fine grain ; the smallness of the tree, maximum diameter being about 160 mm. (6–6½ inches), renders it impossible for most commercial purposes ; tracheal elements are narrow but irregularly differentiated, fibres abundant. The medullary rays and vessels have characteristic large lumina. (See pl. III., fig. 10.)

The coloured materials are absent from the fibres, but are moderately abundant in the medullary ray cells and vessels. The wide pits between adjacent medullary ray cells possessing coloured materials are often completely choked with the coloured material, suggesting the passage of these substances in solution from cell to cell.

Distribution.—This is one of our very rare endemic species, being limited to the wet forests in the south of the Island. It occurs as a very small tree along river sides in the damp forests of Wewella, Pasdun korale, about eight miles north-west of Hinidumkanda. It has also been found at

Hewessa, but nowhere else. It grows in rich clayey soil, and often accompanies D. acuta. When not in flower or fruit it is very difficult to distinguish from small trees of D. Thwaitesii.

Trees with trunks only 25 mm. diameter bear flowers and fruits. Solitary trees are rarely met with in some forests, there being a tendency for them to occur in clumps of 1–7 ; this must be due to some difficulty in transference of seeds; the seeds come up very freely in the forest, the primary root forming a straight axis which pierces the attenuate apex of the fruit and soon establishes itself.

Diospyros acuta, Thw. Enum. Ceyl. Pl., p. 182, n. 17 (1860).

Thw. Enum. 182. C. P. 3,476. Fl. B. Ind. III., 561. Hiern, Mon. Eben. 182.

A small tree, largest measuring 102 mm. diameter (4 inches) and height 10·6 metres (35 feet), flowers when only 25–75 mm. diameter, evergreen, monœcious only ; bark black, when freshly cut is red in colour. *Leaves* alternate, 120–250 mm. long. 30–70 mm. wide, narrowly lanceolate-oblong, tapering gradually to an obtuse or acute apex, narrowing at base, glabrous, very thick, deep green above, pale green below ; venation reticulate but only feebly pellucid, lateral veins never project on either side ; *petiole* stout, slightly channelled above, 25 mm. long ; when not in flower or fruit very difficult to distinguish from D. Moonii. Flowers and fruits September to December.

The sex is only met with in the monœcious state ; the clusters in the axil of a particular leaf usually possess all male or all female flowers ; the female clusters seem characteristic of the younger leaves towards the end of the twigs (*cf.* D. Ebenum ; D. oppositifolia).

Thwaites remarks that the flowers are sometimes monœcious, female above, male below.

The male inflorescence consists of sessile clusters of 1–7 flowers. The bract subtending each flower is green, caducous, pubescent with tapering apex, 5 mm. wide at base

and 7 mm. in length. The flowers are yellowish, 14 mm. long, average diameter in bud 3 mm., diameter of open flower 10 mm. (See pl. VII., figs. 8 and 9.)

Calyx brown, densely pubescent, 7 mm. long; segments 4–5, accrescent, acute apex, 4 mm. long.

Corolla yellow, segments and throat covered with yellowish-brown hairs, 16 mm. long when open; segments 4–5, rotate, very hairy on half of under surface, tapering acuminate apex, 4 mm. long.

Stamens 5–7–9, epipetalous, glabrous, separate or united in pairs, unequal in length; often the inner stamen of a pair is very small and contains very little pollen; *anthers* yellowish-brown, apiculate, 3 mm. long; *filaments* white, 2 mm. long; *pollen* circular, yellowish-green, thick-walled, granular contents.

Pistil absent or rudiment of unicellular hairs terminating receptacle.

The female inflorescence is sessile and usually consists of 1–3 flowers; when solitary a pair of opposite bracts is easily seen; when there is a sessile cyme of three flowers, it is difficult to determine the position of the bracts, which are very early caducous; bracts larger than in male, covered with brown hairs. (See pl. VII., figs. 10–12.)

Flowers large and in bud measure 15 mm. long, 5 mm. diameter.

Calyx large, 12 mm. long, brown, both surfaces densely pubescent; segments 5–6, lanceolate, tapering acute apex, accrescent, small intersegmental groove, margins straight, 8 mm. long.

Corolla yellow, large, 18 mm. long, diameter at base 6 mm., diameter of open flower 14 mm., outer surface pubescent; segments 5–6, rotate, reflexed, hairy beneath, subglabrous above, tapering apex, base 5·5 mm. wide, length 5·5 mm.

Staminodes 5, epipetalous, alternate with corolla segments; *anthers* yellow or brown; *filaments* white.

Pistil large, 13 mm. long; stigmas 2–3, reddish-brown, spathulate, glabrous, and 1·5 mm. long; style densely pubescent, 4 mm. long; ovary globular, apiculate, brown, densely pubescent, 4–6-celled. (See pl. VII., fig. 14.)

Fruit ovoid-attenuate, tapering strongly towards stigmas, 30 mm. long, 15 mm. diameter; fruiting calyx enlarged, segments 15 mm. long, intersegmental groove and reflexed margin pronounced. (See pl. VII., fig. 13.)

Seeds 4–6 per fruit, flattened-elliptical, strongly acuminate at micropylar end, 22 mm. long, 7 mm. diameter; testa umber-brown, smooth and shiny, endosperm copious, equable; embryo white, 12 mm. long.

Seedlings epigeal, cotyledons detached early, 3 traces per cotyledon.

Timber when freshly cut is dirty white, but on exposure turns red; small trunk, no black heartwood, heavy, compact.

The narrow lumined fibres form 88 per cent. of the elements in many parts, and the rings of growth are very inconspicuous.

The elements are never abundantly supplied with contents, the majority being not more than quarter filled; in the sapwood the contents are always yellow and in the form of globules; in the heartwood they are of a deeper colour, occasionally granular, but never abundant. (See pl. III., fig. 11.)

Uses.—Only the timber is used.

Distribution.—This is a very rare endemic species found with D. attenuata in the Wewella, Wirakanda, and Hewessa forests, Pasdun korale. It has not been found outside this very wet area.

The trees usually vary from 4 to 6 metres (20 to 30 feet) in height and 25–75 mm. in diameter, the maximum size being quoted above; they thrive best in clayey or boggy patches and like D. attenuata frequently occur in clumps of 3–14 trees, the leaders being matted together by dense woody roots at the base. The leaves and large stems are very similar, microscopically, to D. Moonii.

Diospyros Gardneri, Thw. Enum. Ceyl. Pl., p. 181, n. 12 (1860).

Kadumberiya, Kallu, S.

Thw. Enum. 181. C. P. 1908. Fl. B. Ind. III., 561. Bedd. Ic. Fl. Ind. Or. t. 132. Hiern, Mon. Eben. 182.

A moderate-sized or large tree, evergreen, dicœcious and polygamous; branches glabrous, young twigs pubescent; bark black, thick, when freshly cut yellowish-red. *Leaves* very variable in size and form, alternate, 75–180 mm. long, 25–55 mm. wide, oblong or oval-lanceolate, acuminate apex, narrowed at base, glabrous and shining, thinly coriaceous, deep green above, paler green beneath, venation reticulate, pellucid, bullate, lateral veins prominent beneath; *petiole* 7–25 mm. long, slightly pubescent below.

The peduncle is usually curved so as to bring the flowers directed downwards, in which case they are partially protected from sun, wind, and rain by the leaves.

Sex.—Some trees are male only, others female only, and others polygamous; several of the latter group are growing at Peradeniya.

The polygamous condition may be observed on many trees growing at Peradeniya, and has been determined for three years in succession; the flowers on polygamous trees may be grouped as follows: (*a*) those with short accrescent calyx segments, fertile anthers, and abortive apiculate pistil; (*b*) those with large deltoid calyx segments, margins of which are straight or recurved, fertile anthers, and abortive apiculate pistil; (*c*) those with large deltoid calyx segments with deep intersegmental grooves, fertile anthers, and fertile pistil producing seeds. Hence the series from male to hermaphrodite flowers on the same tree is gradual and complete. (See pl. XII., figs. 1–8.)

The accessory whorls exhibit very few external characters which enable one to distinguish the male from hermaphrodite flowers. The enlarged recurved calyx segments are the best external indications of a hermaphrodite flower, but

these characters may be absent in such flowers, or may be occasionally present in male flowers.

The development and anatomy of the seedlings was originally studied from seeds obtained from the polygamous trees.

The male and hermaphrodite flowers occur separately or as members of the same axillary inflorescence (*cf.* D. sylvatica and D. Ebenum).

Male inflorescence consists of sessile and subsessile pubescent cymes; developmentally it first appears as a red pubescent bud in the axil of a leaf with or without a peduncle; on either side at right angles to the antero-posterior axis a bract appears, each subsequently bearing a flower in its axil. After a long interval another pair of opposite bracts appear in a plane at right angles to the first, followed by a flower in the axil of each. The primary flower occupying the centre of the inflorescence may be subsessile or supported on a peduncle 10 mm. in length, but each subsequent flower is always sessile. Further complications follow in consequence of the development of pairs of flowers around each of the subsequent flowers mentioned above. Peduncle 1-2-10 mm. long, green, pubescent; bracts small, 2·5 mm. long, 2 mm. wide, caducous, tapering apex, pubescent. (See pl. XII., fig. 5.)

Calyx green, ventral surface pubescent, 5 mm. long; segments 4, 3 mm. long, accrescent, deltoid, acuminate apex, straight or slightly recurved margin.

Corolla yellow, conical in bud, 10–13 mm. long, tube inflated; segments 4, half the length of tube, spreading, glabrous inside, silky pubescence outside.

Stamens 12–16, epipetalous or monadelphous hypogynous group, separate or connate in pairs, inner series always shorter than outer; when 12 only they are usually as 4 pairs and 4 singles, the former being divisible into an outer and inner series; *anthers* inner series 3 mm. long, apiculate,

glabrous or slightly pubescent, 1–5 mm. long; *pollen* yellow, even circular outline. (See pl. XII., figs. 9 and 10.)

Pistil absent or represented by a flattened apiculate disc which often shows in transverse section a crude celled structure.

Female flowers are solitary in axil of leaves, sessile or subsessile; peduncle 4 mm. long, and possesses two pairs of bracts which never bear flowers in their axils, but from comparison one may perceive a similarity with a cymose inflorescence in which all except the primary flower abort (*cf.* D. Embryopteris); first pair of bracts brown, near base of peduncle and at right angles to antero-posterior axis; second pair green, hairy, and at right angles to the first. (See pl. XII., figs. 11 and 12.)

Calyx green, openly campanulate, pubescent; segments 3–4, usually 4, 10 mm. long, deltoid, margin recurved and undulated so as to form a ridge, 2 mm. wide, projecting outwards and downwards, tapering apex.

Corolla white or yellow, tube 8 mm. wide, when mature 15 mm. long and 10 mm. diameter at top, silky pubescent beneath; segments 3–4, 7–10 mm. long, 2 mm. wide, strongly reflexed or spreading in open flower.

Staminodes 8, epipetalous, opposite and alternate with corolla segments, 5 mm. long, 0·5 mm. wide; *filaments* white, hairy, 3 mm. long, adnate to corolla tube at base; *anthers* white, barren. (See pl. XII., fig. 13.)

Pistil with stigmas 3–4, greenish-white; style persistent, 5 mm. long; ovary globose-apiculate, pubescent, 8-celled.

Fruit solitary, green, nearly glabrous, depressed-globose, apiculate, yellow when ripe, 35 mm. high, 25 mm. diameter; fruiting calyx enlarged and hemispherical, deep undulating intersegmental grooves, cup for fruit 15 mm. deep. *Seeds* usually 8 per fruit, thin and flattened, micropylar end slightly recurved, antipolar end straight or rounded, 15–18 mm. long, 8–10 mm. wide, 2 mm. thick; testa olive-brown, shining, not streaked; endosperm copious and equable; embryo white and measures 17 mm. in length.

Seedlings epigeal, cotyledons persistent, epicotyledonary system late in development; *cotyledons* pale green, 40 mm. long, 20–30 mm. broad, cordate, tapering apex, rounded base; *hypocotyl* erect, 90 mm. long, 2–3 mm. diameter, glabrous, becomes black and four-cornered; *epicotyledonary* system does not appear until several weeks or months after cotyledons fully developed; *epicotyledonary* leaves are alternate and measure 25 mm. long, 12 mm. wide, glabrous, deep green, coarse bullate venation; 2 *traces* to each cotyledon, xylem split considerably; epicotyledonary traces 1 per leaf, not continued into root.

Timber yellow with occasional black strands, inferior; similar to D. sylvatica; wood parenchyma wide lumined, tracheal elements rather low percentage number; large radial strands of parenchyma occur in the wood (*cf.* D. quæsita); the coloured contents are not abundant; timber used for buildings. The wide lumined parenchyma and the sparse contents of the secondary xylem elements prove the timber to be of inferior quality. (See pl. II., fig 7.)

Distribution limited to wet and intermediate zones of Ceylon, up to 2,500 feet; Colombo, Ratnapura, Kurunegala, Hantane, Gangaruwa, Ambalawa, Karawita, Sinha Raja forest, Pindeniya, Eratne, Gammaduwa.

Diospyros oocarpa, Thw. Enum. Ceyl. Pl., p. 180, n. 9 (1860).

Kalu kadumberiya, Eta timbiri, S.; Vellai karunkali, T.

Thw. Enum. 180. C. P. 1,914.

Fl. B. Ind. III., 560. Hiern, Mon. Eben. 171.

A moderate-sized or large tree, evergreen, diœcious; bark thick, dark surface, yellowish when cut, young shoots faintly pubescent; flowers in April, fruits in September.

Leaves alternate, 50–90 mm. long, 25–50 mm. wide, ovate or oval, obtusely acuminate at apex, rounded at base, glabrous and shining, thinly coriaceous; venation widely reticulate and faintly pellucid, but inconspicuous in old leaves; *petiole* flat, 5 mm. long. (See pl. VII., fig. 7.)

Male inflorescence consists of an axillary dense sessile or sub-sessile cyme, each flower being subtended by a concave rounded bract.

Flowers bomb-shaped, tapering from base to apex and measuring 12 to 25 mm. when unopened. (See pl. VII., fig. 1–3.)

Calyx green, faintly pubescent, forming a cupule 5 mm. high and 4 mm. diameter; segments indistinct with margins forming an even outlined rim.

Corolla yellow, throat narrow, 13 mm. long; segments usually 3, long and tapering, 6 mm. long, reflexed when flower mature. One of the segments is completely enclosed by the others in bud, the other lobes imbricating sometimes dextrorsely and at other times sinistrorsely (Hiern).

Stamens indefinite, 9–11–12–14, epipetalous or hypogynous, unequal, not apiculate, in pairs or single; *anthers* brown, hairy, 1 mm. long; *filaments* white, glabrous, 0·5–2 mm. long; *pollen* yellow, circular.

Pistil represented by rudimentary hairy disc or absent.

Female inflorescence consists of sessile cluster of 3 flowers; sometimes the flowers are solitary; bracts very small and caducous. (See pl. VII., fig. 4.)

Flowers bomb-shaped when young, 12 mm. long, 4 mm. in diameter.

Calyx brownish-black, thin, glabrous or feebly hairy, forming a cupule 5–7 mm. high; segments indistinct, agreeing with male calyx; calyx of quite specific type.

Corolla greenish-yellow, tapering to apex, 15 mm. long; often closed; segments 3, not very distinct, short, walls very thick.

Staminodes 3, epipetalous, very short, total length being 0·5 mm.; *anther* barren, brown or yellow, hairy towards apex; *filament* white, glabrous and about one-third the length of anther.

Pistil brown, hairy, small; stigma single or bifid, short; ovary 6-celled.

Fruit oblong-ovoid, 35 mm. high, 23 mm. average diameter, wider at the top than towards calyx, rounded at top, apiculate ; carpellary wall green, glabrous, uneven surface first being papillate and finally strongly lobulate, the lobes being conspicuous in one seeded fruits ; usually 4–6-celled, one seeded ; fruiting calyx slightly enlarged, flat, circular, total diameter 11 mm., persistent, glabrous, black. (See pl. VII., fig. 5.)

Seeds flattened, elliptical, with two longitudinal grooves running along the surface, or tending to become as broad as long with a beaked micropyle and as many as five deep longitudinal grooves ; form different from all other species; average length 25 mm., width 15 mm.; testa brown, shiny; endosperm copious, horny, equable ; embryo white, 11 mm. long.

Seedlings epigeal, cotyledons detached early, epicotyledonary leaves slightly enhanced developmentally ; *cotyledons* narrow, yellow, 12 by 4 mm.; *hypocotyl* short type, 10–30 mm. long, 2·5 mm. diameter, at first white, but soon turns brown and black ; epicotyledonary stem long, slender type bearing several small leaves along its length at intervals of about 10-20 mm.; at a distance of about 40 mm. the large leaves are borne alternately ; stem greenish, densely pubescent ; epicotyledonary leaves lanceolate-ovate, even surface, glabrous above except along midrib, pubescent beneath, venation faintly pellucid ; veins not prominent on either side, widely reticulate, petiole short ; *traces* three per cotyledon, xylem splits into 8–13 strands ; one trace per epicotyledonary leaf, continued below cotyledonary node.

Developmentally and morphologically these seedlings are, in many respects, like those of D. insignis. The epicotyledonary leaf rudiments suggest Garcinia.

The timber is very variable. The young trees have usually a small black or brown heartwood, and a sapwood of a faint red tint ; large trees possess a coloured heartwood of considerable size ; one tree having a total diameter of

690 mm. had a heartwood 440 mm. diameter. The heartwood of such trees is invariably irregular in outline and presents a beautiful alternation of black and brown layers, which from an ornamental point of view greatly enhances the value of the timber; such specimens are almost equal to calamander for ornamental purposes. The sapwood of large trees may possess irregular dark lines, which in longitudinal section give good patterns to the coloured timber. The coloured materials occur in all elements of the sapwood except the fibres. The contents of the parenchyma cells is at first granular, but when these granules have disappeared the coloured contents take on the appearance of a gum-resin. In the heartwood all the elements, fibres included, become filled with brown or black contents, with or without a change in the colour of the walls of the elements. The only clear lines in a transverse section of the black heartwood are those of the medullary rays, the comparative clearness of this tissue being due to the thinness of their walls and the partial exhaustion of contents.

Anatomically the timber is characterized by abundance of closely set fibres, and large tracheal elements, and a low percentage number of medullary ray cells. The differentiation is very irregular. Rings of growth are very inconspicuous.

The timber of this tree is rarely met with, and may in some cases furnish the bastard ebony of commerce. (See pl. IV., fig. 15.)

Distribution rare in the dry and intermediate zones: Haragama, Uma-oya, Kurunegala, between Nalanda and Dambulla, Maturata, Kalugalla, Mihintale.

Also in Konkan and Babaloodun hills, Mysore.

Diospyros quæsita, Thw. Enum. Ceyl. Pl., p. 179., n. 7 (1860).

Kalumediriya, S., Calamander.

Thw. Enum. 179. C.P. 3,010. Fl. B. Ind. III., 560. Bedd. Ic. Pl. Ind. Or. Pt. VII., p. 26, t. 128 (1871). Hiern, Mon. Eben. 174.

A large slow-growing evergreen tree, dicœcious; trunk erect and feebly buttressed; branches dark and spreading; bark blackish-gray, 12 to 20 mm. thick in very old trees, peels off in thin sheets exposing brownish layer beneath; bark of twigs shows irregular, narrow, longitudinal ridges; young twigs stout, green, glabrous.

Leaves alternate, 75–180 mm. long, 40–80 mm. wide, oblong-oval, or oblong-lanceolate, shortly acuminate obtuse apex, glabrous, coriaceous; venation feebly pellucid in young leaves, lateral veins inconspicuous, nearly horizontal, prominent when dry; *petiole* 12–20 mm. long, stout, flattened, and canaliculate above.

Male inflorescence occurs in axil of foliage leaf or small caducous bract; in former case there is often congenital concrescence of peduncle and stem for a distance of several mm.; flowers 3–9 on drooping pedicels along the length of primary peduncle at very irregular distances, the first flower occurring at the base or 20 mm. above the base; primary peduncle green, stout, very variable length; each flower is pedicellate and subtended by a caducous bracteole. Each pedicel bears an opposite pair of small bracteoles; pedicels green, slightly pubescent, wide towards flower, 6 mm. long, 1·5 mm. diameter; bracteole subtending pedicel green, pubescent, sessile, tapering obtuse apex, rounded base, caducous, 8 mm. long, 2 mm. wide; basal bracteole and axis green, covered with long unicellular hairs, lanceolate, tapering apex, 4 mm. long, early caducous leaving small scar. Hence there appears to be an inflorescence, which though now approximating to a raceme, possesses the rudiments of a dichasial cyme. (See pl. VI., fig. 7).

The flowers are often closed when the mature pollen is ready for dispersion; the diameter of open throat is small (*cf.* D. Toposia).

Calyx green, forms deep cup for floral parts and in bud is elongate-oval, 9 mm. long, 4 mm. diameter; segments pubescent, deltoid, acute apex.

Corolla yellow, tubular, thick, narrow-throated, basal part swollen, 12 mm. long; segments 4–5, rotate, pubescent beneath, broadly ovate, sub-acute apex.

Stamens indefinite, or about 16, terminating receptacle, 3 mm. long; *anthers* yellowish-brown, nearly sessile, attenuate and pubescent apex; *filaments* white, short, glabrous; *pollen* thin-walled, yellowish-white, feebly granular contents.

Pistil absent or rudimentary.

Female flowers.—My first fresh material was obtained through the kindness of F. Lewis, Esq., from Nahitimukalana, Atakalan korale, 1,800 feet above sea level.

Flowers solitary, pedunculate in axil of foliage leaf, or on lower part of young shoots in axil of caducous bracts; in bud 5 mm. long, 8 mm. diameter, resembling in appearance those of D. Melanoxylon. Open flower measures 20 mm. long, average diameter 3 mm. The peduncle is green, pubescent, measures 20 mm. in length, and bears two small caducous bracts at right angles to antero-posterior axis. (See pl. VI., fig. 5.)

Calyx brown, covered with dense layer of velvety hairs; segments 5, acute apex; when young, margin slightly recurved, but later very wide intersegmental grooves are formed. These pouches are at first nearly horizontal, but subsequently widen and become strongly reflexed, the apices of the segments remaining erect and in contact with corolla.

Corolla yellowish-white, pubescent, 15 mm. long, 12 mm. diameter; segments 5, obtuse or rounded apex, recurved in old flowers, 5 mm. long, 5 mm. wide at base.

Staminodes 5, epipetalous, alternate with corolla lobes and 2 mm. in length, occasionally smaller epipetalous alternating structures occur, probably rudimentary or abortive staminodes; *anthers* barren, yellowish-brown, bluntly apiculate; *filaments* white, short, glabrous.

Pistil green, pubescent, 6 mm. long, 5 mm. diameter; stigmas 5, green, short, undulating apices; ovary 10-celled.

Fruit large, 60–75 mm. long, 50 mm. diameter, sub-globose or ovate, slightly flattened at top, apple-green to black, glabrous or nearly so; fruiting calyx enlarged, flattened, woody, intersegmental groove large, margins strongly reflexed. (See pl. VI., fig. 8.)

Seeds 4–10 in each fruit, 30 mm. long, 15 mm. wide, 5 mm. thick, flattened and elliptical in shape; testa brown, shining, striated; endosperm copious, horny, equable. (See pl. VI., fig. 9.)

Seedlings epigeal, cotyledons detached early, epicotyledonary system enhanced in development and distinguishable in resting embryo (see pl. VI., fig. 6.); *cotyledons* white, when mature measure 25 mm. long, 12 mm. wide, oblong-ovate, blunt apex, squarish base, strong midrib; *hypocotyl* yellowish-green, rapidly turning black, glabrous or nearly so, 90–100 mm. long, diameter 3 mm.; *epicotyledonary* stem yellowish-red, 3 mm. long; *epicotyledonary* leaves, first two form an opposite pair at right angles to the plane of the defunct cotyledons, 60 mm. long, 30 mm. wide; *traces* 3 per cotyledon, median abortive, xylem not much split; epicotyledonary traces, one per leaf, probably continued into the root.

Timber.—The timber of this species—calamander—is considered to be one of the best for durability and ornamental purposes. It would be difficult to find a prettier variegated wood, though samples of D. Kurzii, received from the Conservator of Forests, Andaman Islands, come a good second for ornamental value.

The timber is very scarce; the total amount exported from Ceylon during the last five years being 20 pieces only; these were sold in Colombo for Rs. 150. The specimens were in the form of planks, slabs, and small round pieces, the latter measuring 3 to 4 feet in length and 16 inches in circumference.

The heartwood, when present, is usually of a deep brown colour streaked with black. There is however, considerable uncertainty as to the presence and abundance of coloured

heartwood, and many very old trees have been felled which possessed only dirty white or brownish timber, which was therefore as useless as that obtained from D. Moonii. (See pl. V., fig. 17.)

The relative value of samples of calamander is determined by the quantities of coloured material filling the cells; it is not due to a particular type of histological differentiation. The black portions of calamander are not more durable than the heartwood of D. Melanoxylon or D. Ebenum; the deep brown portions are considerably less so. The value of calamander over other Diospyros woods is due to the particular abundance and more general distribution of the colouring materials characterizing the species.

The percentage of fibres varies from 80–86 per cent.; additional strands of parenchymatous tissue occur in the xylem (*cf.* D. Gardneri).

The rings of growth are inconspicuous.

The timber of D. oocarpa and D. affinis sometimes approximates to calamander in point of distribution of coloured substances in the central timber. In these two species, however, there is always a large proportion of useless sapwood.

Uses.—In addition to the timber being used whenever procurable, the ripe gummy fruits are eaten by the natives.

Distribution endemic, rare, this species being found only in the moist low-country up to 2,000 ft. The scarcity of this tree is not alone due to the value put upon its timber, but (*a*) to a curious mode of development, resulting in the death of many of the germinated seeds, (*b*) to the very slow rate of growth in the seedling and later stages; two-year-old saplings measure only 600 mm. (less than 2 feet) in height, and trees over 60 years old have a circumference of 472 mm. (19 inches) only, (*c*) to the dicœcious flower system and the long interval between flowering periods.

There are a good number of trees on Hinidumkanda, and also in the Sinha Raja forest; Potapitiya, Kukulu korale:

Kuruwiti korale ; Ratnapura, Dotalankanda, Pasdun korale; Yagiralla, near Udugama ; Nahitimukalana, Atakalan korale; Pennelmukalana, Madampe district.

The trees grow well on rocky, porous, damp slopes, rich in silica and iron ; they vary from 0·6 to 2·4 metres (2–8 feet) in circumference, and 12 to 24 metres (40–80 feet) in height.

The largest specimen I have seen measured twelve metres (40 feet) before the first branch, total height 27·4 metres (90 feet), and breast height circumference of 2·4 metres (8 feet); this was a male tree, Yagiralla forest, 900 feet above sea level.

Diospyros sylvatica, *Roxb.* Cor. Pl., p. 37, t. 47 (1795)

Sudu-kadumberiya, S ; Karuppu Thoveria, T.

Alph. D.C. Prodr. VIII., p. 231. (1844). Thw. Enum. 178. C.P. 2,729, Fl.B. Ind. III,. 559 Bedd., Ic. Pl. Ind., Part VII., p. 25, t. 121 (1871). Hiern, Mon. Eben. 161.

A very large tree, attaining a circumference of 4 metres (13½ feet) and height of 61 metres (200 feet), evergreen, dicœcious and polygamous ; trunk erect, buttressed at base, bark of twig shows coarse reticulation, bark of trunk blackish-gray, thick. *Leaves* alternate, 70-130 mm. long, 20-60 mm. wide, oval, acuminate apex, narrowed or rounded at base, glabrous or nearly so ; young leaves thin, old leaves coriaceous, deep green above, paler beneath ; venation reticulate, meshes wide, pellucid, midrib and veins depressed on upper side ; *petiole* flattened, feebly puberulous, 5–12 mm. long.

Polygamous trees.—These are very similar to D. Gardneri and D. Ebenum.

The seeds and seedlings from polygamous trees possess the same characters, anatomically and developmentally, as those obtained from pure female trees. All the flowers on these trees possess fertile stamens and a rudimentary or fertile pistil, those with fertile pistils being usually accompanied with larger accessory whorls. The absence of flowers with fertile pistils during the first few weeks of flowering has been noticed, and it seems quite probable that the production

of unisexual and hermaphrodite flowers may be effected during different periods. There is also a tendency for the hermaphrodite and unisexual flowers to occcur in separate clusters, though the mixed condition in the same inflorescence has been noticed (see pl. XI., fig. 4-6). The flowers are strongly aromatic, and Mr. Willis informs me that they are visited by many bees at Peradeniya.

Male inflorescence arises on lower part of young shoots in axil of caducous bract or foliage leaf ; when the latter the clusters are more crowded and abundant. The bud is enclosed in a sheathing bract ; two small bracteoles appear on the primary peduncle at right angles to the antero-posterior axis, and in the axil of each a flower appears. Each lateral flower becomes the median flower of another cyme, and this is repeated until we have a crowded dichasial cymose inflorescence of 7, 15, or more flowers on a peduncle only 7–10 mm. in length. The first pair of lateral flowers have pedicels over 2 mm. in length, but the subsequent flowers are subsessile along their respective axes ; bract subtending inflorescence green, hairy, caducous, 6–10 mm. long ; the bracteoles are much smaller, green, hairy, caducous ; flowers in April, fruits September-February. The inflorescence attains a length of 20 mm. and is similar to the male of D. Ebenum and D. Toposia. (See pl. XI., fig. 1–2.)

The *flowers* are small, white, fragrant and openly bell-shaped.

Calyx green, total height 3 mm. ; segments 3-4, pubescent or ciliate, rounded apex, accrescent, 1 mm. long.

Corolla white, urceolate or campanulate, total height 8 mm., diameter at top 8 mm. ; segments 3–4, rotate, glabrous, rounded apex, 3 mm. long.

Stamens irregular, 13–22, epipetalous, single or united in 2's or 3's forming usually about 8–10 groups ; when in pairs the shorter anther is innermost (*cf.* D. Gardneri) ; *anthers* yellow, introrse, shortly apiculate, dehiscing laterally from apex ; *filaments* white, united or separate, glabrous except near base of anther.

Pistil absent or rudimentary, flat disc, 2 mm. diameter, undulating, exhibits locular structure.

Female flowers solitary, or as a cyme of 3 flowers on peduncle of varying length; pedicels of each flower short, bracteate. (See pl. XI., fig. 8).

Calyx green, 12 mm. diameter; segments 3–4–5, rounded apex, 8 mm. long.

Corolla yellowish-white, 11 mm. long; segments 4, rounded apex, 3 mm. long.

Staminodes 4, epipetalous, alternating with corolla segments, glabrous, white.

Pistil 3 mm. long, 2 mm. diameter; stigmas 3, deep green, glabrous; ovary 6-celled, broad base, tapering apex, green, glabrous.

Fruit globose, smooth, dark gray, 12–20 mm. high, 10–15 mm. diameter; fruiting calyx enlarged, flat or accrescent, thin and not woody, 15–20 mm. diameter.

Seeds 2–4–6 per fruit, 14 mm. long, 10 mm. wide, 6 mm. thick; ovate or globose in shape; testa brown, streaked; endosperm abundant, strongly ruminate and very rich in tannin; embryo white and small, 6 mm. long. (See pl. XI., fig. 7).

Seedlings epigeal, cotyledons persistent. The whole or greater part of the endosperm is absorbed before the testa splits; *epicotyledonary* system does not appear until several weeks, and in one case five months after cotyledons mature.

Cotyledons cordate, rounded base, tapering obtuse apex, glabrous, 25 mm. long; *hypocotyl* red, glabrous, thin, 80 mm. long; *epicotyledonary* stem very short and developed at a late stage; *epicotyledonary* leaves—first leaf appears about 1 mm. above cotyledonary node, second about 2 mm. above first; alternate, deep green, tapering strongly towards base, rounded apex, venation feebly pellucid, 20 mm. long, 11 mm. maximum width; *traces* two per cotyledon, xylem splits forming 8–15 groups; one trace per epicotyledonary leaf, not prolonged into root. Below the collet most seedlings show a

crude octarch exarch cylinder with protoxylem groups joined by strongly lignified perimedullary zone. (See pl. XVII., fig. 5, 6).

Timber when freshly felled is yellow or white with a variable but usually small quantity of black heartwood: inferior but often used for fancy work and buildings. The yellow colour (*cf.* D. Gardneri) is due to the preserving, in very small quantities, of brown or yellow contents in the parenchymatous and tracheal elements. The medullary ray cells of the sapwood possess contents some of which show signs of disintegration and acquire a distinct colour in passing to the heartwood. The number of parenchymatous cells with such contents increases considerably from without inwards and in addition many of the vessels become partially filled with gum-resin of a yellow colour. (See pl. II., fig. 7). The differentiation of the elements is fairly regular; the percentage number of fibres is rather high. This species is only rarely felled for its timber. The rings of growth are visible to the naked eye; sometimes they have a radial diameter of 1 mm. but occur at very irregular distances from one another.

Uses.—The timber though inferior in quality is sometimes used in fancy work. The fruits when ripe are a trifle fleshy: they are occasionally eaten.

Distribution rather rare and limited to the wet zone up to 4,000 feet; Hantana, Gangaruwa, Watagoda, Ekneligoda, Ambalawa, Sinha Raja forest.

Also in S. India.

Diospyros Melanoxylon *Roxb.* Cor. p. 36, t. 46 (1795).

Kadumberiya, S.

Alph. D. C. Prodr. VIII., p. 224 n. 7 (1884). Fl. B. Ind. III., 564.

Roxb. Cor. Pl. t. 46. Hiern, Mon. Eben. 159.

A medium-sized or large tree, evergreen, dicœcious (polygamous?); bark deeply fissured in alternate grey and black layers, fissures running vertically for a great distance: 100

mm. long, 20 mm. wide; the bark is 10 mm. in thickness on branches 40 mm. diameter; young twigs green, pubescent, become glabrous, white and shiny.

. *Leaves* very variable in position and size; usually opposite, sometimes sub-opposite or alternate, often crowded at end of twig, 40–140 mm. long, 15–70 mm. wide, (on suckers the leaves are often 240 mm. long and 100 mm. wide), oblong-oval, rounded or obtuse apex, tapering base, pubescent when young, glabrous and shiny when old, under-surfaces duller green than upper; venation reticulate, meshes wide, pellucid; lateral veins not very conspicuous above, prominent below; *petiole* green, glabrous or hairy, flat above, 4 mm. diameter, 15 mm. long.

Male inflorescence usually consists of a dichasial cyme, 3-7-flowered, similar to that described for D. sylvatica, D. Toposia, &c., and occurs in lower part of young shoot in axil of leaf or caducous bract; sometimes the lateral flowers do not arise in opposite pairs but at different levels suggesting a racemose type. (See pl. VIII., fig. 8).

When the inflorescence is represented by a central flower only, the bracteoles are nevertheless present; the flowers which should occur in the axil of bracteoles in the plane of the antero-posterior axis are commonly absent.

The main peduncle is pubescent, 3–11 mm. long, 2 mm. diameter; pedicels of first pair of lateral flowers longer than those of second pair and measure 15 mm. in length and 2 mm. in diameter; bracts and bracteoles long, pubescent, size gradually decreasing from bract to youngest bracteole.

Male flowers in bud are green, pubescent, 5 mm. long, 3 mm. diameter; open flower 13 mm. long; there is much variation in the number and orientation of the members of accessory whorls and stamens.

Calyx yellowish-green, pubescent, campanulate, 5–8 mm. long, 5 mm. diameter, occasionally very small; segments 3–6 and accrescent, apex acute, 1·5–3 mm. in length.

Corolla yellowish-white, narrow-throated, outside covered with silky hairs, 12 mm. long, 3 mm. diameter: segments

4–6, usually 5, rotate, rounded or acuminate apex, 2 mm. long, 2 mm. wide.

Stamens indefinite, 8–10–16–20, never epipetalous but terminate central disc, arranged singly or in equal or unequal groups of 2 or 3; in one case 15, arranged (*a*) outer whorl of 8, four in two connate adjacent pairs, and four successive separate stamens; (*b*) inner whorl of 7, two of which were connate (*cf.* D. pruriens); in another case 13, ten in 5 pairs with anthers of inner stamens shorter than outer, two as a pair with anthers of equal length, and one separate stamen with long anther and filament; *anthers* yellow, glabrous, slightly apiculate, 1·8–3 mm. long, opening by longitudinal slits; *filaments* white, glabrous, 1·5–2·5 mm. in length.

Pistil absent or represented by bunch of hairs or apiculate rudiment 2 mm. long.

In one or two cases I suspected polygamy, but was not able to prove the undoubted occurrence of this condition.

Female flowers solitary in axil of foliage leaf, large; in bud measure 5 mm. in length and 6 mm. in diameter; accessory whorls very unequal; peduncle short and stout, covered with light brown hairs, 1·5 mm. long, 3 mm. diameter; two small hairy bracteoles on peduncle forming an opposite pair at right angles to antero-posterior axis (*cf.* D. affinis and D. Ebenum) 2mm. long, broad base, acute apex; occasionally a third bracteole occurs placed between flower and axis. (See pl. VIII., fig. 6).

Calyx green to brown, deeply lobed, pubescent, forming rather shallow cup; segments 4–7, usually 6, accrescent, tapering apex, broad base, margins undulate, 7 mm. long, 5 mm. wide, become more nearly horizontal after fertilization.

Corolla yellow, wide-throated, white base, both surfaces covered with silky hairs, 9 mm. long, 5 mm. diameter; segments 5, tapering apex, 3 mm. long, 2·5 mm. wide.

Staminodes indefinite 8–10–12, rarely epipetalous, when 12 in number they are opposite and alternate to calyx segments; *anthers* reddish-brown, barren, apiculate, glabrous, 1·5 mm. long; *filaments* yellowish-white, glabrous, 2·5 mm. long.

Pistil green, globose, densely pubescent; stigmas 4, green, hairy, and fleshy; ovary globose, 7 mm. long, 4 mm. diameter; 4–6-celled, but orientation of loculi very irregular; ovules usually disposed at right angles to the plane of antero-posterior axis and this apparently in consequence of pressure.

Fruit solitary, green, globose-apiculate with few persistent hairs, 40 mm. high, 30 mm. diameter, 2–4–celled; fruiting calyx slightly enlarged, 25 mm. diameter, pubescent, reflexed and undulated margin, small intersegmental groove; acute apex of segment remains in contact with carpellary wall. (See pl. VIII., fig. 7).

Seeds 1–4 per fruit, oval-wedge shape, 21 mm. long, 10 mm. wide, 8 mm. thick; testa reddish-brown; endosperm copious, horny, ruminate; embryo white, 15 mm. long.

Seedlings.—None of the seeds germinated, but from a study of the embryo the following points were made out:—Traces three per cotyledon, epicotyledonary traces prominent and distinguishable in the resting embryo. The seedlings are very probably of the ordinary epigeal type with cotyledons which become detached at an early stage.

Timber.—This species is one of the main sources of Indian ebony, possessing very durable black or streaked heartwood. It is spoken of as Coromandel wood by Dr. Watt (Econ. Prod.) and it is difficult to understand why Trimen (Fl. Ceyl., p. 99) refers to it as inferior to that of D. Ebenum. The majority of the trees still in Ceylon are certainly small and cannot yield much good heartwood. In one large tree trunk 320 mm. diameter the black heartwood measured 120 mm. in diameter; in another stem 270 mm. diameter, the heartwood measured 110 mm. diameter—a proportion which compares favourably with D. Ebenum. (See pl. I., fig. 5).

The contents of the parenchymatous and tracheal elements are, as one might expect, always conspicuous. In the red sapwood the coloured contents are almost limited to the medullary ray cells, but in the black heartwood every element is filled with reddish-brown materials. A discolouration also appears in the walls.

The differentiation of the elements is comparatively regular. The percentage number of fibres is approximately 81, and the maximum variation is presented in the cells of the wood parenchyma. Insignificant rings of growth can be distinguished, sometimes continuous throughout the section, at other times on one side only. I believe that if old trees of this species were only more abundant we should have a valuable source of ebony, quite equal to D. Ebenum from an economic point of view. Its limited distribution in Ceylon is not due to non-production of fruit.

Distribution.—This species is very rare in Ceylon. It was first found between Bibile and Ekiriankumbura, Uva, in 1888. It was unknown to Thwaites and according to Trimen (Fl. Ceyl. p. 99) there were no known specimens from the Island except from the above locality. The flowers were first obtained in Ceylon, in May, 1901.

It occurs on the patana and coarse forests to the south-west of Bibile in the localities Elukkapudena, Antibuwana, and Diggalrana. At the first-mentioned place at an elevation of 700–900 feet, the tree is found on patana ground, and there rarely exceeds a total height of 9·1 metres (30 feet) and breast height circumference of 305 mm. (1 foot), though the trees are probably very old. At the latter places, the tree reaches a height of 18·3 metres (60 feet) and circumference of 1–1·67 metres ($3\frac{1}{2}$ feet—$5\frac{1}{2}$ feet).

Other trees also occur along the Bibile-Bintenna road, near Bibile, at the base of a small hill.

Uses.—The Sinhalese call the tree Kadumberiya in this district. They collect the unripe fruits and after steeping them in water for two to three days, pronounce them fit to eat. Ripe fruits are abundant from May to July.

This species is abundant in Peninsular India.

Diospyros hirsuta, Linn. fil. Suppl., p. 440 (1781). Thw. Enum. Ceyl. Pl., p. 181. n. 15 (1860). Alph. DC. Prodr. VIII., p. 223, n. 5 (1844). Bedd. Icon. Pl. Ind. Or. 1871. Hiern, Mon. Eben. 163. C. P. 382. Fl. B. Ind. III., 565. Hiern, p. 163–164, includes D. Moonii, Thw. and D. Thwaitesii Bedd., as varieties of D. hirsuta, L., but for reasons given this grouping cannot be maintained.

A small or moderate-sized tree, evergreen, dicœcious, moncœcious, and polygamous; bark black with narrow irregular grooves and ridges; branches pubescent when young, often groups of stiff brown hairs occurring in local areas on young twigs (*cf.* D. Thwaitesii).

Leaves alternate, 90-200 mm. long, 30-60 mm. wide, ovate-lanceolate, tapering apex, obtuse or acute, tapering base; young leaves densely pubescent, hairs persisting on under-surface, lateral veins and midrib; sub-coriaceous, pale green below, venation reticulate; *petiole* 8-11 mm. long.

Flowers March-October; ripe fruits March–August.

The polygamous condition is very frequent as a result of the fertility of the pistil in male flowers; the hermaphrodite flowers occur in any cluster, and consequent on the ripening of the fruit the unisexual flowers become detached leaving only one or two fruiting specimens out of a many-flowered cluster. A single twig or herbarium specimen may therefore appear to be female only.

The moncœcious condition has been observed by Thwaites. I have confirmed this in material obtained from Potgulkanda near Ratnapura. The same inflorescence possesses male and female flowers, the former with rudimentary pistil and the latter with barren staminodes. (See. pl. XV., fig. 9).

The male inflorescence consists of dense axillary cymes, sometimes short, at other times drawn out to a length of 20 mm. All the flowers are sessile or subsessile, but an opposite pair of small pubescent bracteoles occurs at the base of each flower suggesting a suppressed dichasial cyme.

Calyx green, pubescent, irregularly lobed ; segments 4–5, accrescent, acute apex, 36 mm. long.

Corolla yellow, with narrow throat, diameter of mature flower 5 mm. ; segments 4–5, overlapping in bud with exposed half externally pubescent, become horizontal when flower mature, acute apex.

Stamens 5, epipetalous, alternate with corolla segments ; *anthers* brown, glabrous, apiculate, 2·5 mm. long ; *filaments* white, short ; pollen yellow, smooth, circular.

Pistil central rudimentary.

Female inflorescence consists of a sessile cluster of flowers in the axil of a leaf, fewer than male, never solitary except by falling away of young flowers ; bracteoles as in male.

Calyx, larger than in male ; segments 4–5, covered with long brown unicellular hairs, 10 mm. long, accrescent in bud with feeble intersegmental pouch.

Corolla yellow, thick ; segments 5, acute apex.

Staminodes 5, epipetalous, alternate with corolla segments : *anthers* brown, barren, apiculate, glabrous, 2 mm. long ; *filaments* white, glabrous, 0·3 mm. long.

Pistil brown, thickly coated with unicellular hairs which persist in ripe fruit (*cf.* D. Moonii, D. Thwaitesii) ; stigmas 1, sessile ; ovary globose-apiculate, 8–celled (*cf.* D. Thwaitesii).

Fruit broadly globose-ovoid, apiculate, 30 mm. high, 70 mm. in circumference, hairs detached only with difficulty ; fruiting calyx persistent, enlarged, flattened, thick, margins much reflexed and undulated, segments 15 mm. long.

Seeds 1–8, usually 6 per fruit, elliptical-wedge-shaped with beaked micropyle, 20 mm. long, 10 mm. wide, 9 mm. thick ; testa brownish-black, prominently striated transversely ; endosperm copious, horny, ruminate ; embryo white, 10–14 mm. long. (See. pl. XV., fig. 11–12).

Seedlings epigeal, cotyledons detached early, epicotyledonary system enhanced developmentally and can be seen by the naked eye in the seed ; *cotyledons* white, long and narrow, measuring when mature 18 mm. in length and 6 mm.

in width; *hypocotyl* white, stout, glabrous, 60-65 mm. long; *epicotyledonary* stem yellowish-green, pubescent, 3 mm. long; epicotyledonary leaves form an opposite pair and prior to the dropping of the cotyledons attain a length of 15 mm. though within the confines of the seed; hairy on under-surface, particularly midrib and margin; *traces* three per cotyledon, median abortive, laterals splitting considerably; epicotyledonary one per leaf prolonged into root.

The timber possesses no black heartwood, and when freshly cut is dirty white in colour turning reddish on exposure; the colour is due to coloured contents mainly in the wood parenchyma and medullary ray cells; a change in colour of the walls occurs. (See pl. I., fig. 3.)

The percentage number of fibres varies from 74–83 per cent. and that of the tracheal elements from 0·3 to 1·3 per cent.

The rings of growth are inconspicuous.

In the Peak Wilderness I came across a variety of this species characterized by a flattened circular fruit and stout persistent style. It was abundant along the banks of streams and in damp forests near Eratna, Madola, and Kadawatta.

Distribution.—endemic and limited to our wet zone up to 1,500 feet, rather rare but often abundant along the banks of streams and in rocky damp forests.

Katugasella, Potgulkanda, Kukule korale, Galle, Ratnapura, Nawadun korale, Eratna, Kadawatta, Madola.

Diospyros insignis, Thw. Enum. Ceyl. Pl., p. 180., n. 10 (1860).

Gona Poruwa-mara, Wal-mediriya, S.

Thw. Enum. 180. Hiern, Mon. Eben. 157. C. P. 2,730 (3,477).

Fl. B. Ind. III., 564. Bedd. Ic. Fl. Ind. Or. t. 130 (1871).

A moderate-sized tree, rarely exceeding 200 mm. diameter, with a straight stem unbranched until near the top, evergreen, diœcious and polygamous (monœcious ?); bark white or grey, characterized by long shallow irregular

cracks about 10 mm. apart, running vertically through a distance of 100–200 mm.; peels off in large thin flakes exposing brown surface; young twigs thick, green and pubescent; the habit and bark characters are very pronounced.

Leaves alternate or sub-opposite, 140–240 mm. long, 40–120 mm. wide, ovate-lanceolate or oblong, acute apex rounded or narrowed at base, glabrous, toughly membranous, pale green beneath; venation conspicuous, midrib and lateral veins project on lower surface, lateral veins connected by parallel transverse veinlets; *petiole* green, cylindrical, glabrous, 15 mm. long, 2·5 mm. diameter.

The polygamous state is very common; the same stages as determined in D. sylvatica, D. Gardneri, and D. affinis have been observed for this species. The hermaphrodite and male flowers occur on the same tree, showing all stages between a central apiculate disc and a pistil with an 8-celled ovary; the hermaphrodite flowers may occur in the same cluster as the male, or in separate clusters, the occurrence being very erratic. (See pl. XIV., fig. 2).

Male inflorescence consists of an axillary subsessile cluster, 3–10 flowers similar to those described for D. hirsuta; flowers in March on stems 60 mm. diameter. (See pl. XIV., fig. 1).

Calyx green, 4 mm. long; segments 4, short, accrescent, ovate, acute apex, nearly glabrous.

Corolla yellowish-white, shortly tubular, 10 mm. long, narrow-throated when mature: segments 4, rotate, short, pale and hairy outside.

Stamens 14–16–20, epipetalous at base of corolla, single or paired, inner shorter than outer, average length 5 mm., very unequal; *anthers* brown, apiculate, longer than filaments, length 3·5 (outer), 2 mm. (inner); *filaments* white, glabrous or pubescent, length 3 mm. (outer), 0·5 mm. (inner).

Pistil apiculate central disc, pubescent, 5 mm. high; crude locular structure seen in transverse section.

The female flowers have not been previously described.

Female inflorescence consists of solitary or sessile axillary clusters of 1–6 flowers. (See pl. XIV., fig. 3).

Calyx green, pubescent; segments 4, 5 mm. long, accrescent in flower with feebly recurved margin and small intersegmental pouch.

Corolla yellowish-white, tubular, 10 mm. long, throat narrow; segments 4, outside covered with silky hairs, tend to become recurved in mature flower.

Staminodes 4–5, epipetalous; *anthers* barren, apiculate; *filaments* white, glabrous or nearly so.

Pistil green, feebly pubescent; stigmas 4, green, ovary 8–celled; after fertilization becomes enveloped in rapidly growing calyx and only stigma can be seen for some time.

Fruit green, glabrous except near apex, subglobose with cruciform depressed apex, with calyx like an acorn in appearance, 40 mm. high, 75 mm. circumference; fruiting calyx considerably enlarged, segments woody, 20 mm. long, with apices strongly pointed and projecting outwards and downwards, margin recurved and coated with long velvety hairs; in mature fruit the calyx is strongly tetrahedral in outline, and the basal part forms a cup over 20 mm. deep in which fruit rests (*cf.* D. Ebenum). (See pl. XIV., fig. 4).

Seeds 4–7–8 per fruit, oval-wedge shape; 28 mm. long, 11 mm. wide, 7 mm. thick; testa smooth, deep brown, transverse striæ not prominent; endosperm copious, horny, ruminate.

I have often suspected the monœcious condition in this species, but the occurrence of pure male and female flowers on the same tree has yet to be definitely proved. On some male trees I have found young flowers possessing a fertile pistil and a staminal whorl of five members, but whether these anthers were barren in consequence of being young or otherwise I could not satisfy myself.

There appears to be a variety of this species in the Ratnapura District, characterized by smaller leaves and fruits, darker bark, and less feebly cornered fruiting calyx.

Seedlings epigeal, cotyledons detached early, epicotyledonary system slightly enhanced developmentally. *Cotyledons* white, 10–13 mm. long, 4–6 mm. wide; *hypocotyl* white, glabrous, very short type similar to D. oocarpa and suggestive of hypogeal tendency; seeds are never raised above the ground and the hypocotyl is never strongly arched; 15–20 mm. long. Epicotyledonary system is long and narrow and easily frees itself from the confines of the decaying cotyledons and endosperm, and at the time of detachment of cotyledons measures 10 mm. in length and 1–5 mm. diameter.

The *epicotyledonary* stem when 65 mm. long bears 3–5 small leaves about 1 mm. in length and disposed at irregular distances; at the apex there are two larger leaves, opposite, but at different levels; these are glabrous, thin, bullate, and measure 50 mm. in length.

Traces 3 per cotyledon, xylem splits at different levels of hypocotyl and primary root. One trace per epicotyledonary leaf, but on account of splitting of cotyledonary xylem difficult to follow.

Timber.—Trimen (p. 100) describes the heartwood as being small and black with pale streaks, and states that it is one of those called "kalumediriya"—the Sinhalese name for calamander. At Ratnapura I found this belief still strong and it was only after much persuasion that trees on private grounds were felled for my inspection. Every specimen which I have seen is white when freshly cut, turning a dirty colour on exposure. Only on one occasion was the black heartwood present and this was very small and rotten. (See pl. III., fig. 3).

The gum-resin is present in very small quantities; the soft parenchymatous tissues are very abundant, and the timber must therefore be regarded as of an inferior quality. The tree provides excellent straight posts and is therefore frequently felled. The rings of growth are very inconspicuous, sometimes they occur as broad dark bands alternating with narrower and lighter zones. These are sometimes so closely

arranged that a radius of 10 mm. may contain 12 rings, whereas in some specimens very large areas may be free from any such differentiations. Perhaps such rings of growth are the expression of special periods of activity, independent of seasonal forces?

Distribution.—This species is common in the moist low-country up to 2,500 feet; Kandy, Polgahawela, Ambagamuwa, Avisawella, Kuruwiti korale, Hewesse, Kalutara, Kottawa, Potgulkanda, Katugasella, Udugama, Yagarilla, Penjaval, Hinidun, Eratna, Kadawatta, Ambalawa, Pindeniya, Pitigalla.

Also in Anamalai Hills, South India.

Diospyros oppositifolia, Thw. Enum. Ceyl. Pl., p. 181., n. 11 (1860).

Kalumediriya, Kadumberiya, S.

Thw. Enum. 181. Hiern, Mon. Eben. 157. C. P. 3,011.

Fl. B. Ind. III., 565. Bedd. Ic. F. Ind. Or., t. 131.

A moderate-sized or large tree, evergreen, monœcious only; trunk erect, not buttressed, bark black, never deeply grooved but fissures somewhat similar to D. insignis. *Leaves* opposite or sub-opposite, 50–130 mm. long, 35-75 mm. wide, oval, shortly acuminate or obtuse apex, rounded at base, pubescent when young, glabrous when old, coriaceous; venation reticulate, pellucid, lateral veins and parallel transverse connecting veins conspicuous when fresh; *petiole* dark, glabrous, 2-5 mm. long; phyllotaxy, texture and form somewhat similar to D. Melanoxylon.

The male and female flowers are always found together on the same tree. Usually a solitary female flower terminates the young shoot, and in the axils of the lower leaves clusters of male flowers arise. In one specimen male and female flowers were in separate but opposite clusters of 9 and 2 flowers respectively on a young twig; in another case there were two residual flowers of a cluster, one of which was a true male, the other showing a ripening pistil; in other cases the female flowers may occur solitary in the axil of the

lower leaves. There was very little evidence of a constant or annual floral periodicity in the trees examined. It is interesting to note that though this endemic species is monœcious, only the male flowers have been previously described. The sex, female flowers, and fruits are here described from material I obtained in the forest in 1901.

Male inflorescence consists of a sessile or subsessile cluster of 1-9 flowers in the axil of leaves or on old twigs. The male flowers never terminate a young shoot and usually occupy the part below the female flower or flowers ; they are rarely mixed with female flowers in the same cluster. Each flower is subtended by a small caducous green bracteole. The flowers are yellow, fragrant when fresh and measure 10 mm. when unopened. (See pl. VI., figs. 3, 4).

Calyx brown or green, diameter 16 mm.; segments 4, acuminate apex, sub-glabrous, 4 mm. long.

Corolla yellow, tubular, swollen at base, when open measures 15 mm. long ; segments 4, rotate, with tapering acute apex, half of outer surface covered with brown hairs, 5 mm. long, 2·5 mm. wide at base.

Stamens 8 (4+4), epipetalous, usually in pairs but filaments not united, inner shorter than outer ; pairs usually alternate with coroila segments, though liable to variation : *anthers* yellow, apiculate, glabrous apex, hairy at back, 2·5 mm. long ; *filaments* white, covered with long unicellular hairs, 1 mm. long, sometimes absent or very short for inner stamen.

Pistil absent or as a central pubescent apiculate structure.

The female flowers and fruits have not been previously described. Flowers usually solitary terminating young shoot, subsessile or on peduncle measuring 8–15 mm. long, 2 mm. diameter ; peduncle greenish, finely pubescent, and may or may not bear bracteoles ; yellow, fragrant. (See pl. VI., fig. 1).

Calyx green, outside finely pubescent, 9 mm. total length. diameter 4 mm.; segments 4, rarely 3, deeply cut, tapering acute apex, thick, 6 mm. long.

Corolla yellow, outside covered with short white hairs, 16 mm. long when unopened, diameter of open flower at top 20 mm.; segments 4, rarely 3, rotate, tapering acute apex, 10 mm. long.

Staminodes 4, epipetalous, alternate with corolla segments; in one case there were eight separate staminodes each typical in form and having barren anthers; *anthers* barren, brown, tapering apex but not apiculate, 2 mm. long; *filaments* white, glabrous, 1·5 mm. long.

Pistil with 4 stigmas, yellowish-watery appearance, thin and undulating; style stout, 4 mm. long, 1·5 mm. diameter; ovary small, greenish, nearly glabrous, 8-celled, the loculi of adjacent pairs becoming grouped opposite the middle of calyx segments.

Fruit solitary, terminates young shoot, ovoid-attenuate, 30 mm. long, 12 mm. diameter, green, glabrous. Some fruits have a broad base and taper quickly towards apex; others are narrow at base and strongly attenuate at apex; fruiting calyx woody, enlarged, forming deep cup for fruit, total length 18 mm., cup 18 mm. diameter. (See pl. VI., fig. 2).

Seeds 2-5 per fruit, wedge-shaped having convex surface in contact with carpellary wall, tapering strongly towards both ends; 28 mm. long, 10 mm. wide; testa brown, smooth; endosperm copious, horny, equable.

Embryo white.

Timber.—Regarding the wood from this species, Trimen states (Vol. III., p. 101) that according to Thwaites the timber resembles true calamander, but that the tree requires more careful examination and is almost unknown. The Sinhalese name is the same as that applied to calamander. My experience does not confirm this. The timber when freshly felled is white or dirty white in colour, with a hollow decayed centre. Young trees 75 mm. (3 inches) diameter are invariably hollow in the centre, and large trees measuring 480 mm. diameter possess only a narrow peripheral band of dirty white living wood, the central and median portions

being quite rotten. On exposure the timber changes to a darker colour with irregular streaks of black, often giving a pattern to the transverse section similar to what has been noted in D. ovalifolia. (See pl. II., 8).

The discolouration is often due to a change in the colour of the cell walls only. The relative scarcity of gum-resin and the abundance of parenchymatous cells, particularly of the medullary ray, necessarily make the timber very inferior in quality.

The rings of growth are inconspicuous.

Distribution.—This is our rarest species of Diospyros and up to the present has only been found on the upper part of the Haycock mountain, or Hinidumkanda, between 1,500–2,000 feet. The climate there prevailing is unique, the upper part being, more often than not, capped with mist, and arborescent vegetation is of a stunted xerophytic type. There are not more than 40 or 50 trees of this species and these occur mixed with trees of calamander. The character of the erect trunk with its black bark is very similar to that of calamander trees, and the fact of their being so freely mixed with trees of calamander is probably the source of the error regarding the value of the timber. This species should grow well on the steep rocky hill sides in the Peak Wilderness, where the rainfall is high.

Diospyros Thwaitesii, Bedd. Ic. Pl., Ind. Or. 27 (1874).

Kadumberiya, S.

Hiern, Mon. Eben. 164. C. P. 3394. Fl. B. Ind. III., 566. Bedd. Ic. Pl. Ind. Or. t. 135

A small or medium-sized tree, 300–1,500 mm. in circumference, and attaining a height of 18 metres (60 feet), evergreen, dicœcious, moncœcious, and polygamous; bark black, slightly rougher than D. hirsuta, with longitudinal fissures 2 mm. deep and 4 mm. wide; bark 3 mm. thick in tree 110 mm. diameter, young twigs covered with brown hairs becoming green and glabrous. *Leaves* alternate 80–120 mm. long, 20–40 mm. wide, ovate-lanceolate, tapering towards apex:

apex acute or obtuse, tapering base, pubescent on both surfaces when young, especially midrib, glabrous and shining when old, thin, venation reticulate, meshes wide, midrib prominent beneath, lateral veins inconspicuous; petiole green, finely pubescent, slightly grooved above, 8 mm. long, 2 mm. diameter. Flowers in March to June; fruits March-October.

The monœcious condition was seen at Palaketi, near Udugama. The male clusters and female flowers occur irregularly on the same or different twigs. I fully satisfied myself that the 5 staminodes in the fruiting flowers were barren, this being the species in which the monœcious condition was first noticed. The polygamous condition established by the occurrence of male and hermaphrodite flowers on the same tree is very frequent. Pure male and female trees occur in the same district, and it occurred to me that perhaps the trees now bearing unisexual flowers may at another time of the year produce hermaphrodite flowers. The sex appears to be very unstable. (See pl. XVI., fig. 3–4).

At Palaketi there is a variety of this species characterized by broader and coriaceous leaves, in which the lateral veins and midrib are conspicuous on the upper surface, and measure 40–120 mm. long and 30–50 mm. broad.

The male inflorescence consists of a sessile axillary cluster of 4–15 flowers; each flower is subtended by a small bracteole, 2 mm. long, acuminate apex, green and glabrous above, covered with red hairs below. (See pl. XVI., fig. 1).

Calyx green, hairy, 3 mm. diameter, 4 mm. long in open flower; segments 5, accrescent, with tapering apex, not undulate in flower.

Corolla yellowish–white, 8 mm. long, 8 mm. diameter of open flower at top, throat widely open and covered above and below with silky hairs: segments 5, rotate, tapering apex, broad base, half of flower surfaces covered with brown hairs.

Stamens variable but usually 5 epipetalous pairs alternating with corolla segments, attached by separate or united

filaments; in other cases 10–18 arranged in pairs and singles without fixed orientation; *anthers* unequal, reddish-brown, apiculate, apex well pointed with long unicellular hairs to disseminate the pollen, average length 3 mm.; *filaments* yellowish-white, glabrous, 1·5 mm. long; *pollen* yellow, even outline, circular, feebly granular contents.

Pistil rudimentary disc, apiculate, densely pubescent.

The female flowers occur solitary, or as a cyme in the axil of foliage leaves; when solitary the flower is surrounded with an involucre of small bracteoles suggesting 3–7–flowered inflorescences; bracteoles with hairy midrib, acute apex, 9 mm. long, 5 mm. wide. (See pl. XVI., fig. 2).

Calyx brown, pubescent, campanulate in flower measuring 10 mm. in depth; segments 5, tapering apex, slightly reflexed margin, undulating intersegmental groove, pubescent.

Corolla yellowish-white, 10 mm. diameter, corolla throat wide; segments 5, rotate, acute apex, half of under surface densely pubescent.

Staminodes 5, epipetalous, alternate with corolla segments, filaments attached near apex of throat; *anthers* barren, brown, apiculate with silky brown attenuate hairs as in male; *filaments* white, very short. *Pistil* with 2 stigmas, yellowish-white, style absent; ovary globose–apiculate covered with dense coating of brown hairs, 4–celled, one ovule in each cell.

Fruit globose-apiculate covered with long brown hairs when young, but tending to become glabrous when old, 30 mm. long, 60 mm. circumference; fruiting calyx not much enlarged. (See pl. XVI., fig. 5).

Seeds 2 per fruit, oval-elliptical in shape, with strongly beaked micropyle; 18 mm. long, 10 mm. wide, 8 mm. thick; testa brown, transversely striated; endosperm abundant, ruminate. (See pl. XVI., fig. 6).

Seedlings epigeal; *cotyledons* drop, but usually only after persisting as a white lamina, void of palisade tissue, for one or two days. During this time they never develop any chlorophyll though the enhanced epicotyledonary leaves

are of a deep green colour ; cotyledons white, 20 mm. long, 12 mm. wide ; *hypocotyl* white, thinner than D. Moonii, 85-90 mm. long; *epicotyledonary stem* pubescent, a trifle longer than D. Moonii, 6-10 mm. long ; epicotyledonary leaves form an opposite pair, cordate, tapering acute apex, midrib hairy beneath, 25 mm. long, 20 mm. broad. Three *traces* per cotyledon, xylem of median trace abortive and liable to be overlooked in sections not horizontal ; one trace per epicotyledonary leaf, continued into the root but in old seedlings absent from the apical part of the root.

Timber.—The sapwood when freshly cut presents a dirty appearance while the heartwood is light red. There is no real black heartwood, only small black traces here and there. The coloured materials in the various elements are small in quantity ; fibres are abundant and medullary rays poor, hence an even-grained timber results. Rings of growth sometimes conspicuous, the light narrow rings measuring 0·2–1·2 mm. radial diameter and being distanced 2–8 mm. radially from one another. (See pl. II., Fig. 9).

Distribution.—This species is found in the moist low-country forests, rather rarely; it grows well on moist, rocky, or sandy soils, and under close canopy usually measures 4·5–6 metres (15–20 feet) to first branch, and has a total height of 6–9 metres (20–30 feet), the average circumference being about 320 mm. The largest trees occur at Hiniduma at an elevation of 800 feet, measurements already quoted. Ratnapura, Hiniduma, Sinha Raja forest, Hewess, Palaketi.

Diospyros Moonii, Thw. Enum. Ceyl. Pl., p. 182., n. 16 (1860) Kadumberiya, Kaluwella, S.

Thw. Enum. 182, C. P. 2,833. Hiern, Mon. Eben. 164. Fl. B. Ind. III., 566. Bedd. Ic. Fl. Ind. Or. t. 138.

A moderate-sized tree, evergreen, dicœcious ; small trees have a relatively smooth black stem, but larger specimens are deeply grooved and buttressed at the base ; average height from 7·6–10·6 metres mm. (25-30 feet), maximum 13·8 metres (45 feet), breast height circumference 760 mm. (2½ feet) ;

young branches black and smooth ; on old twigs the bark is rather scaly and pinkish-red turning to brown when freshly cut.

Leaves alternate, 190–350 mm. long, 70 mm. wide, ovate-lanceolate, short tapering acute apex, rounded base, pubescent when young, glabrous or nearly so when old, thick and leathery ; venation reticulate, meshes wide, not pellucid, lateral veins rather conspicuous below ; midrib prominent below, channelled above ; *petiole* green, cylindrical, 15 mm. long, 5 mm. diameter. Flowers October, ripe fruits March to October.

Male inflorescence consists of a sessile cluster of 1–8 flowers on old twigs ; bracteole subtending each flower green, pubescent, tapering acuminate apex, broad base early caducous 3 mm. long, 3 mm. wide at base. (See pl. XVI., fig. 7).

Calyx brown, hairy ; segments 5, 4 mm. long, acute apex. *Corolla* yellow and 5-lobed ; *stamens* five ; *pistil* rudimentary. Fresh specimens of open flowers not seen.

Female flowers solitary or as a sessile inflorescence ; a ring of 2–5 bracts at base of solitary flower, 8 mm. long, 4 mm. wide. (See pl. XIV., fig. 6).

Fresh material of young flowers not seen.

Calyx green, pubescent, cupuliform ; segments 5, bluntly apiculate, recurved margin, slight intersegmental groove.

Corolla yellowish-white and 5-lobed ; staminodes present.

Pistil globose, pubescent. *Fruit* solitary or in groups 2–4, sessile or subsessile, globose with depressed apex, 90–130 mm. circumference, 30–50 mm. long, green, slightly hairy, long hairs easily detached, 10-celled ; fruiting calyx persistent to fruit, enlarged, segments measuring 15 mm. in length, flattened, densely pubescent. (See pl. XIV., fig. 7).

Seeds 6–10 per fruit, elliptical-ovate, or rather flattened ; testa brown, transversely striated, outer layer peels off readily ; endosperm strongly ruminate ; 23 mm. long, 15 mm. wide, 6 mm. thick ; embryo white, 15 mm. long. (See pl. XIV., fig. 9–10).

Seedlings epigeal ; cotyledons not readily detached but never function as assimilatory organs and exist as white or shrivelled leaves for a few days ; by the time the cotyledons are dead the enhanced epicotyledonary leaves are deep green and well developed (*cf.* D. Thwaitesii).

Cotyledons white, 13 mm. long ; *hypocotyl* white, glabrous, 90 mm. long ; *epicotyledonary* stem greenish, hairy, 3 mm. long ; epicotyledonary leaves form an opposite pair, ovate, rounded apex, rounded or tapering base, glabrous, 50 mm. long, 25 mm. broad ; *traces* 3 per cotyledon, xylem of median trace weak, xylem of lateral cotyledonary traces much split ; one trace per epicotyledonary leaf, weak and continued into root.

Timber.—A typical red wood with occasional small black strands ; black heartwood absent or small ; the elements are feebly lignified, even the fibres ; vessels have rather large transverse dimensions. The colouring substances are not very abundant. The timber is much inferior to ebony but superior to the yellow and white woods already described. It is rarely felled even where very abundant, and most natives disregard it entirely as a source of durable timber.

Distribution.—Moist lowcountry, rather rare, Kalutara, Hewessa, Penijaval Forests, Kadawatte, Hinidumkanda, near Galle. It grows well in poor sandy or rocky soils providing there is plenty of water ; in some districts it can only be found alongside the streams with roots occasionally submerged ; often accompanies D. Embryopteris and D. quæsita in moist low-country.

Endemic.

The habit of D. Moonii is very different from that of D. hirsuta or D. Thwaitesii, and in this respect greatly resembles D. Embryopteris ; the fleshy leaves resemble those of D. acuta ; the flat relatively thin fruiting calyx and the large globose fruits are widely different from anything met with in D. hirsuta or D. Thwaitesii. D. Thwaitesii resembles D. hirsuta in many features, but can always be distinguished from it in virtue of its 4-celled ovary, larger number of stamens, thinner and smaller leaves.

The three species have therefore been described separately.

Diospyros affinis, Thw. Enum. Ceyl. Pl., p. 179, n. 6 (1860).

Kaluwella (Viriniya), Semel Panachai, S.

Fl. B. Ind. III., 566. C. P. 2,924. Hiern, Mon. Eben. 169. Bedd. Ic. Fl. Ind. Or. t. 127 (1871).

A moderate-sized or large tree, evergreen, dicœcious and polygamous; young twigs green and slightly pubescent, older twigs brown to black and shiny; bark of young branches thick, alternate longitudinal grey and black layers, 10 mm. wide and 40–80 mm. long. In old trees the grey layer becomes the fissure and the dark layer the ridge. The fissures becomes very large and characteristic of the bark. The bark peels away in irregular thick patches.

Leaves alternate, 35–90 mm. long, 13–30 mm. wide, oval or oblong, tapering towards apex, apex obtuse, narrowed at base, glabrous, coriaceous; venation reticulate, meshes wide, not strongly pellucid, net veins rather prominent beneath; *petiole* flattened above, 10 mm. long, 1–5 mm. diameter.

Flowers in June–August; ripe fruits June-October.

The polygamous condition is very frequent. At Viriniya in June, 1902, I obtained abundance of ripe fruit from polygamous trees of this species. The fruits were a trifle smaller than those obtained from true female trees. The hermaphrodite flowers only differ from the male flowers on the same tree in having larger calyces and a fertile pistil, the number and nature of stamens being the same. The hermaphrodite flower when occurring alone on a male cyme usually occupies the position of the median and oldest flower (*cf.* D. oppositifolia). In other cases the majority of the flowers of a particular cyme are hermaphrodite. (See pl. X., fig. 5).

I have also found the polygamous condition on a tree in the Peradeniya Gardens in March, 1903; this particular tree had not been in flower for at least the last three years.

The male inflorescence consists of cymose cluster of 3–7 flowers in axil of caducous bract or foliage leaf. The peduncle is green, hairy, 10 mm. long, 2 mm. diameter. The pedicels vary in length from 2–4 mm., diameter 2 mm.; bracts green, hairy, caducous, 12 mm. long; bracteoles of lateral flowers 9 mm. in length, long tapering apices, green and glabrous, gradually decreasing in size from below upwards, those subtending the ultimate pedicels being very small.

Calyx green, tubular, glabrous, 7 mm. long, 2·5 mm. diameter; segments 4, variable length, apex acute.

Corolla yellowish-white, length 12 mm., average diameter 3 mm.; segments 4, hairy outside, acute apex, broad base, 4 mm. long.

Stamens 6–9–16, forming central hypogynous ring, in pairs or single; *anthers* reddish-brown, glabrous, slightly apiculate, 3–4 mm. long; *filaments* white, glabrous, 1 mm. long; *pollen* circular, yellow.

Pistil rudimentary, represented by a bunch of hairs.

Female flowers solitary on stout peduncles. Peduncles green, nearly glabrous, 5-10 mm. long, 2·5 mm, diameter; pair at right angles to antero-posterior axis near base of flower suggesting a cyme with abortive lateral flowers (*cf.* D. Gardneri); bracteoles caducous, very small. (See pl. X., fig. 1).

Calyx green, hairy inside, sub-glabrate outside, 13 mm. long; segments 4, tapering apex, 10 mm. long, undulating margin, conspicuous intersegmental pouch.

Corolla yellowish-white, tubular; segments 4, short.

Staminodes 6–8, epipetalous at base of corolla or part hypogynous, glabrous, barren anthers.

Pistil green; styles two, each bifid at apex; ovary usually 6-celled, occasionally 8-celled, when latter the loculi are opposite and alternate to calyx lobes, when former four loculi alternate with calyx lobes, the other two taking up any position.

Fruit green or yellow when ripe, globose, slightly apiculate, becomes glabrous, 30 mm. diameter, 25 mm. long; fruiting calyx enlarged, 30 mm. diameter, rather flattened with segments glabrous, black, apices in contact with carpelary wall, margins reflexed, intersegmental pouch large.

Seeds usually 4, ovate, wedge shaped, 18 mm. long, 11 mm. wide, 7 mm. thick; testa deep brown; endosperm copious and ruminate.

Seedlings epigeal, cotyledons detached early, epicotyledonary system well developed before detachment of cotyledons occurs; *cotyledons* white, 11 mm. long, ovate, apex obtuse; *hypocotyl* white, 7 cm. long; *epicotyledonary* stem reddish, pubescent, 4 mm. long; *epicotyledonary* leaves form an opposite pair, ovate, tapering towards base, apex tapering, obtuse; venation reticulate; 35 mm. long, 20 mm. wide; *traces* 3 per cotyledon, fairly equal in strength, xylem of lateral strands split to varying degrees; one epicotyledonary trace per leaf, continued into hypocotyl and root.

Timber.—The coloured heartwood is usually small but occasionally very good; one tree measuring 24·4 metres high (80 feet) and nearly 2 metres circumference, ($6\frac{1}{2}$ feet) possessed a small black heartwood only 100 mm. (4 inches) diameter; in some specimens much smaller than the foregoing the heartwood was large, streaked brown, and probably sold as "bastard" ebony; such samples are often equal to our best woods from an ornamental point of view (*cf.* D. oocarpa). (See pl. I., fig. 4).

The colouring matter is very abundant even in the sapwood; the fibres are very high in percentage number, and possess narrow lumina.

Rings of growth are inconspicuous.

Distribution.—dry and intermediate zones, rather rare; between Uma-oya and Bilihul-oya on the lower Badulla road from Kandy; Viriniya, near Bibile; Bintenna, Kantaḷai, Kalugalla, Vavuniya.

Also in Tinnevelly, S. India.

Diospyros crumenata, Thw. Enum. Ceyl. Pl., p. 179, n. 5 (1860). Fl. B. Ind. III., 567. C. P. 2,438. Hiern, Mon. Eben, 169. Bedd. Ic. Pl. Ind. Or. Part VII., p. 26, t. 126 (1871).

A large evergreen tree, diœcious; bark thick, black, rather scaly: trunk erect, twigs glabrous.

Leaves alternate, 50–120 mm. long, 25–50 mm. wide, oval-oblong, abruptly acuminate apex, rounded or narrowed at base, glabrous and shining, coriaceous, pellucid venation, net veins rather prominent; *petiole* canaliculate above, 6–10 mm. long. Flowers March-August; ripe fruits January-October.

Male inflorescence consists of a pedicellate spreading cyme of 3–7 flowers. (See pl. VIII., fig. 1.)

Flowers yellow, 15 mm. long, throat 4 mm. diameter, top of open flower 11 mm. diameter. Peduncle 3–10 mm. long, green, hairy; ultimate pedicels 1-4 mm. long.

Calyx green, cupuliform, 5–10 mm. long, glabrous inside; segments 4, short or obscure.

Corolla yellow, tubular, 14 mm. long; segments 4, short, rounded apices, broad and recurved in open flower.

Stamens 8-14, hypogynous, 4–6 mm. long; *anthers* brown or yellow, attenuate, glabrous, 4–5 mm. long; *filaments* white, glabrous, 1 mm. long, sometimes absent; *pollen* yellow, circular. (See pl. VIII., fig. 2.)

Pistil absent or rudimentary.

Female flowers solitary, in axil of foliage leaves and usually limited to the lower part of young shoot; approximately spherical in bud, measuring 9 mm. diameter. Peduncle 5–10 mm. long, 2–5 mm. diameter; two or more small caducous bracteoles occur on the peduncle, the first two forming an opposite pair at right angles to antero-posterior axis (cf. D. affinis). (See pl. VIII., fig. 3.)

Calyx green, under surface hairy; segments 4, accrescent in flower, acute apex; margin becomes reflexed, and deep intersegmental pouches are formed after the flower has opened.

Corolla yellowish-white, 15 mm. high, tubular, throat somewhat constricted, basal part swollen ; segments 4, rotate, rounded apices, undulated margins, tomentose on both sides.

Staminodes 8, epipetalous, opposite and alternate with corolla segments, 3 mm. long ; *anthers* barren, glabrous, not apiculate but apex shows signs of bifurcation ; *filaments* white and glabrous. (See pl. VIII., fig. 4.)

Pistil greenish-yellow, pubescent ; stigmas 4, fleshy, short ; ovary 8-celled.

Fruit green, 25–40 mm. diameter, 40 mm. long, depressed-globose, apiculate, glabrous or nearly so ; 8-celled, loculi opposite and alternate with calyx segments. (See pl. VIII., fig. 5.)

Fruiting calyx enlarged, woody, flattened, intersegmental areas are straightened and outline of calyx is tetrahedral (cf. D. insignis).

Seeds 1–8 in each fruit, flattened and elliptical, 45 mm. long, 20 mm. wide, 11 mm. thick ; testa umber-brown, shining ; endosperm copious, ruminate ; embryo white, 24 mm. long.

Seedlings epigeal, cotyledons detached early, epicotyledonary axis well developed ; *cotyledons* white, feebly petiolate, 16 mm. long, 7 mm. wide ; *hypocotyl* white and cylindrical, changing to black and four cornered, 110 mm. long, 3 mm. diameter ; *epicotyledonary* stem red, hairy, 15 mm. long ; traces 3 per cotyledon, much splitting of xylem in collet area ; one epicotyledonary trace per leaf —continued into root, rarely shows splitting of xylem.

Timber.—This is of medium quality and belongs to the red kind. The red colour intensifies from without inwards and local black strands occur here and there. The coloured heartwood is not usually large ; some specimens, however, yield a large black and brown streaked heartwood of considerable beauty and value. The sapwood is much less durable than the heartwood, in consequence of the wide

lumined tracheal and parenchymatous elements there existing. The heartwood contains a fair percentage of fibres of narrow lumen. Trees of this species are certainly worth a little attention, judging from many excellent specimens which I have seen at Ambalawa, near Gampola.

Distribution.—Endemic and rare, limited to moist region, 1,500–4,000 feet; Deltota, Uduwella, below Haputale, Hantane, Gangaruwa, Kalugalla, Ambalawa.

KEYS TO THE CEYLON SPECIES OF DIOSPYROS.

General Characters.

The following key is based on the general characters of the leaves, fruits, and stems, and may be found useful as a substitute for that given by Trimen. With the help of this key and the illustrations of every species showing flowers, fruits, seeds, timber, and leaves there ought to be no difficulty in identifying species of Diospyros in the forests of Ceylon.

ENDOSPERM EQUABLE.

Leaves large, 110 to 300 mm. long.

Fruit flattened or ovoid-globose, covered with glandular hairs ... **D. Embryopteris.**

Fruit attenuate, feebly pubescent... **D. acuta.**

Leaves 50–200 mm. long.

Leaves opposite ... ... **D. oppositifolia.**

Leaves alternate.

Leaves thin, not coriaceous, feebly pellucid.

Fruit depressed-globose, stem spiny ... **D. montana.**

Fruit strongly attenuate, stem smooth ... **D. attenuata.**

Leaves coriaceous, strongly pellucid venation.

Seeds flat.

Fruits depressed-globose, leaves bullate and pellucid ... D. Gardneri.

Fruit globose-ovoid, nervation not pellucid ... D. quæsita.

Seeds wedge-shaped.

Nervation closely reticulate, fruit-calyx thin and flat ... D. Toposia.

Nervation wider mesh, fruit-calyx woody and cup-shaped ... ... D. Ebenum.

Leaves small, 50–120 mm. long.

Leaves and fruits covered with very long hairs ... ... D. pruriens.

Leaves and fruits glabrous.

Veins and calyx segments inconspicuous, seeds deeply grooved ... ... D. oocarpa.

Veins and calyx segments conspicuous, seeds superficially striated ... ... D. ovalifolia.

ENDOSPERM RUMINATE.

Male corolla urceolate, seeds small and rounded ... ... D. sylvatica.

Male corolla tubular, seeds wedge-shaped or flat.

Leaves large, 100–300 mm. long.

Fleshy, veins not prominent, bark thick ... D. Moonii.

Coriaceous, veins prominent, bark thin and scaly ... D. insignis.

Leaves 35–130 mm. long.

Mature fruit hairy ... **D. hirsuta.**

Mature fruit glabrous or nearly so.

* Fruit-calyx much enlarged and woody.

† Leaves oblong-oval, 40–90 mm. long, feebly pellucid venation ... **D. affinis.**

†† Leaves with acuminate apex, 50–130 mm. long, pellucid venation ... **D. crumenata.**

** Fruit-calyx not much enlarged nor woody.

† Fruit globose, 35 mm. high, leaves broadly oval ... **D. Melanoxylon.**

†† Fruit broadly ovoid, 25 mm. high, leaves narrowly lanceolate ... **D. Thwaitesii.**

Seedling and Fruit Characters.

The following key has been constructed mainly from characters of the seeds and seedlings. In several instances the number and behaviour of cotyledonary traces would have been of service, but as such characters cannot be used outside the laboratory those of the fruit have been included as being of more practical importance in determining the identity of species in the forest.

ENDOSPERM EQUABLE.

Cotyledons persistent.

Seeds flat, thin (2 mm.) ... **D. Gardneri.**

Seeds wedge-shaped.

Fruit-calyx large, woody, segments acute, first epicotyledonary leaf small, only 2 mm. long **D. Ebenum.**

Fruit-calyx small, thin, segments rounded, first epicotyl leaf average size, 20 mm. long **D. montana.**

Cotyledons dropping.

Hypocotyls short (10-50 mm.), epicotyledonary stems long (40-70 mm.).

Seeds irregular in shape, deeply grooved, hypocotyl 10-30 mm., fruit—calyx segments undistinguishable ... ... **D. oocarpa.**

Seeds oval - elliptical or wedge-shaped, hypocotyl 40-50 mm. long ... **D. Toposia.**

Hypocotyl long (30-100 mm.), epicotyledonary stems short (3-40 mm.).

Seedlings densely pubescent **D. pruriens.**

Seedling glabrous or nearly so.

* Seeds rounded and short (9 mm.), testa superficially striated ... **D. ovalifolia.**

** Seeds large and flat, 30 mm. long.

Testa transversely striated, epicotyledonary leaves opposite ... **D. quæsita.**

Testa not striated, epicotyledonary leaves sub-opposite .. **D. Embryopteris.**

*** Seeds semi-lunar or wedge-shaped.

Seeds acuminate at micropyle, fruit-calyx large and convolute ... **D. acuta.**
Seeds not acuminate, fruit-calyx small and thin ... **D. attenuata.**
Fruit-calyx forms deep cup (18 mm.) ... **D. oppositifolia.**

ENDOSPERM RUMINATE.

Cotyledons persistent.

Seeds short (14 mm.), globular ... **D. sylvatica.**

Cotyledons dropping.

Hypocotyl short (15 to 20 mm.), epicotyledonary stem long, with leaf rudiments (65 mm.) ... **D. insignis.**
Hypocotyls long (60-110 mm.), epicotyledonary stem short (3–15 mm.).

Fruits small, 27 × 23 mm.

Fruit wall with dense layer of brown hairs, fruit 8-celled ... **D. hirsuta.**
Fruit wall when old nearly glabrous, fruit 4-celled ... **D. Thwaitesii.**

Fruit large, 36 × 33 mm.

Seeds flat and thin.

Testa deeply striated, fruit-calyx small, thin ... **D. Moonii.**
Fruit-calyx large, woody, strongly recurved ... **D. crumenata.**

Seeds wedge-shaped or semi-lunar.

Fruits globular, fruit-calyx large, thick, and undulate **D. Melanoxylon.**
Fruits apiculate or flattened at top, fruit-calyx thin and small ... **D. affinis.**

In conclusion, I take this opportunity of expressing my thanks to Mr. J. C. Willis, for first suggesting the genus Diospyros to me, and for the help received during the progress of this work while enjoying the tenure of my appointment as Scientific Assistant. I have also to thank Messrs. A. F. Broun, F. Lewis, H. P. C. Armitage, A. M. Walker, A. M. Fontyne, and other officers of the Ceylon Forest Department for the time they have spent conducting me through their districts and for the many specimens received from them. For similar favours I must also express my gratitude to Messrs. W. P. Hiern ; J. H. Maiden, Director of the Botanic Gardens, Sydney ; C. A. Barber, Government Botanist, Madras ; Major Prain, Superintendent, Royal Botanic Gardens, Calcutta ; to Mr. J. Wilson, China ; Mr. W. C. Curtis, Penang ; and to the Conservator of Forests of the Andaman Islands.

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Description of Plates I—XX.

Plate I.—Sections of the timber of (1) *D. pruriens*, (2) *D. hirsuta*, (3) *D. Moonii*, (4) *D. affinis*, (5) *D. Melanoxylon*, and (6) *D. ovalifolia*.

The relative sizes of the different trees may be calculated from the measure photographed on Plate V. Obviously, the timber of most of the species here described may be obtained in various sizes, but those on the same plate are selected with a view to illustrating the relative sizes of mature trees of the respective species.

Piate II.—Transverse sections of the timber of (7) *D. sylvatica*, (8) *D. oppositifolia*, and (9) *D. Thwaitesii*.

Figure 8 shows the characteristic hollow decaying protoxylem area and the streaked nature of the remaining wood in D. oppositifolia. The rings of growth in D. sylvatica are perhaps clearer than in any other Diospyros species.

Plate III.—Transverse sections of the timber of (10) *D. attenuata* (12) *D. Toposia*, (13) *D. insignis*, with characteristic bark, and (11) oblique section and log of *D. acuta* showing bark characteristic of most Diospyros species.

Plate IV.—Transverse sections of (14) *D. crumenata*, (15) *D. oocarpa*, and (16) *D. Ebenum*.

The section of D. oocarpa is unusually large and is used to show the large amount of streaked ebony of good quality which is frequently found in this species.

Plate V.—Longitudinal section of (17) *D. quæsita* showing streaked heartwood of varying width, transverse section of (18) *D. Gardneri*, longitudinal and oblique sections of (19) *D. Montana*, and (20) *D. Embryopteris.*

Plate VI.—Nat. size. *(1-4), D. oppositifolia* ; (1) female flower terminating young twig ; (2) mature fruit and fruiting calyx ; (3) and (4) male inflorescence and flowers from woody twig ; *(5-9) D. quæsita* ; (5) female flowers, young and mature ; (6) seed showing transverse striæ on testa and young seedling stage ; (7) male inflorescences : (8) fruit in longitudinal section (reduced $\frac{1}{2}$); (9) longitudinal section of seed showing embryo *in situ.*

Plate VII.—Nat. size. *(1-7), D. oocarpa* ; (1) male inflorescences ; (2) section through male flower, showing position of stamens ; (3) mature male flower showing calyx with insignificant segments ; (4) female flower ; (5) fruit showing insignificant straight rimmed calyx ; (6) seed; (7) leaf. *(8-14), D. acuta* ; (8) male inflorescence ; (9) corolla of male flower ; (10) female inflorescence ; (11) solitary female flower ; (12) corolla of female flower ; (13) fruit with calyx ; (14) pistil from mature flower.

Plate VIII.—Nat. size, except (2) and (4).

1-5, D. crumenata ; (1) male inflorescence ; (2) section of male flower enlarged to show position of stamens ; from drawings in the herbarium ; (3) solitary female flower ; (4) dissected corolla of female flower showing position of staminodes (enlarged); from herbarium drawing ; (5) fruit and recurved fruiting calyx ; *(6-9) D. Melanoxylon* ; (6) female inflorescences ; (7) fruits ; (8) male inflorescences ; (9) male flower.

Plate IX.—Nat. size. *D. Embryopteris.* 1, 2, 3, 4, stages in the development of the female inflorescence showing positions of bracts (for description see Part 1, p. 72); (5) mature female inflorescence ; (6) fruit covered with reddish-brown glandular and unicellular hairs ; 7, 8, 9, and 10 stages in the development of male inflorescence ; described in Part 1, p. 73–74 ; (11) mature male inflorescence ; 12 section through male flower showing position of stamens.

Plate X.—Nat. size, except 4 and 10. *1-6, D. affinis* ; (1) mature female flower ; (2) fruit showing insignificant calyx ; (3) male inflorescences showing positions of detached flowers; (4) section through male flower showing position of stamens and rudimentary pistil enlarged ; from herbarium drawing ; (5) polygamous inflorescence, median female, and lateral male flowers ; (6) fruit from polygamous tree ; *7-10, D. Toposia* ; (7) young and (8) mature male inflorescences ; (9) female inflorescence ; (10) fruit, young, $\frac{1}{2}$ size of mature specimens.

Plate XI.—Nat. size. *1-9, D. sylvatica* ; (1) young male (2) mature male inflorescences ; (3) corolla of male flower dissected to show position of stamens ; (4) polygamous twig bearing upper cluster of male flowers and fruit below ; (5) and (6) sections through flowers from polygamous tree showing development of pistil ; (7) seed showing external rumination ; (8) female inflorescences ; (9) fruit from female tree. *10-15, D. attenuata* ; (10) male inflorescence ; (11) separate male flower ; (12) seed ; (13) mature fruit showing insignificant calyx ; (14) solitary female flower ; (15) leaf.

Plate XII. D. Gardneri. Nat. size, except 2 and 10 ; (1) group of hermaphrodite flowers from polygamous tree ; (2) × ½ section of hermaphrodite flower showing pistil and stamens ; (3) male flower ; (4) section of male flower ; (5) male inflorescense ; (6) male flowers and fruit on same twig from polygamous tree ; (7) flower from true male tree ; (8) section of male flower showing stamens ; (9) corolla of male flower dissected to show position of 8 pairs of epipetalous stamens; (10) ring of stamens (enlarged) to show groups of various sizes, from herbarium drawing ; (11) solitary female flower ; (12) section through female flower showing staminodes and pistil ; (13) corolla of female flower dissected to show the position of eight epipetalous staminodes ; (14) longitudinal section of seed showing equable endosperm and embryo *in situ.*

Plate XIII.—Nat. size.

D. Ebenum1-8. (1) Male flowers ; (2) female cymose inflorescence ; (3) solitary female flowers ; (4) polygamous clusters (*a*) female (*b*) male flowers ; (5) moncœcious group (*a*) female (*b*) male flowers ; (6) group of stamens showing fusion and unequal length ; (7) fruit and recurved calyx ; (8) transverse section of young fruit.

D. pruriens (9–12). (9) Male flowers and leaves ; (10) staminal whorl magnified ; (11) fruit with long hairs ; (12) seed with embryo.

Plate XIV.—Nat. size.

D. insignis (1–5). (1) Male flowers ; (2) polygamous flowers (*a*) female flower ; (*b*) same flower separated from cluster ; (3) female flowers in bud ; (4) fruit with calyx ; (5) L. S. of seed with embryo and showing ruminate endosperm.

D. Moonii (6–10). (6) Young fruits ; (7) male flowers in bud ; (8) fruit with calyx ; (9) seed showing transverse striæ ; (10) longitudinal section of seed to show embryo and ruminate endosperm.

Plate XV.—Nat. size except 4 and 5 which were taken from drawings in the herbarium.

D. ovalifolia (1–5). (1) Male inflorescence ; (2) female flowers, fruit, and leaf ; (3) seed showing irregular striæ ; (4) pistil in situ,

corolla, and staminodes removed ; (5) pistil figured from above to show crenate bifid stigma.

D. hirsuta (*6-12*). (6) Male inflorescence ; (7) female inflorescence; (8) polygamous group (*a*) female flower ; (*b*) male flowers ; (9) monœcious group (*a*) female ; (*b*) male ; (10) fruit and calyx ; (11) seeds exposed after carpellary wall removed ; (12) longitudinal section of seed showing embryo.

Plate XVI.—Nat. size.

D. Thwaitesii (*1–6*). (1) Male flowers ; (2) female flowers ; (3) polygamous group (*a*) female (*b*) male flowers ; (4) monœcious state (*a*) female (*b*) male cluster ; (5) fruit and calyx ; (6) young seedling.

D. montana (*7–10*). (7) fruits and leaf ; (8) section through fruit showing seeds and embryos *in situ ;* (9) male flower ; (10) female inflorescence.

Plate XVII.—Nat. size.

D. insignis (*1–3*). (1) Germinated seed representing a stage of the seedling when the cotyledons are detached, but the epicotyledonary system not liberated ; (2) a later stage showing the hypocotyl less than one cm. in length and young epicotyledonary stem ; (3) an old seedling showing short hypocotyl, long epicotyledonary stem with rudimentary leaves along its length and a pair of large leaves at the apex.

D. Toposia. (4) Seedling showing median length for hypocotyl and long epicotyledonary stem without leaf rudiments.

D. sylvatica (*5–6*). (5) young seedling ; (6) mature seedling with long hypocotyl and a pair of persistent foliaceous cotyledons. Note the absence of epicotyledonary leaves.

The first pair of leaves in the seedlings of these three species are approximately the same height above the ground.

Plate XVIII.—Nat. size except 6 to 8.

D. pruriens (*1–5*). (1) Seed showing embryo ; (2) young seedling ; (3) seedling with white cotyledons attached at cotyledonary node ; (4) stage showing the shrivelled cotyledons after a few hours' exposure and the enhanced epicotyledonary leaves ; (5) mature seedling showing cotyledons detached and a scar at the cotyledonary node, an epicotyledonary stem about one cm. in length, and the first pair of epicotyledonary leaves as an opposite pair similar to the cotyledons of D. sylvatica.

Embryos (*6–8*). (6) D. crumenata (× 2) ; (7) D. Embryopteris (× 2) ; (8) D. Ebenum (× 2) ; (9) seedling of D. Embryopteris showing the pale cotyledons prior to being detached and just exposed by removal of the testa and endosperm ; note the long epicotyledonary hairy stem between cotyledons. (cf. fig 6, pl. XVII.)

Plate XIX.—(All 4×D.).

Sclerotic cells (*1–4*). (1) From cortex of a twig 0·9 mm. diameter; (2) from twig 2 mm. diameter; (3) from branch 70 mm. diameter; (4) from branch 78 mm. diameter.

Hairs (*5–10*). (5) Origin of unicellular hairs from upper surface of calyx, D. Ebenum; (6) pedicellate multicellular gland, from upper surface of calyx, D. Ebenum; (7 and 8) irregular unicellular hairs from leaf bud D. Embryopteris; (9 and 10) multicellular glands usually on long pedicels, from carpellary wall of fruits of D. Embryopteris.

Plate XX.

D. Ebenum (*1–6*). (1) Transverse section of xylem, D × 4; (2) transverse section of twig 2 mm. diameter showing origin of phellogen from subepidermal layer; (3) section, diagramatic, of old xylem with lumina filled with coloured material; (4) rods of black carbon-like material liberated from the cells after treatment with strong sulphuric acid; (5 and 6), sections of the xylem showing the appearance of the deposits in the early stages; transverse and longitudinal.

Correction.

In Cooke's Flora of the Bombay Presidency, Vol. II., Pt. 1, received since the above was completed, D. crumenata is given as common in the forests between Gairsoppa and Dodmune Ghâts. It is therefore not endemic in Ceylon, as stated on p. 199.

On the Growth of Giant Bamboos, with special reference to the relation between Conditions of Moisture and the Rate of Growth.

BY

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(With Plates XXI.—XXIII.)

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INTRODUCTION.

ALMOST all previous detailed observations upon the growth of plants have been made in temperate climates. And the question naturally arises whether a

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repetition of some of these experiments made under the more favourable and uniform conditions of climate obtaining in many parts of the tropics may not lead to interesting results, possibly even indicating the necessity for a revision of some of the generalizations based upon those earlier observations.*

It appeared therefore to be worth while to make a few observations upon growth under natural conditions such as exist in a tropical country. And for a preliminary study of the growth of internodes few plants are so well adapted in many ways as the rapidly growing giant bamboo. Large clumps of Dendrocalamus giganteus constitute a striking feature in the Royal Botanic Gardens at Peradeniya, and it was upon members of this species that the majority of the measurements recorded in the following pages were made.

Sachs has indeed long ago pointed out† the disadvantages of using large and rapidly growing plants for observations upon the physiology of growth, one of the chief being the impossibility of subjecting such plants to experimental conditions. On the other hand by the use of large plants certain factors of error may be avoided. For instance the effect of strain produced by the attachment of the growing region to a recording apparatus can be done away with, if the growth is sufficiently rapid for a simpler method of observation to be used.

Perhaps the most striking fact which the observations here recorded have brought to light is the very large effect produced upon the growth of young culms of Dendrocalamus by relatively small changes in the conditions of moisture. The giant bamboo is no doubt a very highly specialized plant, and its behaviour may therefore be to some extent exceptional. Indeed the small number of plants upon which observations of the rate of growth have hitherto been made seems to warrant the suggestion that in other specific cases.

* *Cf.* Willis, Flowering Plants and Ferns, 2nd Edition, 1904, p. 3.
† Arbeiten d. Bot. Inst. in Würzburg Heft II., p. 100, 1872.

new specific results are to be expected, even in a function generally supposed to be so uniform in its progress as the rate of growth of an internode. But the result is none the less interesting, and may depend at least to some extent upon the marked constancy of the conditions other than those of moisture. The daily alternation of light and darkness is indeed more intense and the change takes place more rapidly in Ceylon than in Europe, and in the case of a plant like the giant bamboo it is almost impossible to determine the exact effect of these changes; but it seems clear that the effect is very small compared to that of changes of moisture.

Previous Observations upon the growth of bamboos in the tropics have not been numerous or elaborate. The best known are those of Kraus * in whose paper will be found a good summary of earlier observations, which consist almost entirely of mere lists of daily measurements. Some of the results of my own measurements at Peradeniya differ rather widely from those which Kraus obtained at Buitenzorg. It will therefore be necessary to give a brief description of his experiments.

Kraus made direct measurements by the aid of a tape with which he took the distance between the sharply pointed apex of the growing bud and a mark near the base of the halm. As the halm grew upwards a Malay was called in to hold the upper end of the tape, and still later a pole was made use of having a cross piece at the end. Kraus states that even towards the close of his observations two consecutive measurements, *i.e.*, made within a few minutes of each other, did not differ by more than 2–3 centimetres. Hence, although the methods which he used appear somewhat crude, and although there may have been a rather greater error in measurements made at intervals of a day, it does not appear possible to explain the wide difference between Kraus's results and those described below as being due to errors of observation.

* Ann. Jard. Buitenzorg, XII., p. 196, 1895.

The climatic conditions during the Buitenzorg experiments are described as having been very regular. In the months November to January, during which the growth of Dendrocalamus was recorded, the temperature varied only between 23° C. and 32° C. On only 5 days out of 57 did no rain fall.

From November, 1894, to January, 1895, Kraus took daily measurements of three halms belonging to a single clump of bamboos, which he describes as being labelled "Dendrocalamus sp. from Ceylon." From his description and measurements there can be no doubt that this was a young clump of Dendrocalamus giganteus *Munro*, a native of Burma introduced into Ceylon in 1856, and now becoming widely distributed. The following are the principal results of these measurements.

The early part of the grand period showed a gradual and steady increase in the rate of growth; later on there was considerable irregularity. When the culms had reached a height of nearly 14 metres there was a marked falling off in the rate of growth, and this Kraus supposed to indicate a rapid setting in of the final part of the grand period, characterized by slower growth. Here the records come to an end, and Kraus gives no indication of the total height which his culms would finally have reached. My own measurements of a clump of corresponding extent indicate 23–24 metres as a likely height.

During the latter part of the period of Kraus's observations some very violent oscillations in the daily rate of growth took place. Thus on six consecutive days the following amounts of growth are recorded for a particular culm 27, 57, 3, 48, 5, and 23 centimetres.

Kraus found an average daily growth of 22·9 cm., the greatest growth recorded during 24 hours being 57 cm. Observations taken at 6 A.M. and at 6 P.M. for seven days showed on the average a ratio of 1·8 : 1 between the amount of growth by night and that by day. On a single occasion growth was more rapid by day than at night; on all other occasions less.

Measurements were made at 12 noon also, and these showed that the rate of growth was sometimes greater in the morning, sometimes in the afternoon.

Kraus did not associate these differences with changes in conditions. Neither did he associate the violent oscillations from day to day with any conditions of climate. On the contrary, he states that temperature, rainfall, and moisture of the air showed practically no oscillations of a corresponding nature. He gives, however, no records of the conditions. Moreover he found different halms on the same plant to show widely different rates of growth on the same day. To illustrate this circumstance I reproduce a small portion of one of the published tables.

Table from Kraus.

Date. 1894.	I.		II.		III.	
	Length in Cm.	Growth.	Length in Cm.	Growth.	Length in Cm.	Growth.
January 1	1,244	47	914	24	923	31
January 2	1,288	44	942	28	964	41
January 3	1,329	41	984	42	971	7
January 4	1,341	12	1,006	22	1,015	45

The disagreement between the growth of the 3 culms was not always so great as on these particular four days. Kraus suggests that these oscillations may either be partly due to the resistance of the enveloping leaf-sheaths being suddenly overcome, or may represent "Stossweise Aenderungen" (of Sachs) of a magnitude previously unrecorded.

In his "Beitrage zur Wachstumsgeschichte der Bambusgewächse,"* Shibata publishes a most interesting table in which is recorded the daily growth of six halms of Phyllostachys mitis in Japan for three weeks during April and May, giving at the same time records of the mean daily temperature and relative humidity of the air. These measurements are given only in illustration of the rate of growth, and there is no discussion of the very interesting points

* Journ. Coll. Sci. Tokyo, 1900, p. 456.

which they present; the reader being referred to the paper of Kraus already mentioned. On plotting the curves of growth for these six halms it is found in the first place that they all show a very striking agreement, amounting indeed to almost complete parallelism, a fact much less clearly seen from the table alone. Further, in spite of very great variations from day to day, the curves show the closest agreement with that of the mean daily temperature. This varied considerably during the period of observation, the range of mean temperatures being from 11·6°C to 20·7°C. There is perhaps also a slight general agreement between the curves of growth and the curve of relative humidity, but this agreement is very largely masked by the more obvious effect of temperature.

The conclusions to be drawn from these figures are therefore entirely opposed to those of Kraus, but it is to be remembered that we are here dealing with quite different plants in quite a different climate.

I now pass on to an account of my own observations.

I.—*HABIT AND MANNER OF GROWTH.*

These are described briefly by Kraus in his paper already alluded to. Most of the clumps at Peradeniya are, however, much older and more extensive than that with which Kraus worked, one of them being indeed the parent—by the vegetative method of propagation—of the Buitenzorg plant. The clumps of Dendrocalamus observed by me had each from 300–400 culms. Kraus describes the conical bud with its equitant leaf scales and terminated by a sharp and acuminate apex, which serves as a convenient terminal point for measurement.

The remarkably upright growth of the young culms does not seem to have been much emphasized. The stems grow very straight upwards and so usually soon pass between the older stems, which are bent outwards by the weight of foliage which they bear. The brittle growing parts are

thus supported in their passage upwards, and the whole clump remains compact and resistant to the wind. As growth continues the young unbranched culms rise high above the bowed stems forming the remainder of the clump, and at this stage they are not unfrequently broken off by the force of the wind. As a rule they do not begin to droop until they are within a few metres of their full height.

When a young culm arises close to an old trunk which is nearly vertical, it may run up quite parallel with the latter for a remarkable distance, so that the appearance is as if the old culm exerted a directive influence upon the young one. But there appears to be no reason for regarding this as actually the case. The fact was utilized, however, in making measurements of the growing culms.

At Peradeniya the elongation of the culms takes place almost entirely during the south-west monsoon, which blows generally speaking from May until the end of September. Branching begins about October or November, and the further development of the branches occupies the greater part of the north-east monsoon, October to April. In the case of different clumps a good deal of variation was shown in the time at which a corresponding stage of growth was reached. The culms of the oldest and largest clump examined (clump A) were also the earliest to begin and to complete their elongation. Other clumps were as much as a month later in this respect.

Individual culms of the same clump reached the same height at periods differing by as much as a fortnight, or sometimes even more. It appears further that in different years elongation may begin at different times. Thus I find the following record in Trimen's report for 1889: "The premature and excessive rainfall in April stimulated the giant bamboos to send up their culms a month or more before the usual time. They grew with great rapidity—one which Mr. Clark measured lengthening at a rate of $13\frac{1}{2}$ inches in 24 hours." The same authority states that in the previous

year, 1888, a flood in June, during which the river rose 30 feet, submerged for two or three days the young culms then just beginning to shoot up, and this proved fatal to most of them; those which survived grew up into weak, spindly, and often crooked stems.

With these qualifications I may proceed to describe the growth of the large original clump during 1903, as far as simple observations, without actual measurements, afforded information. Further on a number of measurements will be found recorded.

The buds appeared above ground at the beginning of June, and at first elongated slowly, but as soon as a height of a metre or less had been reached they began to shoot up at a rapidly increasing rate. Later on this rate appeared to become approximately constant, and then gradually to fall off as the tops of the young culms appeared above the bent trunks of previous years. This stage of growth was arrived at late in September, rather less than four months after the appearance of the buds had been noted. The height reached in this interval was approximately 25 metres, as was ascertained by felling the culms. Soon after this the young halms took on a sharp curve close behind the apex, so that the growing point was henceforth directed almost vertically downwards. By this time the thickness of the internodes had become very small, their diameter being little more than a centimetre at the bend. During the next two months, there was a further growth of 3–4 metres, the rate of growth appearing to become very gradually smaller and smaller.

By the 10th of October branches began to shoot out. These appeared first at the point of sharpest curvature about 3 metres behind the apex. At this stage the end of the halm hung down like the lash of a whip and was very thin and pliable.

In some other clumps branching did not begin untilt he second week of November, by which time the north-east monsoon had thoroughly set in.

II.—*PERIODICITY IN LENGTH OF INTERNODES.*

A number of full grown culms were felled at different times and careful measurements made of them.

In the following table the internodes are numbered from below upwards. No. 1 is the lowest which could be conveniently measured. Below it were a few short internodes obscured by a covering of roots and curving to join the rhizome. The lengths are given in millimetres.

TABLE II.

Internode.	*a.*	*b.*	*c.*	*d.*	Internode.	*a.*	*b.*	*c.*	*d.*
84	—	—	185	—	54	260	301	334	245*
83	—	—	180	—	53	271	317	350	252*
82	155	—	175	—	52	286	322	353	503
81	165	—	215	—	51	303	311	350	330
80	174	—	170	—	50	323	280	358	372
79	179	—	185	—	49	338	310	375	382
78	180	180	180	—	48	351	340	407	430
77	172	180	200	60	47	362	385	432	431
76	165	211	190	75	46	380	387	445	450
75	140	192	210	85	45	385	406	447	452
74	135	231	215	145	44	392	421	450	470
73	140	182	233	139	43	402	445	456	453
72	145	212	230	147	42	414	467	453	492
71	145	201	245	128	41	437	490	460	490
70	141	224	240	185	40	454	505	465	475
69	159	222	260	131	39	475	510	477	453
68	165	253	256	154	38	492	527	496	460
67	178	250	277	140	37	510	528	515	468
66	193	270	283	135	36	527	531	520	477
65	204	261	295	122	35	530	513	542	502
64	220	265	311	102	34	528	553	536	535
63	241	250	305	98	33	533	532	534	563
62	252	252	321	79	32	533	510	531	562
61	252	243	335	90	31	526	515	543	596
60	251	239	330	115	30	532	535	540	568
59	253	240	330	130	29	525	526	540	580
58	251	238	337	165*	28	527	544	535	554
57	245	265	345	180*	27	529	535	545	565
56	245	280	346	185*	26	520	550	532	522
55	247	295	342	207*	25	518	540	554	554

TABLE II.—*contd.*

Internode.	*a.*	*b.*	*c.*	*d.*	Internode.	*a.*	*b.*	*c.*	*d.*
24	512	562	537	552	12	513	510	500	499
23	523	550	558	570	11	502	492	495	491
22	520	577	542	543	10	481	524	460	467
21	539	550	557	532	9	453	486	450	461
20	543	575	536	503	8	444	503	425	448
19	547	539	529	495	7	435	464	400	435
18	531	565	503	482	6	430	462	365	410
17	541	523	495	489	5	397	406	330	387
16	528	557	485	510	4	375	384	270	355
15	525	511	495	523	3	324	343	250	325
14	505	538	510	527	2	290	250	190	260
13	53	497	515	516	1	150	120	150	220

It will be seen that starting from the base of the culm the internodes at first increase rapidly in length. The maximum length is reached at about the 20th to the 30th internode, and from this there is a gradual falling off right up to the apex of the culm.

It thus appears that there is a close general agreement between the grand period of growth and the period of the length of internodes. As will be seen later on the differences in growth are greater than the differences in length of segments here recorded, and would seem to depend mainly on other factors.

The total height of the four culms was as follows:—(*a*) 29·7 metres, (*b*) 30·94 metres, (*c*) 33·3 metres (109 feet), (*d*) 28·6 metres. The circumference a metre from the base of *a* was 62 cm., of *b* 67·5 cm., of *c* 61 cm., and of *d* 57 cm.

From each of the culms measured the actual extremity had been broken off either before or during felling, but not more than 1 or 2 metres was missing in either case.

The steady sequence of increasing and decreasing length is broken here and there by minor irregularities. When there is a very marked break in the sequence, as occurs fairly frequently, there is often evidence that the young

growing culm had been subjected to injury, as in the case of internodes 53–58 of *d* marked with an asterisk(*) where the injury is followed by a series of abnormally short internodes; or to pressure, for example by the apex becoming wedged between two older trunks.

It seems impossible to say whether the smaller irregularities are to be ascribed to smaller strains, to variation in the meteorological condition such as will presently be shown to affect the rate of growth, or to purely internal causes. No relation was to be traced between the curve of growth and the length of internodes in the case of culms cut down after a series of observations upon their growth had been made. Tammes* has shown that in the case of several dicotyledons the removal of one or more leaves from the bud alters the period of length of the internodes. Removal of the leaf sheaths from the growing bud appeared too drastic a measure to apply to Dendrocalamus with any hope of success. But in this case as we have seen, there is other evidence that external causes exert an influence upon the relative lengths of the segments.

In the case of the leaves a complete series of measurements could not be made owing to the fact that the lower leaves become stripped off and fall to the ground long before the growth of the upper part of the culm is completed. The period of the length of the sheathing bases seems to agree with that of the internodes; on the other hand the blades show quite a different periodicity of length. In these organs there is a gradual transition from the condition of mere spines attached to the leaf sheath by a triangular extension, a condition occurring at the base of the culm, to wide leafy blades higher up. Also, unlike the cases of dicotyledonous trees observed by Tammes, the longest blade occurs some way above the longest internode.

* Die Periodicität morphologische Erscheinungen bei den Pflanzen. Verhandelingen der Koninklykke Akademie van Wetenschappen to Amsterdam, 1903.

III.—*CLIMATIC CONDITIONS DURING THE PERIOD OF OBSERVATION.*

During the whole of this period the temperature remained remarkably constant. The extreme range at Peradeniya during the months of June, July, and August was only from 19°C to 30°C. From June to November the extreme limits touched were 17°C and 30°C (62·6°F—86°F). On dull rainy days such as made up quite half of the first three months the range of temperature was usually not beyond 21°C to 25°C (70°F to 77°F).

On the other hand sunshine, rainfall, and moisture of the air varied considerably, On four or five occasions rain fell steadily during the greater part of the day, and the number of days on which the sun shone continuously was not much greater. Intermediate weather of every kind was experienced, and in the tables of daily measurements an attempt has been made to sum up briefly the character of each particular day. A strong wind was rare and was usually accompanied by heavy rain.

Sufficient psychrometric observations were not at first taken. The following general statements however hold good. During the period of observation the air at night was never far from the point of saturation. In the morning there was usually a rapid fall in the psychrometric co-efficient, and in the evening a corresponding rise.* A rapid rise also regularly took place as the sky became overcast previous to a shower. Generally speaking, the moisture of the air varied inversely as sunshine and temperature. The air in the shade was never extremely dry, the percentage of moisture being very rarely lower than 60. The mean driest may have been about 70 per cent.

The following table shows the rainfall to have been somewhat abnormal, as far as can be judged from the average returns. The records here given are only approximate, since

* Cp. also Schimper, Pflanzengeographie, p. 230.

a proper meteorological station has only since been established at Peradeniya. They may be taken however as being very nearly correct. A previous estimate of temperatures* shows that on the whole the range during this period was unusually small. The mean temperature however appears to be remarkably constant.

TABLE III.

Month.	Mean Tem. F.	Mean Max. F.	Mean Min. F.	Rainfall 1903. Mm.	Rainfall Average Mm.	Days, 1903.	Days, Average.
June ...	76	81	71	146	260	17	19
July ...	76·5	79·5	73·5	187	222	23	18
August ...	76	81	71	79	153	17	17
September ...	75·5	80	71	288	166	27	15
October ...	75	80	70·5	348	356	24	20
November ...	74·5	81	68	69	285	13	17

IV.—*METHOD EMPLOYED IN RECORDING GROWTH.*

The growth was recorded by the aid of a home-made instrument of very simple construction. This consisted of a straight piece of glass tubing about 30 cm. long, which was closed at one end and contained alcohol together with a bubble of air. The other end of the tube was plugged with a short piece of lead pencil. By means of this level a mark could be made upon an old halm adjoining the young apex the growth of which was under consideration; and the level of the apex was thus recorded with a considerable degree of accuracy. The error of observation did not exceed one millimetre when the measurement was made fairly close to the ground. At greater heights the error may have reached in some cases a centimetre or more, owing to the relative movements of object and scale. The distance between marks made in this way was measured directly by the aid of a steel rule graduated to $\frac{1}{2}$ mm.

* Willis, Annals, vol. I., p. 5.

In the case of Dendrocalamus, during the earlier periods of growth when the height of the growing halm was from 1-5 metres, the leaf point which formed the apex of the bud opened out and was replaced by the next younger, approximately once in 24 hours. As the halms grew upwards this process took place at an interval gradually increasing up to as much as 48 hours; and later on this became still greater. The new apex appeared in fairly young halms, at a distance of from 1–2 centimetres below the old one. In taking hourly measurements, growth was recorded at the old apex for the hour in which the change took place; the position of the new apex was at the same time noted and the next hour's growth measured from the new point. In making daily records the height was always recorded at the actual apex as it existed at the time when the measurement was taken. The error thus introduced, which is usually less than a centimetre, is not sufficient to affect the character of the curve of growth to a material extent.

As the halms grew upwards bamboo ladders were used in order to reach the apices.

The last few daily measurements of No. 1, those namely from August 1–13, were taken by means of a theodolite. This instrument read only to 1 min. (English scale) corresponding to about 1 centimetre on the vertical culm, since the theodolite was set up at a distance of about 35 metres. The culm under observation bent over at the top towards the instrument in an arc of a circle whose centre was approximately the theodolite. The whole error of these observations does not probably exceed 2–3 centimetres.

Later on a few further observations of still taller culms were taken with the theodolite. But in these cases the culms had become so thin at the upper part as to be swayed by every breath of air and very considerable errors are thus introduced. The curvature of the upper part of the culms also became very marked at this time, and I was unable to

devise any method of recording the growth after this stage had been reached.

In the later part of its growth, from July 15 to August 1, one of the culms (No. 1) was loosely tied to the neighbour on which the growth was marked, in order to bring the apex sufficiently close. The attachment was made by a cloth band which slipped easily upon the smooth surface of the older bamboo so as not to interfere with growth. In all the other cases recorded the young halm grew steadily upwards parallel to an old trunk and at a convenient distance from it. The end of each series of measurements marks the point at which curvature set in and records could no longer be made accurately. A very much larger number of observations were begun than are here published, those halms which showed awkward curvatures at an early stage being then abandoned. None of these however showed phenomena which conflicted with those exhibited in the particular cases chosen to illustrate this paper.

V.—*OBSERVATIONS.*

1.—*Grand Period.*

Daily measurements were made for various periods of time of the growing halms of Dendrocalamus giganteus *Munro*, Gigantochloa aspera *Kurz*, and Bambusa spinosa *Roxb.*

Dendrocalamus giganteus.—Halms Nos. 1, 2, 5, and 6 belonged to a very extensive clump of this species on the west side of the pond, the oldest in the gardens and the parent by vegetative propagation of all the others. The tallest culms of this clump reached a length of from 30–35 metres. Their circumference when fully grown was taken at a height of one metre above the ground; that of No. 1 was 57 cm., that of No. 2 was 61 cm.

No. 3 (circumference 48·5 cm.) belonged to a large clump at a considerable distance from the first. This clump was at

the height of its vegetative growth, and individual culms reached a still greater size than those of the first clump. These three culms were upon the eastern side of the clumps to which they belonged. No. 4 (circumference 59·5 cm.) belonged to a third clump on the east side of the pond and was on the west side of it. A number of halms on the north side of this last clump began to produce flowers about September.

Measurements of No. 1 were started when this culm had reached a height of 3·14 metres ; at a height of 18·84 metres the upper part of it was broken by the wind and the records came to an end. These extend over a period of 55 days, from June 20 to August 13. The average rate of growth during this period was 286 cm. per day, or 12·5 mm. per hour. The greatest growth for any single period of twenty-four hours was 46 cm. on July 29–30.

In the following table (Table IV.) the figures in the first column represent the growth in millimetres of this halm during the previous 24 hours, as recorded every day at 7.30 A.M. At the head of the column is given (in Albion type) the height at which measurements were begun, and at the foot the total height measured is recorded. The readings from which the mean temperature during the same period were deduced were taken at some distance from the plants, and are only approximately correct to half a degree Fahrenheit, but they serve to show the very slight variation in this respect.

The rainfall was recorded in the garden at 9.30 A.M. On no occasion, however, did heavy rain fall in the interval between 7.30 and 9.30 A.M.

The remarks in the last column apply in each case to the weather during the previous day, *i.e.*, the first part (7.30 A.M. to 5.30 P.M.) of the 24 hours for which the corresponding growth is recorded. Growth and rainfall are also represented by curves in Fig. 1, Pl. XXIII.

Table IV.

Date.	No. 1.	No. 2.	No. 3.	Mean Temp.	Rain-fall.	Remarks.
1903.	mm.	mm.	mm.	F.	mm.	
June 14	—	1015	—	—	—	—
15	—	90	—	79	·5	—
16	—	105	—	78·5	10·9	—
17	—	117	—	77	16·6	—
18	—	135	450	78	2·5	—
19	3140	153	22	78	7·5	Dull ; gentle rain
20	224	154	57	78	—	Fairly sunny
21	240	135	36	77·5	·5	Rain at midday
22	232	151	38	78	·5	Some sun
23	266	177	53	77·5	—	Variable
24	239	178	38	76	4·9	Morning sunny
25	309	168	55	77	5·5	Morning sunny
26	281	199	64	76·5	2·5	Dull
27	322	233	54	75	6·5	Dull ; showery
28	300	239	101	78	—	Fairly bright
29	389	295	89	76	26·4	Rain all day
30	420	340	95	77	·2	Variable
July 1	347	307	153	75·5	—	Dull
2	320	280	153	77·5	5·1	Dull
3	350	310	153	75·5	14·7	Dull
4	344	314	167	76	—	Afternoon sunny
5	290	271	195	75·5	—	Rather dull
6	307	268	203	77	3·3	Variable
7	297	286	273	75·5	3·0	Dull
8	281	314	270	76·5	21·1	Very dull
9	285	353	270	77	0·5	Dull
10	314	313	202	76	4·6	Variable
11	308	302	245	77·5	—	Dull
12	284	268	277	78	1·3	Fairly bright
13	323	297	292	77	2·5	Fairly bright
14	286	291	295	76	16·7	Dull ; rain
15	390	370	335	76·5	14·2	Dull ; rain
16	368	303	342	77	9·6	Variable
17	378	8731	365	74·5	7·1	Dull ; rain
18	304	—	345	76	—	Variable
19	270	—	295	75·5	1·0	Dull
20	270	—	290	75·5	—	Bright
21	260	—	305	77·5	—	Fairly sunny
22	190	—	320	77·5	—	Fairly sunny
23	289	—	315	77·5	3·0	Variable
24	290	—	5912	76·5	5·1	Variable
25	302	—	—	76·5	5·1	Variable
26	365	No. 4	—	76·5	12·7	Showery
27	320	860	—	76·5	3·0	Dull ; variable

Table IV.—*contd.*

Date.		No. 1.	No. 4.	No. 3.	Mean Temp.	Rain-fall.	Remarks.
1903.		mm.	mm.	mm.	F.	mm.	
July	28	298	87	—	77·5	3·8	Dull ; variable
	29	312	79	—	76·5	4·5	Dull
	30	460	82	—	74·5	35·9	Wet
	31	320	100	—	74·5	9·1	Dull ; some rain
August	1	290	153	—	74	3·9	Dull ; rainy
	2	260	203	—	77	·5	Afternoon bright
	3	200	235	—	75·5	—	Morning bright
	4	100	229	—	76	1·3	Sun
	5	176	245	—	76	—	Some sunshine
	6	168	242	—	74·5	—	Rather dull
	7	168	235	—	76·5	—	Sun
	8	224	276	—	76·5	2·5	Showery
	9	224	263	—	75·5	—	Sun
	10	192	295	—	76	5·9	Sun
	11	272	320	—	77·5	8·4	Rain
	12	240	302	—	74	7·1	Rain
	13	150	310	—	74	—	Bright
		18844	4516	—	—	—	—

None of the other culms were followed so far as No. 1. A glance at fig. 1 shows that after a height of about 4·5 metres had been reached (on June 26) the growth continued fairly steady, with perhaps some signs of a gradual falling off towards the end of the period of observation. Considerable irregularities, however, occur from day to day, and the agreement which these variations show with the variations in the amount of rainfall is very striking. The greatest difference between the amounts of growth on two consecutive days was 148 mm., between 312 mm. on July 29 and 460 mm. on July 30—a difference which amounts to 32 per cent. of the greater growth. The rainfall on these two days was 4·5 and 35·9 mm. respectively.

The agreement between growth and rainfall is equally marked whether the daily or the three-day curve is taken into account. A drought of one or two days is regularly

accompanied by a falling off in the rate of growth, as for example on July 1, 5, and 22, and on August 1 to 4; whilst heavy rain is accompanied by a marked increase of growth, as on June 28, July 15 and 30. The only exception was on July 8. On the whole the agreement is quite unmistakable.

The variations in rate of growth become more marked in the later part of the grand period than in the earlier, and they appear also in the later portion to show a more marked agreement with the curve of rainfall.

Culm No. 2 grew at a distance of less than a metre from No. 1. Measurements were started on June 14—the halm being then little more than a metre high—and were discontinued on July 17 at a height of 8·73 metres. The average growth during this period was 24·1 cm. per day, or 10 mm. per hour. The less average growth of this culm than in the case of No. 1 is accounted for by the fact that an earlier portion of the grand period is included. The daily measurements are recorded in the second column of Table IV., and a portion of the corresponding curve is shown in fig. 1. This clearly illustrates the steady increase in rate of growth during the earlier part of the grand period. Like those of No. 1 the variations in rate of growth show a close agreement with the variations of rainfall. The greatest growth recorded in 24 hours was 370 cm. on July 15.

Measurements of No. 3 began at a height of 45 cm. The whole of the growth recorded for this culm belongs to the earlier part of the grand period which is characterized by a gradual increase in rate of growth. Here again the daily oscillations of growth show a general agreement with those of rainfall. The total height reached in 35 days was 5·91 metres, showing a rate of growth which agrees closely with that of Nos. 1 and 2 for corresponding parts of their grand periods.

Records of the growth of No. 4 were continued only for 17 days. A part of the curve obtained is shown in fig. 2,

Plate XXII. Some interesting points are to be noticed in this figure. On July 30 35·9 mm. of rain fell. This was accompanied in No. 1 by an immediate increase in the rate of growth, which afterwards fell off rapidly. In the case of No. 4 the immediate increase in rate was very slight, but on the following days the rate became rapidly greater. At the time the height of No. 1 was 15·4 metres, that of No. 4 almost exactly one metre. It may here be pointed out that two halms of Gigantochloa, Nos. 11 and 12, the growth of which is described below, showed upon these days an intermediate behaviour and were intermediate in height between the Dendrocalamus culms, Nos. 1 and 4.

The month of August, 1903, was distinctly drier than the average. At the beginning of September a spell of wet weather set in, and at this time a few further observations were made with a theodolite upon two very upright culms of the same clump as Nos. 1 and 2, but which had not previously been measured. The estimated height of No. 7 on August 28 was 20 metres, that of No. 8 on September 5 being 23 metres. Neither these heights nor the records of daily growth are to be regarded as more than roughly approximate, nevertheless the average growth which they indicate cannot be very far wrong.

From August 29 to September 3 inclusive the average growth of No. 7 was nearly 9 cm. per 24 hours, whilst for the following six days the average was over 21 cm. per day, the weather during the latter period being very much wetter. From September 6 to 10 the average growth of No. 8 was also over 20 cm. per day.

For the whole period of thirteen days the average growth of No. 7 was nearly 16 cm. per day. We have already seen that at heights of from 10–15 metres the rate of growth of Dendrocalamus culms is nearly twice as rapid.

Table V.

Date.	No. 7.	No. 8.	Rainfall.	Mean Temp.	Remarks.
1903.	mm.	mm.	mm.	F.	
August 28	20,000	—	·5	77·5	—
29	70	—	—	77·5	Sunny
30	30	—	—	77·0	Sunny
31	30	—	2·0	75·0	Morning sun; afternoon wet
Sept. 1	120	—	5·1	76·0	—
2	120	—	14·8	75·0	—
3	160	—	7·9	76·0	Dull; wet
4	160	—	66·0	76·0	Heavy rain in evening
5	200	23,000	9·1	77·0	Morning sun; afternoon wet
6	230	240	14·0	75·0	Morning sun
7	230	240	·2	74·0	
8	220	110	1·3	75·5	Dull
9	230	220	12·0	75 0	Dull; wet
10	230	220	32·1	74·5	Dull; wet

The table shows again a very obvious relation between growth and rainfall.

In the above table a bracket indicates that an observation was taken only on the second of the two days so connected. The figures in these cases represent the average growth for each of the two days.

Gigantochloa aspera.—Measurements were made of three growing culms Nos. 11, 12, and 13 belonging to a single clump and all situated on the north side of it. This clump grew on a slight mound, whereas the clumps of Dendrocalamus were all in damp hollows. The heights at which measurements of growth was begun were as follows: No. 11, 103·5 cm.; No. 12, 610 cm.; No. 13, 960 cm. And the ultimate circumferences a metre above the ground: No. 11, 50·8 cm.; No. 12, 49·5 cm.; No. 13, 49 cm. In

the following table the daily growth of these culms is recorded for comparison with that of Dendrocalamus.

Table VI.

Date.		No. 11.	No. 12.	No. 13.	Rain-fall.	Remarks.
1903.		mm.	mm.	mm.	mm.	
July	13	1035	610	—	2·5	Fairly bright
	14	68	34	—	16·7	Dull ; rain
	15	84	43	—	14·2	Dull ; rain
	16	112	45	—	9·6	Variable
	17	132	54	—	7·1	Dull ; rain
	18	126	59	—	—	Variable
	19	130	55	—	1·0	Dull
	20	143	60	—	—	Bright
	21	131	53	960	—	Fairly sunny
	22	132	57	56	—	Fairly sunny
	23	127	62	58	3·0	Variable
	24	145	68	67	5·1	Variable
	25	154	78	77	5·1	Variable
	26	165	83	79	12·7	Showery
	27	186	107	94	3·0	Dull ; variable
	28	157	84	78	3·8	Dull ; variable
	29	145	83	87	4·5	Dull
	30	273	153	148	35·9	Heavy rain
	31	282	173	171	9·1	Dull ; rain
August	1	280	201	202	3·9	Dull ; rain
	2	296	221	197	·5	Afternoon bright
	3	297	265	255	—	Morning bright
	4	290	266	222	1·3	Sunny
	5	260	249	237	—	Fine ; some sun
	6	215	219	2,988	—	Fine to dull
	7	165	179	—	—	Sunny
	8	162	194	—	2·5	Showery
	9	139	166	—	—	Sun
	10	190	222	—	5·9	Sun
	11	225	256	—	8·4	Rain
	12	240	303	—	7·1	Rain
	13	252	303	—	—	Bright
	14	245 }	4,905	—	—	Variable
	15	245 }	—	—	—	Variable
	16	193	—	—	5·1	Rain in afternoon
	17	170	—	—	—	Sunny
	18	6,611	—	—	3·0	Rain in afternoon

In addition to the figures given in the above table No. 11 grew 385 mm. from July 6 to 13, an average growth of 55 mm. per day, and in the same time No. 12 grew 230 mm., an average of 33 mm. per day. On August 25 No. 11 showed a further growth of 1,112 mm., being an average of 159 mm. per day from August 19–25, inclusive.

Examination of the table will show that in the case of Gigantochloa, as well as in that of Dendrocalamus, there is a remarkable correspondence between rate of growth and daily rainfall. A portion of the curves of growth for Nos. 11 and 12 is shown in fig. 2. The sudden increase in rate of growth accompanying the heavy rainfall on July 30 is very noticeable.

In Table VII. under No. 18 is recorded the growth from July 26 to August 31 of a culm belonging to another clump, probably also of Gigantochloa aspera, but much younger. The circumference of this culm was only 26 cm.; its rate of growth during the month of August is relatively slow, and this is probably connected with the low rainfall for the month, for it is to be noticed that the growth of No. 11 fell off considerably about August 17.

Bambusa spinosa.—A few measurements of growing halms of this species were taken for the sake of comparison with the larger bamboos. No. 15 belonged to a very young clump, having only a few adult halms; its circumference was 140 mm. Nos. 16 and 17 belonged to another much larger clump. The circumference of No. 16 was 203 mm.; of No. 17, 191 mm. The growth of these halms is on the whole somewhat slower than in the case of Dendrocalamus, but it is to be remembered that by the time the halms had reached a fair height a somewhat dry period had set in. In the case of all these halms the rate of growth shows a general agreement with the rainfall, whereas the small oscillations in mean temperature appear to produce no more recognizable effect than in the case of Gigantochloa or Dendrocalamus.

Table VII.

Date.	No. 15.	No. 16.	No. 17.	No. 18.	Mean Temp.	Rain-fall.	Remarks.
1903.	mm.	mm.	mm.	mm.	F.	mm.	
July 26	280	450	350	550	—	12·7	Showery
25	12	17	15	26	76·5	3·0	Dull ; variable
28	22	34	26	29	77·5	3·8	Dull ; variable
29	21	38	25	37	76·5	4·5	Dull
30	35	55	38	45	74·5	35·9	Heavy rain
31	35	60	44	48	74·5	9·1	Dull ; rain
Aug. 1	41	76	48	37	74	3·9	Dull ; rain
2	51	94	52	32	77	·5	Afternoon bright
3	52	109	65	30	75·5	—	Morning bright
4	82	121	96	56	76	1·3	Sunny
5	74	125	91	69	76	—	Fine ; some sun
6	78	130	99	76	74·5	—	Fine to dull
7	75	130	100	83	76·5	—	Sunny
8	73	139	113	96	76·5	2·5	Showery
9	78	138	105	92	75·5	—	Sun
10	87	167	147	122	76	5·9	Sun
11	88	190	164	131	77·5	8·4	Rain
12	89	180	181	130	74	7·1	Rain
13	94	159	157	127	74	—	Bright
14	90	170	160	157	77	—	Variable
15	90	170	160	157	75	—	Variable
16	87	147	160	147	77·5	5·1	Rain in after-noon
17	89	2899	143	132	76	—	Sunny
18	95	—	157	167	75·5	3·0	Rain in after-noon
19	95	—	157	167	75·5	4·5	Rain in after-noon
20	1913	—	182	166	75·5	—	Brighter
21	—	—	135	143	78	—	Sun
22	—	—	145	140	77·5	—	Bright
23	—	—	192	162	78	5·1	Morning sun ; rain in after-noon
24	—	—	192	162	75·5	2·0	
25	—	—	192	162	75	8·7	
26	—	—	192	162	75·5	18·1	Dull ; rain
27	—	—	243	172	78·	1·0	Dull
28	—	—	228	148	77·5	·5	Bright
29	—	—	155	133	77·5	—	Sunny
30	—	—	150	147	77	—	Sunny
31	—	—	150	147	75	2·0	Afternoon rain
			5014	4592			

2.—*Length of Growing Region of Dendrocalamus.*

On July 3 to 10 a series of the lower internodes of No. 1 were measured with the following result :—

Table VIII.

Length in mm. of internodes 12–17 from base of halm on July 3-10.

July		3rd.	4th.	5th.	6th.	7th.	8th.	9th.	10th.
Internode.	17	—	—	—	421	451	467	486	486
	16	—	—	—	490	510	510	510	510
	15	433	454	473	484	484	484	484	484
	14	476	490	490	495	495	495	495	495
	13	440	445	443	445	445	—	—	—
	12	433	440	440	440	440	—	—	—

And from these measurements together with those of the total growth of the culm previously recorded the following table is obtained :—

Table IX.

Date. 1903.		Height of Halm.		Distance of Base of lowest growing Node from Apex.
July 3	...	7·379 m.	...	5·549 m.
4	...	7·723	...	5·453
5	...	8·013	...	4·810
6	...	8·320	...	4·647
7	...	8·617	...	4·520
8	...	8·898	...	4·701
9	...	9·183	...	4·986
10	...	9·497	...	4·814

So that during this period the average distance of the base of the lowest growing node from the apex of the halm was 4·935 metres.

When No. 1 was broken down by the wind on August 14 the lengths of the successive internodes were carefully

measured, and the result is recorded in the following table :—

Table X.

Internode.	Length. mm.	Difference.	Internode.	Length. mm.	Difference.	Internode.	Length. mm.	Difference.
67*	13	—	45	180	22	23	450	—27
66	15	2	44	209	29	22	466	16
65	16	1	43	236	27	21	452	—14
64	17	1	42	266	30	20	494	42
63	19	2	41	282	16	19	480	—14
62	21	2	40	300	18	18	515	35
61	23	2	39	332	32	17	480	—35
60	25	2	38	353	21	16	503	23
59	28	3	37	333	—20	15	435	—68
58	32	4	36	374	41	14	446	11
57	33	1	35	395	21	13	375	—71
56	35	2	34	455	60	12	410	35
55	40	5	33	467	12	11	337	—73
54	50	10	32	496	31	10	328	— 9
53	58	8	31	475	—21	9	280	—48
52	63	5	30	480	5	8	255	—25
51	75	12	29	475	— 5	7	240	—15
50	84	92	28	486	11	6	185	—55
49	99	15	27	477	— 9	5	160	—25
48	118	19	26	495	18	4	120	—40
47	137	19	25	470	—25	1 + 2 + 3	300	—
46	158	21	24	477	7	—	—	—

It will be seen that the internodes increase in length from the base upwards to about the sixteenth at a height of 4·37 metres. Above this their length is approximately equal up to the 32nd at a height of 11·55 metres. Beyond this point growth appeared to be still going on, the point at which growth had ceased being some 6 metres from the extreme apex.

Later on, judging from the appearance of other culms which were felled at a later date, the growing region soon became much reduced in length, until elongation was at last confined to the extremity of the hanging lash-like apex, where slow growth continued for a considerable time.

* Beyond the 67th internode the culm was damaged in felling : this point is some 15 cm. from the tip of the bud.

3.—*Growth by Day and Night.*

Dendrocalamus.—Measurements of culms Nos. 1 and 2 were made daily from June 19 to July 18 at 7.30 A.M. and 5.30 P.M. Hourly measurements showed that these times divide the periods of more and of less rapid growth somewhat sharply.

In the following table (Table XI.) the average growth per hour from 7.30 A.M. to 5.30 P.M. (day) and from 5.30 P.M. to 7.30 A.M. (night) is recorded in mm. The date in each case refers to the end of the 24-hour period. And the height at this time (7.30 A.M.) is recorded in centimetres. The remarks apply to the weather during the first ten hours of the period in each case.

Table XI.

Date.	No. 1.			No. 2.			Remarks.
	Height. cm.	Day. mm.	Night. mm.	Height. cm.	Day. mm.	Night. mm.	
1903.							
June 19	314	—	—	161	4·9	7·5	Dull; some rain
20	336	3·6	13·4	177	3·0	8·8	Fairly sunny
21	360	4·6	13·8	190	3·1	7·7	Rain at midday
22	384	2·7	14 6	205	2·7	8·8	Some sun
23	410	4·0	16·3	223	3·2	10·3	Variable
24	434	4·6	13·8	241	3·4	10·3	Morning sunny
25	465	5·0	18·5	258	3·0	9·8	Morning sunny
26	493	4·5	16·8	278	4·0	11·3	Dull
27	525	8·4	17·8	301	6·1	12·3	Dull; showery
28	555	3·2	19·1	325	3·3	14·7	Fairly bright
29	594	15·0	17·0	354	12·4	12·2	Rain all day
30	636	9·8	23·0	388	10·5	16·8	Variable
July 1	671	10·7	17·1	419	9·7	15·0	Dull
2	703	6·0	18·5	447	5·0	16·4	—
3	738	8·0	19·3	478	8·0	16·4	—
4	772	11·6	16·3	509	7·2	17·3	Morning rain; afternoon sun
5	801	2·5	18·9	536	3·6	16·9	Rather dull
6	832	2·7	20·0	563	2·3	17·4	Variable
7	862	5·2	17·4	592	4·9	17·0	Dull
8	890	8·6	13·9	623	10·2	16·5	Very dull
9	918	4·8	17·0	659	9·6	18·3	Dull
10	949	3 8	19·7	690	6·7	17·5	Variable
11	980	2·5	20·2	720	3·4	19·2	Rather dull

Table XI.—*contd.*

Date.	No. 1.			No. 2.			Remarks.
	Height. cm.	Day. mm.	Night. mm.	Height. cm.	Day. mm.	Night. mm.	
1903.							
July 12	1,009	—	—	747	—	—	—
13	1,041	3·5	20·5	776	3·6	18·6	Fairly bright
14	1,070	5·8	16·3	806	5·9	16·5	Dull ; rain
15	1,109	13·0	18·5	843	10·0	19·3	Dull ; rain
16	1,145	6·8	21·4	873	4·3	18·5	Variable
17	1,183	10·0	19·8	—	—	—	Dull ; rain
18	1,214	4·8	18·2	—	—	—	Variable

In the case of No. 1 the average hourly growth during the day for the whole period was 6·27 mm. During the night (5.30 P.M. to 7.30 A.M.) it was 17·75 mm. or nearly three times as rapid. The most rapid growth on any day was 15·0 mm. per hour on June 28, rain having fallen steadily nearly all day. The rate of growth during the following night was 17·0 mm. per hour. The least growth in the day time was 2·5 mm. per hour recorded on July 4 and 9. Both days were rainless. The greatest growth at night was 23·0 mm. per hour and the least 13·9 per hour, which is more than twice the average hourly growth by day.

For No. 2 the average hourly growth by day was 5·7 mm. and by night 14·5 mm., again approaching a ratio of 1 : 3. The greatest growth by day was on June 28 being 12·4 mm. per hour ; during the following night it was 12·2 mm. per hour, this being the only case in which the rate of growth by day was observed to exceed that during the night.

For the period during which records were made it appears that in the case of Dendrocalamus the ratio of the hourly growth by day to that during the following night varied between one of equality and one of nearly 1 : 8 ; the former on an exceptionally wet and dull day. At no time during the period under consideration did the sun shine steadily all day long.

Gigantochloa.—In Table XII. records are given for seven days only. Average growth by day for No. 11, 2·5 mm., for No. 12, 1·2 mm. per hour; and by night No. 11, 6·2 mm., No. 12, 2·7 mm.; here again the average rates of growth by day and by night are nearly as 1 : 3.

The explanation of Table XI. applies to Table XII. also.

Table XII.

Date.	No. 11.			No. 12.			Weather.
	Height. cm.	Day. mm.	Night. mm.	Height. cm.	Day. mm.	Night. mm.	
June 14	110	2·0	3·4	64	·8	1·4	Dull; rain
15	119	2·0	4·6	69	·9	2·4	Dull; rain
16	130	2·4	6·3	73	1·1	2·4	Variable
17	143	4·7	6·1	78	2·0	2·4	Dull; rain
18	156	3·1	6·8	84	1·6	3·1	Variable
22	209	1·6	8·3	107	1·0	3·4	Morning sunny; afternoon dull
23	212	1·5	8·0	113	·9	3·8	Morning sunny; afternoon dull

4.—*Daily Period. Dendrocalamus.*

It will next be advisable to consider more in detail the course of growth by day and night. For this purpose hourly observations were made of the growth of culms o Dendrocalamus on June 22–23 and again on June 29–30 in connection with notes on the state of the weather.

Table XIII. shows the hourly growth in mm. of Nos. 1 and 2 from 3.30 P.M. on June 22 to 11.30 A.M. on June 23. Both before and after this interval readings were taken every two hours, bringing up the total period to one of 36 hours extending from 7.30 A.M. June 22 to 7.30 P.M. June 23. The curve of growth is shown in fig. 3, Pl. XXI.

Table XIII.

Time.	No. 1.	No. 2.	Weather.
9.30 A.M.	3·5	3·5	Dull
11.30 ,,	3	2	Brighter
1.30 P.M.	2·5	4	Showery

Table XIII.—*contd.*

Time.		No. 1.		No. 2.		Weather.
3.30	P.M.	3·5	...	4	...	Showery
4.30	,,	6	...	3	...	Sun
5.30	,,	7	...	1·5	...	Some sun
6.30	,,	8	...	9	...	Clear
7.30	,,	19	...	10	...	Clear
8.30	,,	15	...	9·5	...	Clear
9.30	,,	16	...	11	...	Clear
10.30	,,	19	...	13	...	Clear
11.30	,,	18	...	11	...	Clear
12·30	A.M.	17	...	10	...	Shower
1.30	,,	17	...	10	...	Shower
2.30	,,	15	...	10	...	Clear
3.30	,,	16	...	12	...	Clear
4.30	,,	17	...	11	...	Clear
5.30	,,	17	...	10	...	Clear
6.30	,,	14	...	9	...	Dull
7.30	,,	8	...	10	...	Dull
8.30	,,	6	...	3	...	Sun
9.30	,,	0	...	0	...	Sun
10.30	,,	1·5	...	1	...	Sun
11.30	,,	2	...	3	...	Showery
1.30	P.M.	1	...	1·5	...	Showery
3.30	,,	4	...	3·5	...	Showery
5.30	,,	13	...	8·5	...	Dull
7.30	,,	16	...	10	...	Dull

In the month of June in Ceylon there is a moderately rapid change from light to darkness and from darkness to light at about 6 P.M. and 6 A.M. respectively. The first signs of light begin to appear a little before 5.30 A.M., and by 6.30 P.M. darkness is nearly complete. Turning now to the curve of growth it will be seen that during the day the rate of growth is low though somewhat variable. In the evening the curve rises rapidly and reaches a maximum soon after dark. During the night the rate of growth remains high and fairly constant. At daybreak it falls again rapidly.

The variations of growth during the day show a marked parallelism with changes of weather. Thus the evening of the 22nd was dry and fairly sunny, on the 23rd the

evening was dull and showery, and in the latter case there was a marked increase in the rate of growth some time before darkness set in. From 7–10.30 A.M. on the 23rd the sun shone brightly right on to the culms under observation, which were on the east side of the clump; and from 8.30 to 9.30 no growth could be detected for either culm.

The curves of growth of the two separate culms agree somewhat closely, and if some allowance is made for the "individuality" of the two, the agreement between them and of both with the external condition is remarkably close. A similar series of measurements of the same two culms was taken hourly from 5.30 A.M. on June 29 to 5.30 P.M. on June 30. The result is shown in Table XIV. and the curves of growth in fig. 4, Pl. XXI.

Table XIV.

Date.	Time.	No. 1. Growth mm.	No. 2. Growth mm.	No. 5. Growth mm.	No. 6. Growth mm.	Temp. F°	Remarks.
1903.	P.M.						
June 28	5.30	—	—	—	—	—	
	A.M.						
29	5.30	217	152	61	37	70	Clear sky
	6.30	16	9	9	6	70·5	Clear sky
	7.30	6	10	6	1	71	Some sun
	8.30	11	12	4	3	73	Rather dull
	9.30	7	11	3·5	3	75	Some sun
	10.30	6	3	3	2	77	Sun
	11 30	3	3·5	2	2	78·5	Sun
	P.M.						
	12.30	6	9	3	2	78	Variable
	1.30	11	8	4	2	78	Showery
	2.30	14	12	5	5	78	Some sun
	3.30	8	10	4	3	77	Some sun
	4.30	15	13	4	3	76	Variable
	5.30	17	14	5	4	75·5	Dull
	6.30	27	22	7	4	74·5	—
	7·30	26	18	6	5	74	—
	8·30	26	20	8	5	74	—
	9.30	27	15	6	7	74	—
	10.30	20	18	7	6	74	—
	11.30	23	16	7	4	74	—

Table XIV.—*contd.*

Date.	Time.	No. 1. Growth mm.	No. 2. Growth mm.	No. 5. Growth mm.	No. 6. Growth mm.	Temp. F°.	Remarks.
1903.	A.M.						
June 30	12.30	25	19	8	5	73·5	—
	1.30	19	16	7	6	73·5	—
	2.30	23	17	8	5	73	—
	3.30	23	16	7	5	73	—
	4.30	19	15	9	7	72·5	—
	5.30	22	19	8	4	72	—
	6.30	22	16	8	4	72	Dull
	7.30	20	17	8	7	73	Dull
	8.30	11	11	7	3	74	Dull
	9.30	8	11	5	5	75	Dull
	10.30	8	7	4	2	76	Dull
	11.30	3	6	4	2	77	Dull
	P.M.						
	12.30	6	7	5	1·5	77	Dull
	1.30	5	5	3·5	3	77	Dull
	2.30	5	7	3	2·5	77	Dull
	3.30	16	13	6	3	76	Dull
	4.30	22	15	7	5	76	Shower
	5.30	23	15	7	5	75	Dull

The curves agree in their general features with those last described. Both culms were growing more rapidly by this time, and the variations in rate of growth are also somewhat greater. There was also considerable variation in the conditions and the table shows that a fair degree of parallelism could still be traced.

At first sight it might appear that we have here a marked example of the influence of light upon growth. But there are several reasons which forbid this conclusion. In the first place conditions other than illumination are quite uncontrolled. Moreover the changes in rate of growth are much greater than any which have hitherto been shown to depend upon the stimulus of changed illumination. Further, the culms do not appear to be at all heliotropic, and it is indeed hard to imagine how light can greatly affect the growing region through its thick and opaque armour of leaf sheaths.

A glance at the table shows that the temperature during the period of observation underwent only very slight and gradual changes, and the direction of these changes is generally speaking opposite to that of variations in the rate of growth. We may conclude that temperature has no material effect upon the observed results.

An attempt was made to test the effect of light by shading a small halm by means of a cylindrical cover of tin. This experiment took place also on June 29 and 30, and is recorded in Table XIV. Halms Nos. 5 and 6 grew on the east side of the same clump as Nos. 1 and 2; they were of nearly equal height (No. 5 116 cm. and No. 6 103 cm. at 5.30 P.M. on June 28) and were less than half a metre apart. From 5.30 A.M. to 5.30 P.M. on June 30 No. 5 was covered with an opaque cylinder of tin, the base of which rested upon dry leaves heaped loosely round the base of the halm so as to allow as much ventilation as possible. The cover was removed every hour for some thirty seconds to allow of the growth being recorded. The table and curve seem to indicate that growth was very little affected by this treatment.

And the same thing is shown still more clearly by another experiment, in this case upon a culm of Gigantochloa. A small shoot of this species (No. 13) was continuously covered up from 7.30 A.M. July 23 to 7.30 A.M. July 24. A shoot of equal height (No. 12) which was growing at nearly the same rate was used as a control. The experiment is recorded in Table XV.

Table XV.

Date. 1903.	Time.	Growth in mm. No. 12.	No. 13.
July 21 ...	5.30 P.M. ...	10 ...	9·5
22 ...	7.30 A.M. ...	47 ...	46
22 ...	5.30 P.M. ...	9 ...	9·5
23 ...	7.30 A.M. ...	53 ...	48
24 ...	7.30 „ ...	68 ...	(67)
25 ...	7.30 „ ...	78 ...	77
26 ...	7.30 „ ...	83 ...	79

It appears that the treatment had no effect such as could be detected by the method employed.

No great stress however is to be laid upon these experiments which were discontinued owing to the large number of uncontrollable factors. For example the moisture of the air inside the covering cylinder was not known, moreover the young shoots are intimately connected through the rhizomes with the other members of the clump to which they belong, and this is much too large to be subjected to experimental conditions. Taken together these experiments may be regarded as indicating that the effect of light upon the young halms themselves cannot cause any large proportion of the oscillations of growth observed.

5.—*Effect of Changes in the Moisture of the Air.*

In the open air changes in intensity of light appeared to run closely parallel with changes in the moisture of the air. Thus in full sunlight the temperature is higher and the air is proportionately further from its saturation point, whilst the darkest portions of many days were those during which rain was actually falling. It has been shown above that in the latter case growth is more rapid, whilst in the former it was slower, or even sometimes altogether ceased. Moreover it has already been shown that moisture has a very large effect upon the nature of the oscillations of growth from day to day.

A series of observations were therefore made in order to discover whether a similar parallelism could be demonstrated between the oscillations of growth from hour to hour and changes in the moisture of the air. For this purpose hourly measurements were made of the growth of two halms of Dendrocalamus Nos. 9 and 10 and of one halm of Gigantochloa No. 14. The respective heights of these culms at 5 P.M. on August 16 were :—No. 9, 337 cm., No. 10, 233 cm., and No. 14, 161 cm.

The measurements were carried out on August 17-19 and the results are recorded in Table XVI. The curve of

growth for No. 9 is shown in fig 6, Pl. XXIII., together with the curves of temperature and percentage moisture of the air. In the table the columns headed No. 9, No. 10, No. 14 show in each case at the times recorded the growth in mm. since the last observation. Under H is recorded the moisture of the air reckoned as the percentage of complete saturation.

Table XVI.

Aug.	Time.	No. 9.	No. 10.	No. 14.	Wet Bulb.	Dry Bulb.	H.	Remarks.
16	5 P.M.	3,370	2,330	—	°C	°C	—	Fine sunny day, except shower, 2.30
	6 „	14	11	2	22·01	24·5	79·5	
	7 „	16	16	8·5	21·7	23·0	88·5	Clear sky
	9 „	37	30	18	20·7	21·0	97	Clear sky
17	6 A.M.	132	120	72	19·6	19·9	97	Overcast
	7 „	15	12	6	20·05	21·3	88	Sun
	8 „	11	9	2	20·56	22·0	87	Sun
	9 „	5	9	0	21·4	24·3	76	Sun
	10 „	5	4	—3	21·55	25·3	70	Sun
	11 „	0	1	0	21·9	25·9	69	Some sun
	12 „	—1	2	0	22·1	26·0	69·5	Clouding over
	1 P.M.	5	6	1	22·85	25·35	79·5	Overcast ; dull
	2 „	12	9	2	22·9	24·0	90·5	Heavy shower, 1.15
	3 „	3	5	0	23·3	25·75	79·5	Variable
	4 „	3·5	4·5	1	21·9	24·6	78	Getting duller
	5 „	17	12	5	22·2	24·5	83	Fairly dull
	6 „	15	13	7	21·4	23·8	80	Dull
	7 „	17	14	7	21·1	22·8	85	Overcast
18	7 A.M.	227	188	103	20·7	21·9	89	Dull
	8 „	9	11	6	21·1	22·6	87	Dull
	9 „	11	12	5	21·3	23·0	85	Shower at 8.15
	10 „	7	6	0	21·5	24·0	79	Bright to dull
	11 „	11	8	1	22·6	23·9	89	Variable, showery
	12 „	2	2	—1	21·9	25·5	71	Sun
	1 P.M.	1	3	0	22·6	25·9	74	Variable ; sunny

Table XVI.—*contd.*

Aug.	Time.	No. 9.	No. 10.	No. 14.	Wet Bulb.	Dry Bulb.	H.	Remarks.
	2 P.M.	2	3	0	22·2	24·5	81	Variable ; rain at 1.15
	3 „	6	5	1	22·3	24·9	79	Variable to dull
	4 „	2	2·5	1	22·0	25·9	69·5	Variable ; some sun
	5 „	3	4	0	20·1	24·6	64	Variable to sunny
	6 „	15	11	5	21·4	23·7	81	Dull
19	7 A.M.	225	180	117	20·6	22·1	87	Dull
	8 „	11	17	3	21·25	22·35	90	Dull
	9 „	15	15	9	21·3	21·9	94	Rain
	10 „	12	10	2	21·1	23·1	83	Getting brighter
	11 „	4	6	1	21·8	23·9	82·5	Rather dull
1	12 „	13	11	6	20·9	21·6	93	Heavy rain
	1 P.M.	14	12	7	21·8	23·5	85·5	Rain ; dull
	2 „	2	3·5	·5	22·0	24·7	78	Dull
	3 „	1	1·5	0	21·4	23 9	79·5	Dull
	4 „	7	5	1	21·6	23·9	81	Dull
	5 „	12	11	7	21·6	23·6	83	Dull
	6 „	17	15	11	20·7	21·7	91	Rain at 5
20	7. A.M.	208	183	118	20·9	23·2	81	—

It will be seen that the agreement between growth and changes of moisture is very striking, almost every marked alteration in the moisture of the air being accompanied by a corresponding change in rate of growth. And all three culms agree very closely in this respect. The parallelism was specially marked on August 19, on which day practically no corresponding oscillations could be noticed in the degree of light, the whole day on the contrary being continuously dull.

In the following table is given the average hourly growth in mm. from 7 A.M. to 6 P.M. and from 6 A.M. to 7 P.M. for each of the three halms on the three days of observation. There is a close agreement between these averages and the average moisture of the air on the respective days.

Table XVII.

Date.	Percentage of Moisture.	No. 9.		No. 10.		No. 14.	
		Day.	Night.	Day.	Night.	Day.	Night.
17	78·4	6·9	18·8	6·7	15·5	1·3	8·4
18	78·2	6·3	17·3	6·1	13·8	1·6	9·0
19	85·6	8·2	16·0	8·2	14·0	3·5	9·1

VI.—DISCUSSION OF OBSERVATIONS.

1.—*Recapitulation.*

In the preceding pages, before describing the result of observations on the rate of growth, some account of the habit of Dendrocalamus was given. The periodicity in the length of successive internodes was illustrated by measurements of a series of culms, and certain irregularities in some of these periods were ascribed to mechanical pressure and injuries. Unlike the cases observed by Tammes, the longest leaf blade occurs higher up the culm than the longest internode—a state of things which seems to be clearly associated with the function of the leaves at different positions, the function of protection being more marked below, that of assimilation higher up.

At Peradeniya the elongation of the halms begins as a rule early in June and is nearly completed by the end of October. At Buitenzorg on the other hand the buds first appear above ground at the beginning of November. This very marked alteration in the yearly periodicity of the plant following a change of locality from one side of the equator to the other is a fact of considerable interest, and none the less so because the method of propagation in this case was vegetative, namely by cuttings.

The observations recorded show that the culms of the giant bamboo pass through a definite grand period of growth. At first, when the bud is just appearing above ground, elongation is slow. Soon, however, a rapid increase in the rate of growth sets in, and is continued until a height of some 5 metres has been attained. For the next 10 metres or more, growth, apart from oscillations which can be ascribed to the effect of external conditions, appears to remain fairly steady. Later on the rate of elongation falls gradually and finally becomes very slow. This slow growth is continued for a considerable time at the apex of the halm.

If now a cause of this phenomenon be sought, it may be found at once in the varying length of the growing region. Up to a height of nearly 5 metres the intercalary growing areas are spread over almost the whole length of the young culm. And we should therefore perhaps expect growth to be proportionate to length. But at the earlier stages a larger proportion of the young culm, then less than half a metre high, is in the embryonic phase of growth, and consequently elongation is proportionately slower. When a length of something over 5 metres has been reached, the older internodes at the base of the culm gradually cease to elongate. The growing region is thus kept at approximately the same length, and growth also remains nearly constant. As the end of the growing period is approached it appears certain that reduction in length of the growing region must be accompanied by a steady falling off in the growth of the culm regarded as a whole, until the adult length is reached and growth ceases altogether. It was not found possible to make any trustworthy observations at this final period. Neither could observations be made upon the growth of individual internodes, since these are completely covered by the sheathing bases of the leaves until their growth is very nearly completed.

The rate of elongation of the various developing cells at different stages of growth also doubtless plays a part in

determining the course of the grand period of the culm. But in the case before us this factor is largely obscured by the much larger effect of the length of the growing region. In this respect bamboos are probably unique, and cannot, strictly speaking, be compared with other plants whose growth has been more usually studied.

In addition to and partly obscuring these periodic changes of growth the tables and curves already given show considerable oscillations from day to day. The corresponding records of rainfall show very clearly that there is a connection between the two phenomena. Unfortunately complete psychrometric records were not taken, nor indeed was this possible in the absence of recording instruments. The moisture of the air is however to a large extent proportional to rainfall, so that the effects of the two must be dealt with together, whereas sunshine and temperature would show an almost inverse curve compared with the curve of rainfall. It appears therefore that the oscillations from day to day are determined almost entirely by conditions of moisture, including in this term moisture of the air and of the soil, in addition to the direct effect of rain in moistening the leaves of the clump and the surfaces of the growing culms themselves. The conclusion that changes in atmospheric moisture have a large effect was fully borne out by the results of more detailed observations made every hour.

Within certain limits the effect of moisture appeared to be greater and more immediate the greater the height which had been reached by the culm under observation. This effect is very clearly illustrated in pl. XXII., fig. 2. Unfortunately it was impossible to make very accurate hourly observations at any great height. The result is probably partly due to the more rapid growth, and the larger number of internodes concerned in active growth at the greater height; perhaps partly also to the greater distance from the source of water which might make the effect of drought more acutely felt. At the later stage too the young culm itself possesses

a fairly large surface of transpiring leaves, whereas in the early stages of growth its own transpiration must be very small.

Growth during the day was almost always considerably slower than at night. On a single occasion only was a greater hourly growth recorded for the period from 7 A.M. to 5 P.M. than for the following period from 5 P.M. to 7 A.M. On this occasion rain fell continuously during the whole of the day, and in consequence of this the psychrometric condition of the air closely approached saturation, and the day therefore equalled in moisture, or possibly even exceeded the following night.

Observations taken hourly showed a very regular periodicity of growth during the 24 hours. During the night growth was rapid and, as far as errors of observation allowed of judging, nearly constant. Soon after sunrise the growth fell off rapidly and, during the day, was on the whole low, rising again shortly before sunset.

During a considerable series of days measurements of several halms were made every two hours. The majority of these I have not found space to record, and they were in many ways incomplete. But they showed quite clearly, and without any actual psychrometric records, the marked relationship between growth and meteorological conditions. In bright sunshine elongation was always slow or even ceased altogether, and sometimes an actual shrinkage was observed. When clouds gathered growth increased, and when rain was falling it was still more rapid. On several occasions the morning was sunny, the middle of the day overcast, and the afternoon again bright. And on such days the rate of growth always rose towards noon whether rain actually fell or not, and this rise was often followed by a falling off later on.

Experiments made by covering up young growing culms seemed to show that the effect of light upon these had very

little to do with the changes of growth.* On the other hand observations taken hourly in conjunction with readings of the psychrometer gave evidence of a marked parallelism between the two curves, whilst the curve of temperature had an almost exactly opposite character.

In this connection it is to be noted that in the early part of the period of growth when these observations were made, drops of water were excreted from the tips of the sheathing leaves in considerable quantities during the whole night, the night being regularly the period of most rapid growth.

This rapid excretion of water has been noticed by Molisch.† This observer found however that it was impossible to make records of the pressures normally existing in the stems owing to the remarkable disturbing influence exerted when a manometer was introduced.

During the hotter and drier parts of the day a slight reduction in length was sometimes observable. This was always small in amount, and usually only just to be detected by the method of measurement employed. It never amounted to more than 2 or 3 mm. per hour.

It is thus clearly established that changes of moisture are the chief cause of the observed oscillations in the rate of growth of the culms of Dendrocalamus. The temperature in the shade beneath the clump, where the young growing culms are protected during the early part of their growth, shows only slight and slow changes. On the other hand when the sun is brightly shining the older members of the clump are exposed to a much higher temperature, and this, in

* In another way however light has probably an important, though subsidiary effect. Increased illumination as a rule causes opening of stomata and decreased illumination closing of stomata when other conditions are unchanged, so that unless Dendrocalamus is quite exceptional in this respect the periodic changes in illumination must co-operate with the nearly parallel changes of moisture in inducing corresponding changes in the rate of transpiration of the full grown culms, and may thus exert an appreciable indirect influence upon the rate of growth of the young culms, although the direct effect is very small.

† Ann. Jard. Buit., 2nd Supplement, 1898, p. 30 *et. seq.*

combination with the greater dryness of the air, must promote transpiration, and may thus influence the rate of growth of the younger members.

2.—*Comparison with Previous Observations.*

The results of the observations here recorded agree with those made by Kraus at Buitenzorg (1) in the average rate of growth recorded, and (2) in finding growth to be almost always more rapid during the night. Kraus also recorded a more rapid growth by day than by night on a single occasion.

On the other hand Kraus states that the very marked oscillations from day to day which he observed showed no relation to external conditions. Since no record of these conditions is given, beyond the general statement of their marked uniformity, it is impossible to judge how far Kraus was correct in this conclusion. As far as I am aware, the only important differences between the conditions at Buitenzorg and those under which my observations were made consist in (1), the fact that the single clump observed by Kraus was younger than any of mine, and (2), that the climatic conditions were more uniform and probably on the whole more favourable for rapid growth. Whether these differences are sufficient to account for the discrepancies in the two results appears to me to be somewhat questionable.

Kraus suggested that the oscillations which he observed were discontinuous variations of growth ("Stossweise Aenderungen" of Sachs) of an extent hitherto quite unsuspected. Reinke* showed however that what Sachs took to be spontaneous variations were probably to a large extent determined by small changes in the external conditions. He found that such "Stossweise Aenderungen" do take place in the plants which he examined, but that they required the most accurate methods of measurement applied at short intervals of time for their demonstration. It seems

* Reinke. Untersuchungen über Wachsthum, Bot. Zeit. 1876.

therefore in the highest degree improbable that daily measurements could show anything analogous even in the rapidly growing giant bamboo. However, my own measurements, whether daily or hourly, have indicated nothing which can be ascribed with certainty to this phenomenon.

I was not able to observe any such sudden reduction in the rate of growth as Kraus records towards the end of his series of observations.

The results of the daily observations at Peradeniya are supported by the earlier figures of Shibata.* The measurements made by this observer clearly show that the growth of Phyllostachys in the climate of Japan is also in a high degree sensitive to changes in the external conditions. The mean daily temperature varied greatly during Shibata's observations, and the curves of growth show a very close agreement with the curve representing this variation. Changes in atmospheric moisture had obviously a very much smaller effect; yet some agreement can, I think, be traced when the curves are plotted and compared closely. The agreement between the curves representing the growth of separate halms is even closer than in the case of my own observations of Dendrocalamus.

In the light of these results it seems clear that the possibility of demonstrating a marked effect upon growth from changes in the conditions of moisture depends, at least in part, upon the existence at Peradeniya during the period of observation of a very constant mean temperature, and one at the same time highly favourable to rapid growth. It is possible that at Buitenzorg, as Kraus suggests, the conditions of moisture also are so constant, that in the absence of controlling factors individual variations in the rate of growth become very marked.

3.—*Factors influencing the Grand Period of Growth.*

Although my observations were not sufficiently exact or complete to enable me to set forth in an orderly manner, all

* *Loc. cit.*

the factors upon which the course of elongation of the culms depends, it may yet be worth while to enumerate some of the circumstances which would make any such elucidation a matter of great complexity.

As has been already stated, the course of the grand period of growth of the culm regarded as a whole must depend very largely upon the total length of the growing region at various stages. And in this connection it is to be remembered that the elongation of the older internodes takes place at an intercalary region of growth at the base of each internode, at which point elongation continues after the upper part of the internode has ceased to grow in length. In speaking of the growing region then, I here mean to imply the whole section of the culm situated between its apex and the base of the lowest growing internode. In the earlier stages this region is short and growth is slow. Later on, as the region of active growth becomes longer, the rate of elongation rapidly increases, and during the middle period of rapid growth the lowest growing internode may be more than 5 metres from the growing point. Later on the region of growth is shorter and growth becomes slower.

When the bud begins to elongate a very large number of internodes are already laid down in it. The formation of new internodes continues during the elongation of the culm; but in the later stages of elongation, the number of young internodes enclosed in the bud is small. It follows therefore that at first new leaves unfold and new internodes take on their most rapid phase of elongation at a shorter interval than that between the formation of new internodes at the growing point.

The leaves moreover were observed to unfold at a gradually increasing interval of time, this interval being about 24 hours when the culms were 2-3 metres high, and gradually becoming longer as the height increased. At the earlier stages of development of the bud this interval must also have been longer, so that we have here another

periodicity, not exactly corresponding with that of rate of growth, but still showing some agreement.

The periodicity in the final length of the internodes themselves must also have some influence, if only a small one, upon the grand period of growth of a culm taken as a whole. I have already mentioned certain abnormalities in this period which are apparently to be associated with external injuries and pressures. But the final period of length of internodes is usually very regular, and this would seem to indicate that certain irregularities of length in the young internodes, as observed in longitudinal section of the bud, are more or less fully compensated for as growth continues.

It may be supposed that the external meteorological conditions, of which moisture is the only one here closely examined, affects chiefly the turgour and rate of elongation of the individual growing cells of the internodes. To what extent and in what way the other factors here enumerated affect the result it seems impossible to say in the present state of knowledge of the subject.

4.—*The Effect of Changes of Moisture upon the Growth of Plants.*

It is remarkable that so little attention has hitherto been paid to the reaction of the growth of plants to changes of moisture. Pfeffer* connects the fact that light has much more influence than temperature upon the form of plants with the greater importance of light in the economy of the plant. Moisture, however, is an even more necessary condition for the growth of plants than light itself, since growth can take place in darkness, but not in the absence of moisture. Nevertheless the effects of light and of temperature have been closely studied by physiologists, but the effect of moisture much less fully.

* Pflanzenphysiologie Bd. 2, p. 81

Of the experiments which have been carried out in this direction, by far the greater number have consisted in exposing the growing cells to the direct action of saline solutions according to the method introduced by H. de Vries.* Observations of this kind have established the important part played by turgour in the process of elongation, but they can give little information as to the sensitive reaction of the growing regions of the plant to changes of moisture, owing to the essentially abnormal conditions under which such experiments are made. Moreover, except in the case of de Vries' own experiments, which were concerned chiefly with the determination of the length of the growing region in a variety of cases, the number of plants which have been tested in this way is very limited. For several workers the roots of Vicia faba have provided the sole object of study.

There is no need to dwell further on this class of experiments. Reference may next be made to the principal papers in which the question of the effect of atmospheric moisture upon the growth of internodes is dealt with.

Sachs in his well-known paper dealing with the effect of temperature and light upon the growth of internodes† quotes observations made by W. H. de Vries upon the flowering scape of Agavea mericana in 1847. During the period from August 9 to September 1, measurements showed that on five occasions growth almost ceased during the morning, on twelve occasions there was a slight shrinking, and during two mornings, both of which were dull, there was a slight elongation. Some of the observations upon Dendrocalamus recorded above closely recall these measurements of de Vries upon Agave.

Sachs himself made no experiments upon the effect of moisture. He took psychrometric observations during his experiments, but kept his wet and dry thermometers standing

* Untersuchungen über die Mechanischen Ursachen der Zellstreckung. Leipzig, 1877.

† Arbeiten d. Bot. Inst. in Würzburg, II., p. 101, 1872.

over moist earth in a separate receptacle from that which held the plant which was under observation. Thus there was no record at all of changes caused by the transpiration of the plant itself. Furthermore a glance at Sachs' figure* does not encourage a belief that his plants, if none were treated better than the one there shown, could have been in anything like a normal condition as regards the important function of transpiration;† nevertheless Sachs fully recognized the important effect which alterations in atmospheric moisture may have upon the growth of internodes, as the following words show: "In the day-time, also, the difference of tension of the aqueous vapour in the atmosphere is usually greater than during the night, and transpiration is thus increased, and it may easily happen that turgescence during the day is less than at night, and growth likewise may be retarded thereby."‡ But he does not appear to regard this as a normally recurrent phenomenon.

J. Reinke in 1876 published a valuable paper on growth§ in which the importance of atmospheric moisture is fully recognized. His observations upon the growth of Juncus and Scirpus, in which plants the growing region of the single long internode is buried in the earth, showed that in these cases psychrometric changes had practically no influence upon elongation.

Experiments upon seedlings of Helianthus exposed to hourly alternations of light plus less moisture and darkness plus more moisture showed that moisture of the air distinctly favoured growth, but light had a marked effect also.

But in making records of the growth in *thickness* of the stem of Datura stramonium, Reinke discovered a much more

* *Loc. cit.*, p. 113.

† Kraus has shown that the removal of leaves affects the period of alternation of the volume of water in different parts of the stem. Ueber die Wasservertheilung in der Pflanze, III., p. 58, 1881.

‡ *Loc. cit.* I quote from the English Ed. of Sachs' Lectures on the Physiology of plants translated by Marshall Ward.

§ Untersuchungen über Wachsthum, Bot. Zeit. 1876.

marked effect resulting from changes in the humidity of the air. His fig. IV. and Table III. shows a very marked parallelism to exist between the curve of growth and that constructed from readings of the psychrometer.

The following are Reinke's principal conclusions:—

(*a*) Generally speaking the change in volume is proportional to the relative moisture of the air.

(*b*) With a high degree of moisture an energetic increase in volume of the stem takes place. With a marked reduction of moisture there occur, not only a smaller increase, but an actual and marked shrinking of the stem volume.

(*c*) Not infrequently the curve of growth sinks below zero when moisture has sunk only a few degrees from a high point on the psychrometric scale. If the moisture now remains constant at this lower point, growth finally begins once more.

In this case the plant becomes acclimatized, as Reinke phrases it, to a low degree of moisture which was at first harmful.

These changes are connected by the author with the evaporation of water from the leaves.

The whole of this effect ought perhaps not to be attributed to changes of growth, for Kraus has shown* that in the case of certain plants, in branches not actually growing, there is a regular periodic interchange of water between the wood and the cortex accompanied by a change in the total diameter of the stem.

The facts with regard to the elongation of bamboo internodes agree closely with these results of Reinke's, except that in the case of the former the contraction which was sometimes observed to take place when the air was dry was never very large.

To explain why the internodes examined by him showed no such changes in the course of their elongation, Reinke suggested that these were less easily affected because of the

* Gregor Kraus, Ueber die Wasservertheilung in der Pflanze, Part I., Festschrift der Naturforsch. Ges. zu Halle, 1879.

greater intensity of their growth. On the other hand in the giant bamboo, for which the intensity of growth is proverbial, a very marked sensitiveness was manifested to changes of moisture. The absence of a marked contraction when circumstances are adverse may however very well be due in the case of the bamboo to the greater vigour of its growth.

Working with internodes of Phaseolus, Godlewski* found that a sudden decrease in the moisture of the surrounding air had a marked immediate effect upon elongation; this was however quite temporary, hardly extending into a second half hour from the time of application of the stimulus. Thus a fall of saturation from 63 per cent. to 36 per cent. was accompanied by a reduction in the half-hourly growth from ·7 mm to ·2 mm. And in the first few minutes there was even a slight shrinkage.

My curves seem to show more agreement with Reinke's "acclimatization" result than with the extremely temporary effect which Godlewski obtained. Like Reinke's curves they show a rate of growth actually proportional to the relative moisture of the air.

One other more recent paper requires special mention here, namely that of F. Darwin, "On the Growth of the Fruit of Cucurbita."† Darwin found variations in the rate of growth of the fruit to be chiefly dependent upon the hygrometric condition of the atmosphere. In this case also increased dryness of the air was frequently accompanied by a diminution in size and weight.

Here again we have a case which closely resembles the growth in thickness of Datura and the elongation of the halms of Dendrocalamus. So closely parallel do the cases appear to be that Darwin's most general conclusions‡ apply almost equally well to the results of my own observations upon the latter plant.

* Emil. Godlewski. Studyja Nad Wzrostem Roslin, Krakow, 1891, p. 73. German abstract. Anzeiger der. Akad. Wiss. in Krakau, 1890, p. 170.

† Annals of Botany, Vol. VII., p. 459, 1893.

‡ 1, 4, 5, 6, 8, and 11 p. 485, *loc. cit.*

5.—*The Daily Periodicity of Plant Functions.*

The daily periodicity exhibited by many of the functions of plants has long excited considerable interest. Pfeffer* definitely associates such a periodicity in the case of growth with the daily alternations of light and darkness. This association rests principally upon the observations of Sachs and of Baranetzky. And for the relatively small number of plants with which they worked such a conclusion seems to have been well established, although it does not appear quite certain in either case that periodic changes in the psychrometric condition of the atmosphere were entirely excluded.

Baranetzky† records no observations upon the psychrometric conditions of the air. And although the atmosphere of a closed room does not exhibit any such marked changes in this respect as does the free air outside, yet the suggestion arises that changes of moisture may have had some influence upon the marked irregularities in periodicity which appeared in Baranetzky's plants. On the other hand this author states that sprinkling the floor with water had no effect upon the growth of the plants.

Baranetzky ascribed every case of periodicity observed by him to the action of alternating light and darkness. Those which appeared in continued darkness were explained as being due to an after effect; and in some cases such an effect seems to have been clearly demonstrated.

The case of Brassica Rapa is more difficult. Etiolated shoots of this plant which had developed in the dark from tuberous roots, and were never exposed to light, showed nevertheless a clear daily periodicity. The plants exhibited—as clearly appears from Tables XXIX. and XXX.‡—a marked tendency to an increase of growth by night and a falling off during the day. The temperature during these experiments

* Pflanzenphysiologie, Bd. II., p. 252

† Baranetzky—Die Tägliche Periodicität im Langenwachsthum der Stengel. Mem. Acad. Imp. St. Petersburg. 1879.

‡ P. 79, 80, *loc. cit.*

was nearly constant, and we are bound to suppose the conditions of moisture to have been so also, but we are not told to what conditions of atmospheric moisture the plants had previously been exposed. Is there not a possibility that an after effect from previous alternations of a drier atmosphere by day and a moister by night might become apparent in this manner? This seems to me to be more likely than that there should be inheritance of the effect of still earlier alternations of darkness and light.

Sachs regarded this experiment as showing that plants normally exhibit a daily periodicity quite apart from changes of light and temperature. But the effect of changes of moisture must also be excluded before this periodicity can be called spontaneous; and it appears doubtful whether this has ever been done completely.

Almost all the investigations which have been made in this direction have had for their object plants exposed to quite unnatural conditions. And recent experiments, for example those of Singer* and of Richter† upon the influence of the air of a laboratory upon the growth of plants, show very clearly how powerful an influence may be exerted upon the processes of growth by factors which have been probably very largely overlooked in the older experiments. It seems very desirable that careful records should be made of really normal growth in a number of different plants.

The great importance of moisture for growth and the very regular occurrence of the change from drier air by day to moister air by night, the existence of which is a matter of common observation both in England and at Peradeniya, makes it highly probable that periodicity of growth may be found in other cases to be connected with periodic changes of moisture.

Another function, the periodicity of which may show a like relationship, is that of root pressure. This has been

* Berichte der deut. Bot. Ges. XXI., 3, p. 175, 1903.
† Berichte der deut. Bot. Ges. XXI., 3, p. 180.

studied likewise by Baranetzky who attributed the periodicity in this case also to the action of the alternating changes of light and darkness. The root pressure maximum occurs usually in the afternoon. At this time Kraus* found the volume and turgour pressure of the cortex of woody branches to be at a minimum, the minimum amount of water being then present in the cortical cells. It seems probable that the increased transpiration by day may afford a rational explanation of both these phenomena as well as of others.

For these reasons I would submit that the question requires further examination whether the daily periodicity so widely observed in the functions of plants may not be partly or even largely determined in a considerable number of cases by periodic changes in the psychrometric condition of the atmosphere, and whether the influence of the daily alterations of light and darkness may not have been somewhat exaggerated.

6.—*The Mechanism of the Effect of Moisture.*

6. Baranetzky† suggested that the periodic after-effect of light was due to the existence of an 'elastic reaction' in the plant. The effect of the stimulus of darkness was to increase the rate of growth up to the limit of 'elastic stretching,' and this was followed by a series of oscillations of opposite phases until equilibrium had been restored. The differences in length of the periods of oscillation which were observed in different cases were regarded by Baranetzky as being due to differences in the amount of energy which had been imparted in starting the oscillations. If this is the case it is plain that there can be no true analogy with any purely mechanical action; the periodicity must be essentially a vital phenomenon.

Godlewski‡ from the sudden and temporary nature of the response to a change of atmospheric moisture in the case of

* *Loc. cit.* p. 45.
† *Loc. cit.*, p. 14.
‡ Anzeiger d. Akad. d. Wissenschaften in Krakau, 1890, p. 392.

Phaseolus supposed the effect to be simply one of turgour, as opposed to the other of the two factors to which he ascribes changes in the rate of growth, namely, a direct action of the protoplasm upon the extensibility of the cell-wall. And this seems to be very probably the case in Dendrocalamus as well. But it is to be remembered that the control of turgour is just as much a function of the living protoplasm as is the latter method of control of growth.

It seems certain that the reaction of changes of moisture in the case of the young growing culms of Dendrocalamus depends largely upon the transpiration of the adult members of the clump. The growing region is so closely covered by an impenetrable armour of stout sheathing leaf bases that the possibility of a direct action of small changes of atmospheric moisture would appear to be quite excluded. The presence of this thick and practically opaque covering also probably explains the fact that changes of illumination have very little effect. We must suppose that transpiration produces changes in the pressure of water in the rhizome, and that these changes of pressure react upon the turgour of the growing cells.

The rapidity with which this reaction takes place is remarkable when we consider the great size of the plant and the distance of the foliage of the mature shoots from the rhizome and from this to the growing points of the young culms. It seems most probable also from this consideration that the transmission of the effect must be by changes of hydrostatic pressure, and not by any direct conduction of a stimulus through living organs.

Conclusion.

In the preceding pages some account has been given of a preliminary study of the growth of internodes, made in a tropical country by the use of the simplest methods only, applied to a particular plant of very rapid growth. The result of these experiments seems to justify the conclusion that

further observations upon tropical plants of other orders may lead to results of equal interest. Hitherto practically all the generalizations of plant physiology have been based upon experiments carried out with plants native to the temperate zone. An extension of such experiments to the tropics is highly desirable and the work is so far almost untouched.

The effect of changes of moisture upon the *normal* growth of plants has been very little attended to even in temperate climates, so that there seems to be still considerable scope for experiments in this direction. And the examination of a considerable number of plants belonging to as many different natural orders as possible is especially to be advocated from this point of view.

Finally I desire to express my thanks to Mr. F. Darwin and to Mr. J. C. Willis, Director of the Peradeniya Gardens, who have aided me during my work both by encouragement and advice. To the latter I am especially indebted for many valuable suggestions.

SUMMARY OF RESULTS.

These are based upon observations of the growth of culms arising from large (full grown) clumps of Dendrocalamus giganteus.

1. The culms show a gradually increasing rate of growth up to a height of approximately 5 metres. Afterwards growth remains nearly constant up to about 15 metres and then slowly falls off until the final height of 30 or more metres has been reached.

2. The greatest observed length of the whole growing region was from 5–6 metres.

3. The average daily rate of growth agrees closely with that in Java; at a height of 1 metre it is approximately 10 cm. per day, at heights from 5–15 metres 30 cm., and at 20–25 metres 15 cm. in 24 hours.

4. The greatest growth actually recorded in 24 hours was 46 cm.

5. The daily rate of growth is strongly affected by external factors, among which the principal are rainfall and the psychrometric condition of the air.

6. This effect appears to be greater the greater the height which the growing halm has reached.

7. The greatest observed change in the rate of growth between two consecutive days amounted to 50 per cent. of the average rate of growth.

8. Growth is almost always more rapid by night than by day, but on one exceptionally wet day a particular culm grew more rapidly than during the following night.

9. The average hourly growth between 7 A.M. and 5 P.M. (day) was 6 mm., between 5 P.M. and 7 A.M. (night) 16 mm. at heights of 3–12 metres.

10. The maximum rate of growth was reached soon after dark, but throughout the night growth was fairly constant. And with this is to be associated the fact that water was excreted from the tips of the sheathing leaves during the greater part of the night.

11. The most rapid growth recorded at night was 23 mm. per hour.

12. During some parts of the day a slight shrinkage was recorded on several occasions. This never amounted to more than 2 mm. per hour and was always preceded by one or more hours of sunshine.

13. The curve of growth by day follows very closely that of the percentage moisture of the air.

14. This effect is probably (to a large extent) due to the transpiration of the adult members of the clump.

15. Any effect of the change from night to daylight or *vice versa* apart from psychometric changes was not great enough to be recognized by the methods employed.

Peradeniya, March 25, 1904.

DESCRIPTION OF PLATES.

Plate XXI., fig. 3. The curves represent by vertical lengths the hourly growth of culms Nos. 1 and 2 (Table XIII., p. 239) recorded in mm. on June 22 and 23. At the beginning and end of the curve records were taken at 2-hour intervals and the *average* hourly growth is given.

Scale : 2 mm. in the fig. represents 1 mm. actual growth.

Plate XXI., fig. 4. Hourly growth of Nos. 1 and 2 on June 29 and 30 (Table XIV., p. 24) scale the same as in fig. 3.

Plate XXII., fig. 5. Hourly growth of culms Nos. 5 and 6 on June 29 and 30 (Table XIV., p. 24). On June 30 from 5.30 A.M. onwards. No. 5 was covered with an opaque cylinder which was removed hourly for about 30 seconds whilst the growth was recorded. No. 6 remained uncovered.

Scale: 3 mm. in the fig. represents 1 mm. actual growth.

Plate XXII., fig. 2. The four upper curves represent the daily growth from July 21 to August 10 of—

No. 1, Dendrocalamus, see Table IV., p. 227.
No. 4, Dendrocalamus, see Table IV., p. 227.
No. 11, Gigantochloa see Table VI., p. 232.
No. 12, Dendrocalamus, see Table VI., p. 232.

Scale: 1 mm. in the figure represents 4 mm. actual growth. The lower curve represents the daily rainfall. Scale $\times_1$

Plate XXIII., fig. 1. The upper curve represents the daily growth of Culm No. 1 and the dotted curve that of No. 2. The lower curve represents the daily rainfall from June 14 to August 16. The broken line in each case represents the average growth (or rainfall) for consecutive periods of three days. Scale, daily growth : a height of 1 mm. = 5 mm. growth. Three-day : 1 mm. = 15 mm. growth. Rainfall, daily and Three-day : 1 mm. = 1 mm. rainfall.

Plate XXIII., fig. 6. The curve *g*. represents the hourly growth of culm No. 9 on August 17, 18, and 19 (Table XVI., p. 245). The average rate of growth for each hour is here more correctly represented by the vertical height above the base line of a horizontal, the length of which represents 1 hour. The curve *p.s.* represents changes in the percentage moisture of the air; *t.* represents temperatures.

Scale : 2 mm. = 1 mm. growth. Psychrometer : 1 mm. = 1 per cent. Temperature : 1 mm. = 0·5°C.

On the Life-History of Enalus acoroides.*

(A Contribution to the Ecology of the Hydrophilous Plants.)

BY

NILS SVEDELIUS.†

(With Plate XXIV., A and B, and seven figures in the Text.)

DURING my stay in Ceylon in 1902–03 to study the marine algæ I had also many opportunities to make observations on the marine phanerogamic plants. Among these, the family of Hydrocharitaceæ is represented on the Ceylon shores by the three genera: Enalus, Thalassia, and Halophila, and each genus by one species. Upon the first mentioned of these plants, Enalus acoroides (*L. fil.*), *Steud.*, I shall now record some observations.

This plant was first observed by the Indian explorer Johan Gerhard .König "inter insulas Zeylonicas." According to a description by König it was named Stratiotes acoroides by the younger Linné. Afterwards the plant was separated by Richard as a special genus under the name of Enalus.

That Enalus acoroides belongs to that group of hydrophilous plants, of which Vallisneria spiralis is the oldest known example, and which is characterized by the male flower being detached underneath the surface of the water and conveyed by floating to the female flower, is already evident in Zollinger's notes about this plant‡: "flores ♂ citissime

* *E. acoroides*, Aschers. and Gürke in Engl. and Prantl, Nat. Pflanzenfam.: *Enhalus Koenigii*, Rich.

† Written in English by the author, and the diction corrected so far as necessary by the Editor.

‡ According to Ascherson (2), p. 176.

[Annals of the Royal Botanic Gardens, Peradeniya, vol. II., Pt. II., August 1904.]

a pedicellis soluti in aquæ superficie natantes." Zollinger, however, was of the peculiar opinion—which is in strong contrast with the real circumstances—that the female flowers were drawn down to the male flowers underneath the surface by the spiral contraction of the pedicels.

As no observations have been made upon this plant in its living condition or natural habitat, and as it is only from analogy that the inferences are drawn by which we have the notices on its pollination which occur in botanical literature, I shall give an account of the life-history as detailed as is possible with my material, the rather as I think that it will appear that the pollination does not agree in detail with that of Vallisneria, as perhaps one might think from the statement of Ascherson and Gürke (5).

In the Ceylon flora Enalus acoroides only occurs in a rather limited district in the north, viz., around the islands in the Gulf of Mannar, *e.g.*, at Jaffna and at Paumben on the Indian island of Ramisseram, where I first had the opportunity to investigate this plant. There it occurs around the shores in the shallow water to a great extent, sometimes in large masses forming a kind of submarine meadows on a depth at most of about a meter and a half at flood-tide. It occurs only on soft muddy bottom, where the shoots grow deeply down in the silt.

In regard to general organization and vegetative structure this plant is already known in its principal features, so that I may refer to the papers of Griffith (12), Ascherson (2–5), P. Magnus (4), and Sauvageau (27, 28).

The Root.—From the rootstock emerge few but rather large roots of uniform character. In their anatomy they show normal root-structure. The epidermis with very few root-hairs is in function only at an early stage. The outermost layer of the cortex is developed as exodermis; the other cells of the cortex are arranged in radial layers with intercellular spaces. In the external part there arise large air-chambers separated by (in a cross section) radial rows of tissue. The

central cylinder, which occupies a rather small part of the whole volume of the root, is surrounded by a slightly developed endodermis with thin walls. The xylem has only very few feebly-developed vessels, whereas the phloem is relatively better developed. Tannin cells occur in the root, though rather few, and not one inside the endodermis.

The Stem.—The cortex is strongly developed, its external cell-layers are cutinized and without cell-contents; the internal layers on the contrary quite filled up with large starch grains, which may reach a diameter of 40–50 μ, and which show an evident stratification just like potato-starch. The starch reaches its maximum in the cells close outside the endodermis, which itself is entirely free from starch. The endodermis differs very little from the other tissue, its walls are not thickened but the cells are extended in the tangential direction. The vascular system is also little developed. The vessels are very few and just as in the root are not lignified. Also in the parenchyma inside the endodermis there is some starch, whereas the tannin cells in the stem are very numerous, especially inside the endodermis where they often lie very close together, while those in the cortex are more scattered. They all have a coarse-grained content.

The Leaves.—Sauvageau (28) has given us a detailed description of the structure of the leaves of Enalus, to which nothing needs to be added. In regard to the lignification of the mechanical elements it may be observed that so far as I have found in my material these elements in the leaves, whether young or old, never showed any reaction of lignification. Treatment with aniline chloride and with phloroglucin and hydrochloric acid showed negative results, while on the contrary iodine-zinc chloride (Schulz's solution) gave an evident cellulose reaction. An examination of the old fibres also, which after the decay of the leaves still remain around the stem, indicates that their lignification is extremely slight, almost none. They dissolve almost

entirely in concentrated sulphuric acid and leave only a very little remainder of the wall behind, whereas the stains for lignification give negative results. It is apparently only the middle lamella which is slightly lignified, whereas the thickening layers consist of unchanged cellulose. Sauvageau (28), however, states concerning these "fibres scléreuses," that they are totally lignified at an older stage, though lignification takes place very slowly, just as in Posidonia. Commonly water plants are distinguished by the fact that lignified elements are not developed in any high degree. Among the water plants examined by Sauvageau (27) Zostera marina proved most striking in that respect, as it lacked every trace of lignification. Other species, however, *e.g.*, Cymodocea æquorea, proved variable; sometimes they totally lacked, sometimes again they had, lignified elements. To judge from the account of Sauvageau (28), compared with my own observations, Enalus acoroides seems also sometimes to be like Cymodocea æquorea.

The Flowers.—Enalus acoroides is diœcious. Both the axis with the male flowers and the therewith homologous single female flower are surrounded by two spathe-leaves of partly different structure and development in both sexes. (Pl. XXIV., A fig. 1, 8). This seems to be in connection with the pollination in so far as their form in the female flower helps to keep the flower floating, and especially to give it that horizontal exposure, which plays an important part in the pollination and particularly in the catching of the male flowers, as will be shown below.

The Male Flower.—The spathe-leaves of the male inflorescence (Pl. XXIV., A fig. 1) are widely ovate-lanceolate and somewhat keeled just like the female spathe-leaves. Their length does not much exceed 5 cm. Their breadth is about 3 cm., or perhaps a little more. At the base one of them overlaps the other with both margins. The breadth of the whole spathe at the time of the anthesis or discharge of the male flowers is about 25 mm. Both during the early stages,

and during the discharge of the male flowers, they are directed straight upwards. The position of the axis is always vertical. During the anthesis the spathe opens a little by gaping asunder at the top. At the same time the edges of the spathe-leaves are slightly rolled back, whereby an open passage is afforded to the loosening male flowers.

Along the principal veins—especially on the midrib which forms the keel—the spathe-leaves are richly trimmed with long rough hairs, which are developed in especially great numbers at the top of the leaves.

The male flowers are formed just as in Vallisneria, a great number on a common axis (Pl. XXIV., A, fig. 2), on which every flower is fixed by a thin pedicel often 5–6 times longer than the flower (Pl. XXIV., A, fig. 3).

In the pedicel occur a lot of large tannin cells. That these really contain tannin and not Raciborski's "myriophyllin," which has been discovered by him in so many waterplants, is evident from the fact that ferric chloride causes typical tannin staining (dark black-green), and by the fact that no reaction occurs with Fehling's fluid. Tannin cells were also observed by H. Schenck (29) in Vallisneria, even in the vascular bundles. Similar tannin cells occur in all vegetative parts of the plant, especially in the rhizome. In the male pedicel they lie equally distributed, except just below the perianth, where they are lacking on the spot where the crack takes place when the male flowers are detached. Here the tissue of the pedicel consists only of short rounded cells, which are poor in contents. The tannin cells appear again in the perianth.

At the rupture of the pedicel the male flower suddenly floats up to the surface, where at the same time the leaves of the perianth turn up explosively, probably owing to the great difference in the external pressure. At the opening of the flower the anthers are raised aloft in the same manner as in Vallisneria (Pl. XXIV., A, fig. 4, 5). So far the agreement with this plant is complete. But in Enalus the perianth

is double, viz., with six leaves, but nearly uniform (fig. 1). The number of the anthers is also always three, whereas in Vallisneria the perianth is always single, and commonly one anther is lacking. But a more remarkable difference is that in Enalus the filaments are particularly short, scarcely developed at all, and are also directed straight upwards, so

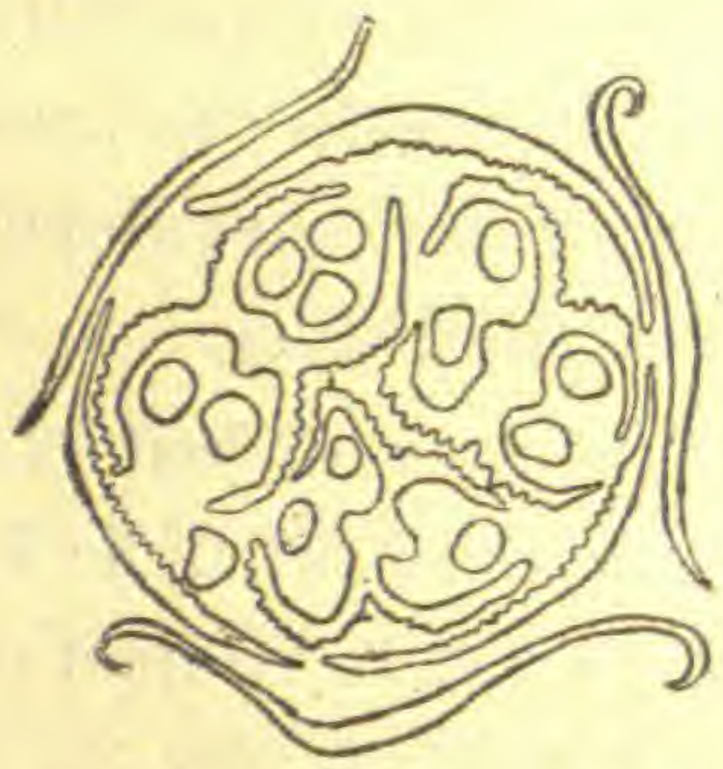

Fig. 1.—Transverse section of a male flower (15×1).

that the three anthers stay close together in the centre of the flower and point vertically upwards (Pl. XXIV., A, fig. 4, 5). In Vallisneria on the contrary—at least to judge from the figure and description given by Kerner (16, II., p. 130)—the filaments are well developed and "ragen in *schräger** Richtung in die Luft empor." The difference may easily be seen by comparing my fig. 4, 5 (Pl. XXIV., A) with that of Kerner (16, II., p. 130). This difference is also in close connection

Fig. 2.—Transverse section of a male sepal with a tannin cell (225×1).

with the different manner in which the pollination takes place in these two plants.

The further organization of the male flowers may be understood by referring to the figures. The perianth whorls show to some extent a different development, as the exterior

* Italicized by the author.

circle, the sepals (fig. 2) has very few papillæ, but rather many tannin cells ; the interior circle, the petals, on the contrary, which after the bursting of the flower becomes situated on the outer side, has very well-developed papillæ (fig. 3), but rather few tannin cells.

I have not been able to follow the development of the anthers and pollen grains in their earliest stages. It may be

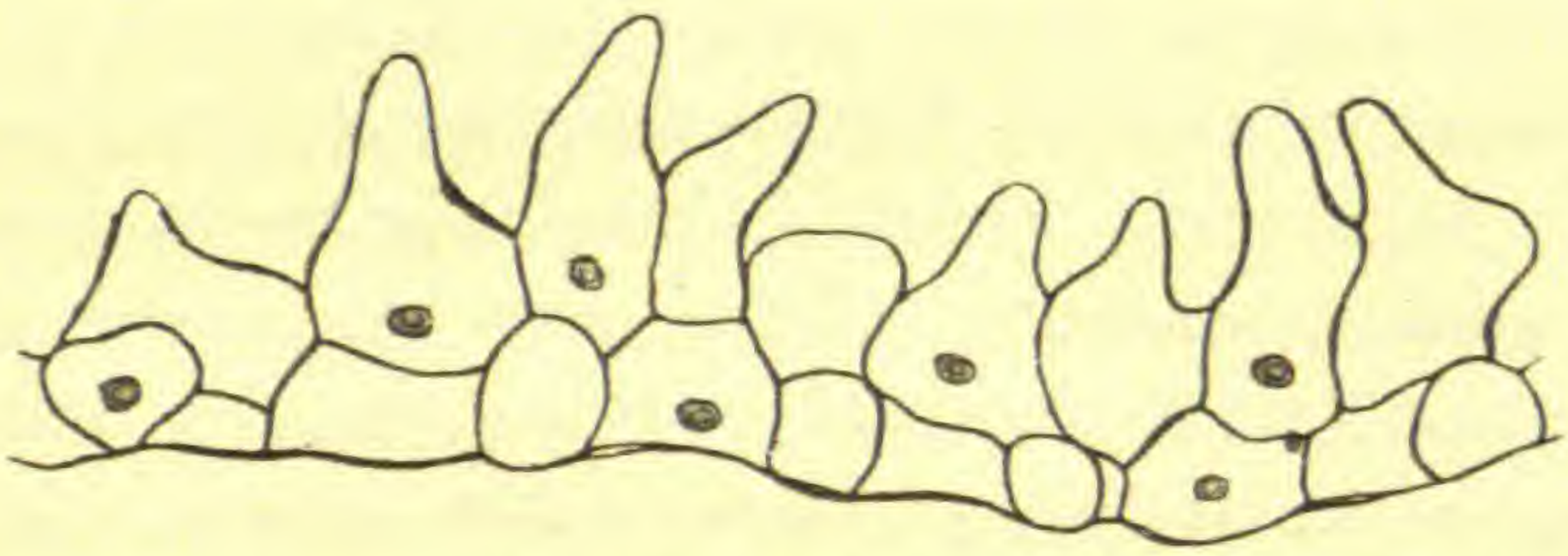

Fig. 3.—Transverse section of a male petal with papillæ (225×1).

observed that in the sporangia probably only one row of pollen mother cells develops, as is the case in many other plants, for instance Knautia arvensis (*cf.* Goebel 9, p. 396). A transverse section of a ripe microsporangium shows always only very few pollen grains (2–3), apparently from the same tetrad (fig. 4). The number of the pollen mother

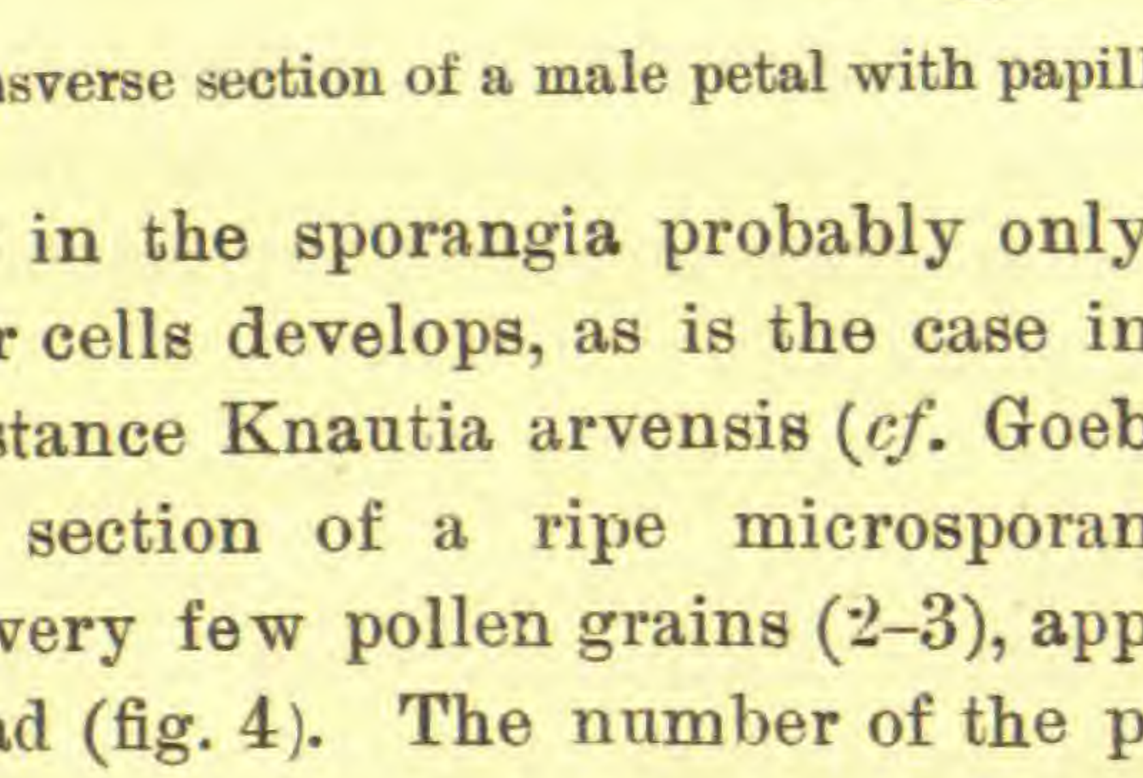

Fig. 4.—Transverse section of a microsporangium in an anther with a tetrad (112×1).

cells is not great, for in a longitudinal section there are at most only 8 tetrads to be seen and if always only one row is developed, there will thus be only very few—about 30—pollen grains developed in each of the four sporangia in every anther. The wall-layer of the anther is thin, and a

fibrous layer is not developed (fig. 4), just as in so many other water plants. The anthers are clothed on the outside with rather large papillæ (Pl. XXIV., A, fig. 6) which are supplied with a series of delicate reticular folds.

The pollen grains (Pl. XXIV., A, fig. 21) are very large: they average about 170–175μ in diameter, consequently Enalus in this respect belongs to that group of plants which have the largest known pollen (*cf.* Kerner 16, p. 96). The pollen grains contain besides drops of oil a large number of finely distributed starch grains; they are thus very heavy and sink in sea-water. Thus they behave like the pollen grains of Najas, examined and described by Jönsson (15). Also, as in so many other water plants, *e.g.*, Ruppia (Murbeck, 20), Zannichellia, Najas (Jönsson, 15), and Ceratophyllum (Strasburger, 32) the pollen grains of Enalus have no intine, and are quite smooth on the surface (Pl. XXIV., A, fig. 21).

The number of the pollen grains seems always to be in a certain correlation to their size (*cf.* Kerner, Pflanzenleben, II., p. 94). But in Enalus there are so many male flowers developed—a whole male inflorescence is homologous with a single female flower—that the diminished chance of securing pollination, which a smaller number of developed pollen grains must otherwise cause, is neutralized.

The Female Flower.—The spathe-leaves of the female flower when fully developed (Pl. XXIV., A, fig. 8) are rather different in shape from those of the male inflorescence. These differences are closely dependent on the arrangements for the pollination of the flower. At an earlier stage (Pl. XXIV., A, fig. 7) they agree more with the male spathe-leaves as to their form and the position of the leaves, but in regard to the size there is a difference, as they are much narrower, so that the breadth of the whole bud would not much exceed 10 mm., and during the whole anthesis the spathe maintains this breadth at the base. After the pollination, during the increase of the fruit, the spathe-leaves are pressed more

asunder whereby the breadth is augmented (Pl. XXIV., A. fig. 14). Fully developed—at the stage of pollination—the female spathe-leaves (Pl. XXIV., A, fig. 8) are narrowly oblong, not exceeding 2 cm. in breadth. In length they agree with the male spathe-leaves, but differ in their form and situation. A little before the time of pollination they curve outwards; besides they are so stiffly keeled that both halves of the leaves, at least at the top, have their surfaces nearly pressed together. The edges of the leaf never roll up. By this arrangement—which perhaps is best understood by looking at fig. 8 (Pl. XXIV., A) compared with fig. 1 (Pl. XXIV., A)—the double advantage is obtained that the petals are freely exposed—which, as I shall show below, is of fundamental importance for the pollination—and also that the whole flower, by means of the wing-like spathe-leaves, is kept floating on the surface in a *horizontal* position.

The female flower of Enalus (Pl. XXIV., A, fig. 9) has a double perianth of three sepals and three petals. The ovary while still young is already densely clothed with rather large hair-like projections. The sepals are short, oval, smooth with entire edges. The petals are much longer, up to 3–4 times the length of the sepals. They show a very characteristic folding which certainly may be partly caused by the fact that the petals increase while the closed sepals still prevent their free development (*cf.* Arnoldi, 1, p. 440). The folding is partly lengthwise, partly crosswise (Pl. XXIV., A fig. 9). While the folds in the length are two only, running at a rather short distance from each other parallel to the edge of the leaves, the cross folds are numerous, the edges of the petals are consequently just roughly denticulate. The tannin cells are present in great numbers spread all over the lamina, not gathered together in a few strings in the middle of the leaves as in the male flower. Concerning the structure of the petals it may be noted that the epidermal cells are provided with papillæ, the walls of which have the same structure as in the

male flowers and the anthers (Pl. XXIV., A fig. 6). The petals have a faintly reddish colour which later on changes into brown; also after the pollination the folds of the petals become smoothed out and fade.

The appearance of the ovary is already mentioned. No style is developed. The stigmas are 6, bilobed, so that there are 12 lobes of the same size (Pl. XXIV., A, fig. 10, *st.*). These are narrowly lanceolate with long points, and at the base somewhat enlarged (Pl. XXIV., A, fig. 11). Excepting a part of the top they are clothed on their inner sides and on their edges with rather long stigma-papillæ. These papillæ are especially large, with rather thick walls, on the edges, where they are also extended laterally, so that the stigmas, especially at the base, look as if fringed (Pl. XXIV., A, fig. 11). It is also noteworthy, that the tops of the stigmas completely lack papillæ. The stigmas contain plenty of tannin cells. They are parallel to the axis of the flower and thus form an erect group to catch the pollen grains when the flower is in *vertical* position (Pl. XXIV., A, fig. 9, 10).

The gynœceum is composed of six carpels which form a unilocular ovary divided into six cavities (fig. 5). The

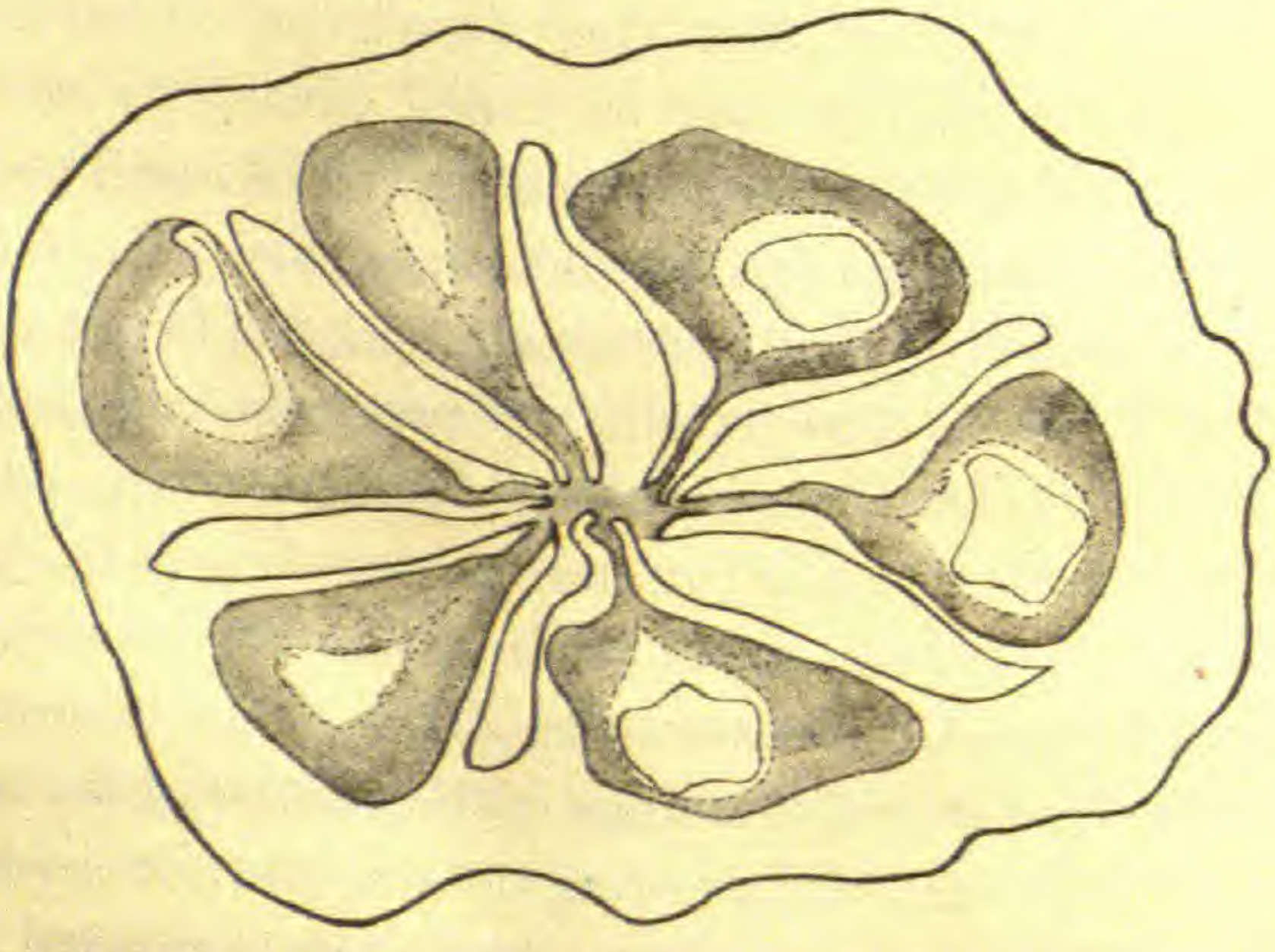

Fig. 5.—Transverse section of a young ovary ; the ovules enclosed in mucilage and the placentæ split into air-chambers (15 × 1).

parietal placentæ project to the middle of the ovary and are, as in so many of the Hydrocharitaceæ (*cf.* Eichler, 8), split quite into two lamellæ. During an early stage there are rather

Fig 6.—Transverse section of a fruit with embryos. Nearly all mucilage gone and the air-chambers pressed together (15 × 1).

large air-chambers between these, but when the embryos grow out they disappear as the lamellæ become pressed together (fig. 6). It is the low specific gravity due to these and also some other air-chambers in the ovary that keeps the flower floating before the pollination. Afterwards when the fruit

Fig. 7.—Ovule (35 × 1).

is drawn down by the spiral rolling up of the pedicel, the air-chambers between the split placentæ disappear.

The ovules are anatropous (fig. 7) with two integuments. The ovarial cavities, but *not* the air-chambers formed by the split placentæ, are quite filled up with mucilage before fertilization and during the early stages of the embryo-development (fig. 6). It is a secretion from the outermost cell-layer of the wall of the ovarial cavities, the cells of which are rather large and high (Pl. XXIV., A, fig. 22). The nucleus is always situated at the inside wall of the cell. The layer that secretes the mucilage just inside is rich in starch, contrary to the condition in the other tissues of the ovary. The external cells bordering on the air-chambers do not differ from the others in the tissue of the fruit, nor do they form any mucilage.

The mucilage is deeply stained by fuchsin, methyl violet, methyl green, and gentian violet, but not by Congo red. Iodine in potassium iodide and iodine-zinc-chloride only cause a feeble yellowish stain. Thus it appears that the mucilage is a pectin-mucilage, like most mucilages which swell in water.

It is evident that the occurrence of starch in the outside cells of the placentæ may be in some relation to the secretion of the mucilage. That starch is used to form mucilage by plants has been especially observed in seeds, *e. g.*, in the Cistaceæ the seeds produce mucilage, the formation of which has been studied by Rosenberg (24). In the outer coats of the seeds, especially in species with abundant mucilage formation, there is often much starch in the epidermal cells which cannot be used for the embryo but apparently is in connection with the mucilage-formation, so that it is partly employed for the formation of mucilage. A product is thus formed called " red starch " (*cf.* A. Meyer *sec.* Rosenberg 24), which is supposed to be an excretion which, at a more advanced stage, is stored in the epidermal cells or also further used for mucilage. Also the common starch, " blue starch," occurs in some species and is transformed into mucilage.

In the placentæ of Enalus it is noteworthy that the starch is rather more abundant at a more advanced stage than at an earlier one. After treatment with iodine-zinc-chloride at an older stage a transverse section of a young fruit shows a dark blue line following the walls of the fruit-cavities, especially in the placentæ. This is the starch-filled cells below the mucilage-layer (Pl. XXIV, A, fig. 22 *st.*). At an earlier stage there is also a considerable quantity of starch in the other tissues of the ovary, but not so much and especially not so strictly localized as at a later stage. That the starch is more abundant at a later stage, when the secretion of mucilage rather begins to cease, may be explained by considering it either as a secretion formed in connection with the formation of mucilage and stored in the more superficial cells, or as stored because at a later stage it is no longer consumed for the mucilage formation. At all events the starch here seems to be of the common type which is stained blue, not brownish-red, by iodine.

The result of this formation of mucilage from the walls is that the young ovules are quite covered by mucilage, whereas at a more advanced stage there is much less mucilage, and at the bursting of the fruit the valves are quite free from it upon their inner surfaces.

No mucilage is developed from the testa as in so many other of the Hydrocharitaceæ. According to the description of the Hydrocharitaceæ by Ascherson and Gürke (5) the formation of mucilage in their fruits is exclusively caused by the mucilaginous testæ. They say (5, p. 245): "Die Höhlung der Frucht ist in der Regel mit einer Gallertmasse angefüllt, welche meist zum grossten Teile der verschleimten Aussenzellschicht der Samenschale ihren Ursprung verdankt." That this is not the case in Enalus I have already shown above, and according to Raunkiær (22, p. 137) the mucilage is also formed from the placentæ in Elodea canadensis.

Concerning the importance of the mucilage for the plant Goebel (10) has pointed out that the penetrability for

solutions is rendered much more difficult by mucilage. On this account he considers the covering of young parts of plants with mucilage as a protection against destructive osmotic disturbances. Besides this, of course, the mucilage in fruits has often a more mechanical object, to effect the bursting of fruits, as for instance in Utricularia and in some other Hydrocharitaceæ, where it is formed from the seeds, or in Calla palustris, where according to a notice of Sernander (31, p. 156) it is formed by the funicle.

As an osmotic protection the mucilage has a special importance for young parts of plants. This has been more closely investigated by Schilling (30), who has shown that a coating of mucilage is very common in young parts of plants, but disappears when they grow a little bigger. The same thing has been first shown by Goebel, especially in liverworts, where the mucilage glands at the growing point function only at an early stage of the development of the young parts of the plant. That the mucilage in the ovary of Enalus is to be considered as an osmotic protection for the young ovules is, I think, fairly evident. It appears directly from the fact that it was very difficult, or rather impossible, to make the fixing solution penetrate into the ovules, apparently on account of their protection by mucilage. The period of the development of the mucilage also confirms this, because only when the ovaries are young—and thus their tissues more feeble—is there a plentiful secretion, but no more when the embryos are more advanced, and when the fruit is ripe it is nearly all gone.

Phenomena of Pollination.—That Enalus acoroides belongs to that group of plants which Delpino has called hydrophilous has long been known. The notes in the literature about its pollination all agree in stating that it completely corresponds to the long-known and very interesting method of pollination in Vallisneria spiralis. Thus Aschersson and Gürke (5, p. 244.) say in speaking of this plant

after having given an account of the phenomena of pollination of Vallisneria: "Genau derselbe Vorgang findet bei Enalus statt." *Cf.* also Goebel in "Pflanzenbiol. Schilderungen" II., 2, p. 365. To some extent there is an agreement, as the male flowers break off, rise to the surface and float isolated, driven by stream and wind, thus being carried to the pistillate flower. But as regards the manner in which the pollen is actually carried over to the stigmas of the female flower and—in connection therewith—also as regards the floral organization of both these plants there are considerable differences. These depend upon the fact that *Enalus is an oceanic plant exposed to the changes of high and low water*. And it is with regard to this fact that the differences in the pollination between Vallisneria and Enalus obtain their full explanation.

When the female flower of Enalus is in full anthesis the pedicel reaches such a height that the flowers during *low* water float on the surface, and during the lowest tide the uppermost part of the pedicel is also on the level of the surface of the water. By means of the above described wing-like spathe leaves the flower is kept floating in a *horizontal* position, viz., with the axis of the flower on a level with the surface of the water. The petals are now extended and float on the surface of the water without being wet, and as the spathe leaves are more or less strongly recurved they do not prevent the full exposition of the petals. The sepals still remain. The stigmas again are not so pushed out that they are exposed, but are covered as well by the basal parts of the petals as by the sepals (*cf.* Pl. XXIV., A, fig. 8).

When the male flowers arrive floating on the surface of the water they very easily get caught upon the petals, especially upon the folded edges, which are especially fitted to hold them fast, being just like the petals, very papillose. One may also observe little rows of captured male flowers along the edges of the petals, which hold them fast in spite of wind and currents. But no transport of pollen from these

male flowers which are caught by the long petals can take place now, partly because the stigmas are not fully exposed, partly because the stamens, owing to their lack of filaments and to their straight position, can scarcely transport any pollen directly to the stigmas, even if they were brought far in towards the centre of the flower. It is to be observed also that the pollen grains—as I have mentioned above—are so heavy that they sink in sea water. Hence it is impossible that any shed pollen grains could be carried to the stigmas by their own flotation.

The pollination here takes place in fact in an entirely different manner. If during low water one slowly pulls the pedicel of a flower, whose petals have caught some male flowers, below the surface level, one finds that the petals at once fold together owing to the pressure of the water, so that they catch the male flower between themselves. When I studied this plant in Jaffna I often had occasion to observe this fact. The male flowers were always enclosed by the embracing petals which shut rather closely together. But thus it, of course, also occurs that the anthers get an occasion to drop their pollen, and since this is heavier than the water it sinks down and can scarcely escape falling upon the stigmas, which stand *vertically and in a circle*, owing to the *changed position underneath the level of the water*. Probably also the strongly extended papillæ on the edges of the stigmas, which I have described above, aid the whole stigma apparatus with more certainty to carry on its work of catching and retaining the pollen grains.

What is thus effected by pulling the flower under water happens naturally in the sea twice in one day and night during high water, and no flowers of Enalus can at that time be observed above the surface of the water, because they are all submerged.

Whether the air bubbles, which when the petals close together are also caught inside the flower, are any obstacle or not for the pollination I cannot say. At any rate it is not

impossible that they are dissolved in the water long before the next low water period. As a comparison I have made an experiment: if a seed with long hairs, for instance that of a Strobilanthes, is dropped into a jar of boiled water which contains no air, the air bubbles which are always present between the hairs require 3–8 hours to be dissolved. Of course, this result cannot be regarded as absolutely decisive as the conditions are not the same, but it makes it nevertheless probable that air bubbles, possibly a hindrance, may be dissolved during the time the flowers are submerged.

It is remarkable that the discharge of the male flowers also occurs somewhat exclusively during low water, as I had frequently occasion to observe in Jaffna. My attention was called to this fact in a singular way. One morning during low water I had observed the loosening and catching of the male flowers, and had also preserved some of them for investigation. In the meantime, wanting more material, I visited the same place later on in the same day, but in spite of eager search and long waiting I could not see any male flowers at all. I did not then understand the reason. Next morning when it was low water again I made a new attempt at the same place, and then with better success. Just as during low water the previous day, male flowers in great numbers floated up and swam about as before. Afterwards during my stay in Jaffna I repeatedly had the opportunity to notice the same thing, viz., that it is during low water that the loosening of the male flowers take place.

This phenomenon may easily be explained by the differences in the pressure of the water during high and low water. The male flowers are like balloons when closed. When ripe they are filled with gases, and the sudden recurving of the sepals and petals may apparently be due to the pressure of the gas bubbles on reaching the air. As the perianth, within certain limits, can easily be more or less pressed together, the explanation of this periodical

phenomenon may be the following. With increased pressure, *i.e.*, during high water, the buds are somewhat compressed, and consequently the volume diminishes, but since their absolute weight is the same it follows that the specific gravity is increased and consequently the power of attraction upwards diminished. With diminished pressure again, during low water, the volume of the buds is augmented and thus the specific gravity diminished, so that the power of attraction upwards is augmented. The chance for the male flowers to rise to the surface during low water is consequently greater than during high water, in otherwise similar circumstances.

Thus there is in this plant a remarkable correlation between the exposition of the female flowers and the loosening of the male flowers, in that both these phenomena always occur at the same time, during low water.

For the full comprehension of the significance of this fact the occurrence and geographical distribution of Enalus may be of some interest. The difference in the rise and the fall of the tide in Ceylon is rather small, about $\frac{1}{2}$ m. or more, but great enough to keep the Enalus flower submerged during high water. But this plant occurs in other parts of the world where the difference in the tide levels is very great. Thus Balansa notes (*sec.* Sauvageau 28, p. 269) that Enalus acoroides in New Caledonia grows in a depth of (at high water) 2–3 m. and Volkens (36, p. 455) states that in the Caroline Islands it is 1-2 m. below the surface level at high water. As Enalus never reaches more than about 1 m. in height, it is evident that in these parts of the world the female flowers of this plant never have any chance to reach the surface except during low water.

As may be seen from this description, there are somewhat essential differences between Enalus and Vallisneria in the mode of pollination, and these are closely connected with the different morphological organization of the flowers.

One may compare, for instance, Kerner's description (16, p. 129) of the pollination of Vallisneria. As regards the

difference in the organization of the flower it may be noticed that the spathe leaves in Vallisneria are little developed and always submerged; that the flower is kept floating always in a *vertical* position by the relatively well-developed sepals. The petals of Vallisneria are very little or not at all developed, which is explained by Kerner as an adaptation for the exposition of the stigmas. These are placed *between* the sepals, so that they can be easily reached by the anthers if the petals are reduced. And as regards the male flowers in Vallisneria the anthers have rather long filaments obliquely stretched out, so that the anthers can come into *direct* contact with the stigmas.

In all these respects Enalus is opposed to Vallisneria. A superficial comparison shows that the petals are developed as organs to catch the male flowers; that the pollination is arranged by the changed position (due to the tides) of the flower, which is horizontal on the surface, but vertical below it; the filaments in Enalus are quite reduced, so that a direct transport of pollen from the anthers, which besides are directed straight upwards, is impossible. The pollen grains are also heavier than water, and therefore they can scarcely reach the stigmas by floating. Finally, all these differences must be considered in relation to the fact that *Enalus is a sea plant exposed to the differences of the tide*, which cause a periodical change in the exposition of the female and loosening of the male flowers. Vallisneria, on the contrary, is a lake plant without any such changes in the level of the surface.

The Ripening of the Fruit and the Development of the Embryo.—After the pollination and fertilization the fruit is pulled down to the bottom by the spiral twisting of the pedicel, just as in Vallisneria (Pl. XXIV., A, fig. 14). Regarding the real nature of this movement, and what it is really due to, very little is known, except that it belongs to the "autonomous movements." J. F. Müller (21) in his paper on Vallisneria has examined the anatomy of the pedicel

to discover whether perhaps its internal structure might provide any explanation of this phenomenon. Already at an early stage the anatomical structure of the pedicel is somewhat monosymmetrical (*cf.* Müller, 21, tab. 3, fig. 23). Besides the central larger vascular bundle there is also a smaller one close by, making the transverse section more or less monosymmetrical. If the growth of these two bundles is different, *i.e.*, if one still increases after the growth of the other has already stopped, the result might be a coiling of the pedicel.

Enalus also has a somewhat monosymmetrical structure of the female pedicel, especially at the place where the closest spiral forms. For comparison it is also of interest to know the structure of the pedicel of the male inflorescence. Fig. 1, Pl. XXIV., B shows a transverse section through the male pedicel. Under the epidermis there are a few cell layers (2–3) which fit closely together without any air chambers. Within these the tissue is very full of air, with a lot of lacunæ separated by single cell layers. The vascular system is represented by two bundles of the same size in the middle and also a few other very small ones at the periphery. Thus the structure is bisymmetrical. The vessels in the bundle are few and small. There are also some tannin cells in the tissue, but not many. The pedicel of the male inflorescence has the same structure throughout its whole length and also during its whole life. The female pedicel (Pl. XXIV. B, 2–3) on the contrary has a rather different structure. Its structure during a later stage differs somewhat from its structure during an earlier stage, and also differs in different parts. In the female pedicel the coherent cell layers under the epidermis are more developed, while the air chambers are few, but the vascular bundles are rather large and numerous. But just as in the male pedicel, there are two vascular bundles in the middle, much larger than the rest. At the base of the pedicel they are also of about the same size as the air chambers around them. But higher up

about the point where the spiral begins (Pl. XXIV., B, 2) one of them is already a little larger and also especially the air chambers around it. These have apparently a tendency to originate radially around the larger bundle. The stem, originally bisymmetrical like that of the male inflorescence, thus becomes more and more monosymmetrical. In the general structure of the female pedicel Enalus thus agrees with Vallisneria, according to the description and figure given by Müller (21, tab. III., fig. 23). If now the different structure of the two larger bundles is accompanied by a different increase in length obliquely to the axis of the pedicel, the result must be a spiral twisting of the pedicel.

The differences in the anatomical structure at various stages appear in the different degrees of development of the mechanical elements before and after the pollination and fertilization. After the fertilization (Pl. XXIV., B. 3), the smaller peripheral bundles are all combined on their outer sides with groups of mechanical cells. The walls of these outer cells have become thickened, but are not at all lignified, staining violet with iodine-zinc-chloride and not at all with aniline chloride, or phloroglucin and hydrochloric acid. They thus consist exclusively of cellulose. This development of mechanical elements at an older stage in the female pedicel corresponds, of course, to the augmented demand for strength when the fruit ripens, and this the more as the currents in the sea where Enalus lives are often very strong. In the pedicel of the male inflorescence these mechanical elements never occur, as is commonly the case in diclinous phanerogams (*cf.* Grevillius, 11).

The remarkable increase of the hair-like emergences on the fruit after fertilization may also be regarded as an adaptation to protect the fruit from being broken off by the currents. Certainly they keep the fruit well anchored in the mud, where this plant commonly grows. This seems to be the case wherever this plant lives; it was so at Paumben and all around Jaffna, and Kurz (19) has made the same

observation at the Nicobar Islands. The currents near Paumben and Jaffna just where this plant lives are in fact very strong. According to Walther (34) the current in the Paumben channel often reaches a speed of 5–6 knots in an hour.

The ovules are anatropous with two integuments (fig. 7). These are both fully developed, whereas, according to Müller (21), in Vallisneria the outer integument after some time ceases to grow, so that only half the length of the nucellus is provided with two integuments, and thus the micropyle is formed by one integument only.

I have not been able to investigate the development of the embryo sac and the fertilization in my material, owing to the difficulty of making the fixing solution penetrate the copious mucilage in the young ovaries.

In the embryo sac the antipodals are rather large. (Pl. XXIV., A, fig. 13). Sometimes the embryo sac has a pouch-like deepening in its antipodal end, though not so large as in Elodea (*cf.* Wylie, 35). The cells of the tissue of the nucellus are here but little different from the rest. They are smaller, but their walls are thicker and stain better. From these smaller cells some larger ones radiate in a semi-circle, probably because they have some nutritive function in connection with the antipodal cells. The fertilization itself I have not observed, but have often seen pollen tubes in the micropyle.

The young embryo has a very large suspensor cell (Pl. XXIV., A, fig. 12) just as in Elodea (Wylie, 35). The embryo seems otherwise to be of the usual monocotyledonous type. Very few endosperm cells are formed in the embryo sac. Thus the embryo is suspended as if in a great vacuole.

It is remarkable that during the further development of the embryo the integuments do not develop any more, but simply stretch so much that they equal the growing embryo. No lignification takes place in their tissue, and when the fruit

is ripe and bursts (Pl. XXIV., A, fig. 15) the testa also breaks off around the hypocotyl and remains only as a ragged easily-loosened cap on the top of the cotyledon (Pl. XXIV., A, fig. 17.) *Thus this plant can scarcely be considered to have any seeds, because it is the young embryos which are dispersed at the opening of the fruit* (Pl. XXIV., A, fig. 16, 18). Enalus acoroides is thus a new example of a "viviparous" plant.

These embryos are rather highly developed, as is generally the case in the Hydrocharitaceæ. Fig. 20 (Pl. XXIV., A) shows an embryo with the testa a little before the bursting of the fruit. The cotyledon is very large and covers the young plumule, with its many young well-developed leaves, like a sheath. The hypocotyl is also large and contains much starch, just like the cotyledon. At the end may be seen the young primary root, which probably never functions, but at the side under the plumule a secondary root is seen pushing out at the base.

The young embryos are rather heavy. They soon sink down into the mud, where *they at once begin to grow out.* Some embryos cultivated by myself in Jaffna after about a week already showed several leaves more than 1 cm. in length (Pl. XXIV., A fig. 19).

Enalus acoroides thus belongs to that group of plants where the young embryos or spores develop directly without any period of rest. Goebel especially has shown that this phenomenon is not rare in plants growing in wet localities, and that the well-known "vivipary" in the Rhizophoraceæ and other mangrove plants may be in some respects regarded as a special case of this rather common general phenomenon. Another example is Crinum asiaticum, where the embryo, however, is provided with a well-developed endosperm but no testa owing to the lack of integuments. Another similar case is Cryptocoryne ciliata, where the embryo leaves the cotyledon behind and only the well-developed plumule is detached, after having reached a high degree of development in connection with the mother plant.

It is evident that the difference between such plants and Enalus is not great. Vivipary also frequently occurs in a genus where other species, even if not viviparous, have seeds in which the germination commences immediately after reaching the ground (F. E. Lloyd, 37). One of the characteristics of Enalus is that the young embryos are dispersed directly, the plant having no seeds. These embryos, however, have not reached so high a degree of development in connection with the mother plant as in the Rhizophoraceæ, nor are they provided with any endosperm. But the cotyledon is plentifully provided with food, and the further development can go on directly, because the plant lives under conditions in a tropical sea where the period of vegetation is never interrupted by external influences.

The observations made by Borzi (7) upon Inga Feuillei show that it is not always plants living under wet conditions which show the phenomenon of the embryos being directly dispersed, a phenomenon which is closely allied to the vivipary. In Inga Feuillei the young embryos are directly dispersed, and according to Borzi, by the aid of birds. But it is remarkable that these embryos are very resistent to drought, so it is evident that it is not necessary for them to develop at once.

Comparison with other Hydrophilous Plants.— The hydrophilous plants were first distinguished as a special pollination type by Delpino. Knuth in his great work "Handbuch der Blütenbiologie" (18, I., p. 83) has divided them into two groups: the Hypohydrogamics, where the pollination takes place below, and the Epihydrogamics where it takes place above the water. It is rather remarkable that, though the hydrophilous plants are very few in number, they yet represent so many different types of pollination. For even among the hypohydrogamics, there are several very well distinguished types. The most divergent among them are perhaps Zostera, Posidonia,

Cymodocea, and Halophila, where the pollen is vermiform. But the epihydrogamics also represent many different methods of pollination. I have already shown above that Enalus does not agree so completely with Vallisneria in this respect as was perhaps previously supposed. But it may also be of some interest to make a further comparison with some other hydrophilous plants.

A careful examination of Elodea canadensis has recently been made by Wylie (35). As regards the female flower it is of interest to see that in Elodea also its floating upon the surface is due to the buoyancy of the gases in large lacunæ, which here arise in the long floral tube according to Wylie (35), but in the elongated part of the ovary according to Raunkiær (22, p. 135, fig. 63). In Enalus the lacunæ are formed by the split placentæ (fig. 5). The organization of Elodea otherwise reminds one more of the female flower of Vallisneria than of Enalus; the perianth, however, is double, but the flower floats with the axis vertical, the weight of the flower resting chiefly upon the stigmas (Wylie). The pollen grains of Elodea are very remarkable. The male flowers develop just as in Vallisneria and Enalus; they loosen at maturity and rise to the surface in the same manner.

It is interesting to note that Wylie has observed a periodicity in the detachment of the male flowers in Elodea also. They are chiefly raised to the surface during the early part of the forenoon, and very few in the evening. This phenomenon, Wylie suggests, may be due to the first photosynthesis of the day. The oxygen hereby accumulated makes the flowers which have ripened during the hours of darkness float up. I have made no observations on the influence of the light upon the male flowers of Enalus and their detachment, but, as I have already mentioned above, the male flowers of Enalus almost without exception float up only during low water, which I think is due to the pressure of the water. But Elodea is never exposed to any such changes, as it lives in lakes and rivers.

In Elodea the pollen is nearly all discharged before the male flower reaches the surface, so that, according to Wylie, the floating male flowers themselves do not play any important part in the pollination. But instead the pollen itself shows a very remarkable organization for floating. The tetrads remain joined together so strongly that violent shaking seldom breaks them apart. In organization they rather resemble a Pediastrum or Hydrodictyon or other such plankton-alga with the different cells more or less closely joined together with interjacent spaces between (*cf.* Wylie, 35, Pl. III., fig. 51, 53). The pollen grains have not only a well-developed intine, but also a strongly cutinized exine beset with spines, which retain air in their interspaces, so that the whole tetrad is kept floating. Thus the pollen itself in Elodea shows a remarkable adaptation for floating and in this way reaches and comes into contact with the floating stigmas. Consequently Elodea is strikingly epihydrogamic, but also represents a distinct type of hydrophilous pollination owing to the pollen tetrads being especially adapted for floating.

In the structure of the pollen grains Enalus agrees much more closely with some of the hypohydrogamic plants. These might, I think, also be divided into two more or less different groups with respect to their pollen grains. One is distinguished by the pollen grains having the same specific gravity as the water, or at any rate not being much heavier. Often the pollen grains also have a remarkable shape, viz., vermiform. In connection with this Goebel (10, II., p. 367) has pointed out that the stigmas are especially adapted for catching such pollen, as they are more or less curved but never infundibuliform. This form on the contrary is very characteristic of hypohydrogamics with pollen heavier than the water (owing to numerous starch grains). These hypohydrogamics are always so constructed that the sinking pollen is collected by a special "appareil collecteur," which in different plants is of somewhat

different origin. Thus in Najas (Jönsson, 15, p. 14) it is the lobes of the corolla which act as collecting apparatus, in Zannichellia (Goebel, 10, II., 2, p. 365) it is the funnel-like stigma itself. In these respects Enalus apparently agrees with the hypohydrogamics whose pollen grains are heavier than water and are collected by a special "appareil collecteur"; this in Enalus is effected by the erected funnel-like group of the twelve stigma lobes (Pl. XXIV., A, fig. 9, 10).

Very characteristic of Enalus, and which makes this plant a very singular pollination type, is the part which the petals take in the pollination, viz., as collecting apparatus for the male *flowers*. Afterwards the sinking *pollen grains* are collected by the funnel-like stigma apparatus. Among the Hydrocharitaceæ the genera Blyxa and Limnobium also have long and narrow petals like Enalus, but the pollination of these plants has not been observed.

Thus Enalus acoroides takes a singular intermediate position among the hydrophilous plants, as it is epihydrogamic in that the male flowers on the water are carried to the female flowers, but hypohydrogamic in that the pollen grains in the water sink down to the stigmas *underneath the surface*.

Summary.

1. The male flowers differ from those of Vallisneria—except as regards the perianth—in that the filaments are scarcely developed and the anthers are directed straight upwards.

2. The pollen-grains are very large—about 170 μ in diameter—and are heavier than sea-water, owing to the presence of numerous starch-grains.

3. The pollen-grains have only a single smooth wall, probably the exine.

4. The wing-like female spathe leaves aid to keep the female flower floating in a horizontal position.

5. The petals are specially adapted to catch the floating male flowers.

6. The exposure of the female flowers and the loosening of the male flowers only occur during low water.

7. During high water the position of the female flower is changed from horizontal to vertical. The heavy, sinking pollen grains can scarcely avoid sinking down upon the erected stigmas, which form a striking "appareil collecteur."

8. Enalus thus as regards pollination takes an intermediate place between the epihydrogamic and the hypohydrogamic hydrophilous plants.

9. The ovules when young are enclosed in mucilage developed from the inner walls of the ovarial cavities. At the maturity of the fruit the mucilage is nearly all gone.

10. The suspensor-cell is very large. The embryo-development is of the common monocotyledonous type.

11. The integuments are never lignified. At maturity the testa is only an easily loosened cap around the embryo.

12. Thus Enalus disperses the embryos directly, or has no seeds. These embryos develop immediately.

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EXPLANATION OF PLATES XXIV., A AND XXIV., B.

Pl. XXIV., A.

Fig. 1. ♂—spathe (1 × 1).
" 2. ♂—spathe, longitudinal section (1 × 1).
" 3. ♂—flower with pedicel (3, 5 × 1).
" 4. } ♂—flowers (3·5 × 1).
" 5. }
" 6. Papillæ from an anther (225 × 1).

Fig. 7. ♀—spathe (bud) (1 × 1).
„ 8. ♀—flower in anthesis (1 × 1).
„ 9. ♀—flower; the spathe-leaves cut away. *co* = corolla; *ca*= calyx; *st* = stigma (1 × 1).
„ 10. The stigma-apparatus (2 × 1).
„ 11. Stigma-lobes with tannin cells (outside) (15 × 1).
„ 12. Embryo-sac with a young embryo. *s* = suspensor-cell (225 × 1).
„ 13. Embryo-sac with antipodals (*ant.*) (225 × 1).
„ 14. Fruit, nearly ripe (1 × 1).
„ 15. Fruit, opened, with seeds (1 × 1).
„ 16. Embryo at the opening of the fruit, in side-view. *p* = plumule (1 × 1).
„ 17. Cap-like testa, loosening from the embryo at the opening of the fruit (1 × 1).
„ 18. Embryo at the opening of the fruit, front-view (1 × 1).
„ 19. Embryo, six days after the opening of the fruit (1 × 1).
„ 20. Seed in longitudinal section. *p* = plumule; *r* = radicle (20 × 1).
„ 21. Pollen-grain (250 × 1).
„ 22. Transverse section through a placenta with mucilage and starch-filled outer-cells. *m* = mucilage; *st* = starch (450 × 1).

Pl. XXIV., B.

Fig 1. Cross-section of a pedicel of the male inflorescence. The section is bisymmetrical (12·5 × 1).
„ 2. Cross-section of a female pedicel *before* the pollination. The section shows a tendency to be monosymmetrical: the air chambers around one of the two longer vascular bundles are greater than around the other one. The walls of the mechanical cells not yet thickened (18 × 1).
„ 3. Cross-section of a female pedicel after the pollination. The section is monosymmetrical. The walls of the mechanical cells are strongly thickened but not lignified. They consist of cellulose (18 × 1).

Studies in Plant Breeding in the Tropics.

BY

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I.—INTRODUCTORY: THE WORK OF MENDEL AND AN ACCOUNT OF RECENT PROGRESS ON THE SAME LINES; WITH SOME NEW ILLUSTRATIONS.

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Introduction: Brief historical notes.
I.—Mendel's observations.
(1) Monohybrids.
(2) Dihybrids.
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(4) The theory of purity of the gametes.
(5) The paper on Hieracium.
II.—Recent confirmation and criticisms.
III.—The shape and colour of the seeds of peas.
IV.—The views of de Vries.
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VI.—Latency of characters.
VII.—Correlation.
VIII.—De Vries' analysis of floral colour.
Conclusion.
Summary.
List of literature.

THE rediscovery in the year 1900 of Mendel's Paper on plant hybrids (49*) instituted a new phase in the study of the problems regarding the nature of species, and the

* Figures in brackets ( ) refer to the list of literature at the end of the paper.

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importance of applying the direct methods of experiment to these questions was at once widely recognized. Already after an interval of only four years, real and solid advances in knowledge have been made, and on every hand the range of facts explicable on the Mendelian theory has been extended. Although the work has not yet passed beyond the foundations of a great branch of evolutionary science, a brief general account of the progress which has been so far made may not be without interest, in view of the great importance of the subject.

Mendel's own work is now fully familiar to the majority of naturalists, and for the publication of yet another summary of his conclusions an apology would be wanting did it not appear that in some quarters the full importance of Mendel's discovery has still failed to be grasped. Thus Vernon writing in 1903 (64) still lays stress on the perfection or imperfection of dominance as if this were a prime issue, whereas the principal law of Mendel, as it is very clearly stated by Correns in the paper which Vernon quotes, takes no account of dominance at all.

Pearson again, in the course of a valuable investigation into the relation between the principle of gametic purity and the law of ancestral heredity (54), entirely ignores Mendel's demonstration of the truth of his hypothesis by the process of recrossing with the parental forms. Pearson, too, would confine the term "Mendelian theory" to the particular cases where dominance appears. But it cannot be too forcibly stated that the facts of dominance were merely incidental to Mendel's experiments, and constitute no fundamental portion of his theory.

The idea of discontinuity in evolutionary processes is one which is now fully familiar through the labours especially of Bateson (1) and de Vries (69). All the most recent work upon the subject of species has confirmed more and more fully the importance of this conception, and the progress here dealt with is concerned throughout with the

behaviour of discontinuous characters. The statistical study of continuous variations has been greatly elaborated during the past decade by the Biometric school : for the purpose of the present paper, however, it is sufficient to assume such a knowledge of "normal" variability (53), as may be obtained from a perusal of Galton's "Natural Inheritance."

In giving an account of recent progress, it appeared that interest might be added to the discussion by illustrating it with concrete examples drawn from experiments in plant-breeding which have been carried out by the writer at Peradeniya during the past two years. The present paper is to be regarded as an introduction to a full account of these experiments which it is hoped will appear shortly. An indication will also be made here of some of the most important results which these experiments have afforded, since at the present stage of the inquiry a prompt publication of data is desirable even when these differ only in detail from facts already known. Work of a merely confirmatory nature is also not without value. A few of the facts here recorded are new in a somewhat more marked degree.

To the experiments here described certain necessary limitations have been attached. The majority of them were concerned in the first place with the acclimatization of plants from a more temperate country, and with the production from these, by crossing, of strains better adapted to a tropical climate. The number of plants found to be suitable for these experiments was limited ; and many of those which were tried would hardly grow at all. Serious difficulties were met with in the attempt to grow several generations in the course of a single year, and the majority of European plants tested were found to grow well only at one particular season. At other times of year unexpected vicissitudes of climate were often attended with disastrous results.

An account of these effects will appear later, together with details of the experiments here briefly summarized. At present I need only emphasize the fact that, in spite of

conditions frequently very unfavourable, the results obtained by other observers in Europe and America, establishing the excellence and accuracy of Mendel's work, were on the whole fully confirmed.

Observations were made upon several plants native to the tropics, in the hope of discovering suitable objects for further experiments. But only a few were found to fulfil all the necessary conditions. In the present case a short period of growth, reasonable facility of manipulation, and a ready success of artificial pollination were essential in addition to the requirements postulated by Mendel (49) for his experimental plants, viz., the possession of constant differentiating characters, facility of protection from foreign pollen, and an absence of disturbances in the fertility of the cross-bred plants. In fact, like Mendel and Knight (44) before me, I have found "no plant so calculated to answer my purpose as the common pea," although Indian corn has also yielded results of considerable interest.

Work previous to the Rediscovery in 1900 of Mendel's Papers.

The following brief historical notes make no kind of pretence to completeness. They are intended merely to recall a few of the principal steps by which the present state of our knowledge has been reached :—

J. G. Kölreuter (46) was the first to attack the problem of inheritance in cross-bred plants by experimental methods. As early as 1761 he established the fundamental fact that the contribution of the two parents to the offspring is substantially equal. And in the following years he carried out a series of experiments by which his knowledge of hybrid plants reached a level which was hardly excelled previous to the publication of Mendel's papers. These experiments showed, among a number of other facts now equally familiar, that in plants the results of reciprocal crosses are usually identical, although not always carried out with equal facility; that hybrids between different races of the same species are

usually more fertile than those between different species; and that hybrid plants often excel their parents in luxuriance of growth. Kölreuter attached importance to the number of generations in which by continually fertilizing the successive offspring of a hybrid with the pollen of one parent, plants exactly resembling this parent could be obtained.

These latter facts were subsequently discussed by Mendel and explained by him in terms of his own theory.

T. A. Knight was the earliest observer to lay stress upon the practical side of the study of hybrids, and he was largely concerned with the improvement of useful races of plants by cross-breeding. The account of his experiments with peas (44) was published in 1779. The agreement of the facts then described with those of Mendel has been pointed out by Bateson (2).

Between 1800 and 1860 a large number of workers were concerned with the raising of hybrids, but there was no great advance in theoretical knowledge. Gaertner, in 1849, published an enormous mass of observations largely confirming and amplifying those of Kölreuter.

C. Naudin's essay entitled "New Researches on Hybridity in Plants" appeared in 1862 (52). He pointed out that the facts of the return of hybrids to the specific forms of their parents, already observed by Kölreuter and Gaertner, were naturally explained by the hypothesis of the disjunction of the two specific essences in the pollen and ovules of the hybrid. In cases where this is complete, forms exactly resembling the parents might be obtained. This hypothesis comes remarkably near to that of Mendel; and the importance of the uniformity of the first hybrid generation, as contrasted with the diversity of the second, is clearly recognized. Naudin considered the hybrid in the adult state to consist of an aggregate of particles, homogeneous and characteristic of a single species when taken separately, but mingled in various proportions in the organs of the hybrid plant, which is thus looked upon as a "living mosaic."

Darwin's "Origin of Species" was published in 1859, his "Variation in Animals and Plants in 1868."

Mendel's paper on peas was read in 1865, and that on Hieracium in 1869. In 1865 also appeared Wichura's account of willow hybrids (78), in which the strictly intermediate form of most of the hybrids examined was strongly emphasized.

In 1881 Focke in his "Die Pflanzen-Mischlinge" gave an able account of the progress of the knowledge of hybrids up to that date. This work contains also a useful historical summary. Mendel's work is briefly referred to, but its full importance is not recognized.

Nægeli's "Mechanisch-physiologische Theorie der Abstammungslehre" was published in 1884, and Weismann's well-known essays upon Heredity were appearing about the same time.

In 1889 Galton in his "Natural Inheritance" gave a very clear account of his application of statistics to the problems of heredity. From various human characters he deduced the value $\frac{1}{3}$ for "filial regression." Although most of his own observations were directed to the elucidation of the laws of "normal variability" Galton recognized the probable importance of discontinuous variations in evolution.

Macfarlane in 1892 (48) showed that the minute structure of plant hybrids agrees with their external appearance in showing characters usually intermediate between those of the parental forms.

Millardet's remarkable account of "False hybrids" appeared in 1894. In the same year Bateson's work "Materials for the Study of Variation" was published. The author criticized a number of biological conceptions then current, and showed that the whole tendency of the material accumulated was to indicate the importance of discontinuous variations in the origin of species. Without attempting a rigid definition—hardly possible at that stage of the inquiry—Bateson indicated the difference between the two kinds of

variation by a number of instructive examples. The recent advances in knowledge following upon a return to the experimental method were in one place explicitly foretold.

A number of further important contributions towards a solution of the problems of variation and inheritance will be found mentioned in the list of literature at the end of this paper.

I.—MENDEL'S OBSERVATIONS.

It will now be necessary to consider those remarkable discoveries of Mendel, which were independently rediscovered and confirmed in the year 1900 by de Vries (67), Correns (11), and Tschermak (58). An essential point in Mendel's treatment of the subject of hybrids is the separate study which he applied to separate pairs of differentiating or alternative characters (one member of such a pair being exhibited by one of the parent forms, the second by the other, *e.g.*, the presence of coloured flowers upon one, and of white flowers upon the other). Following the terminology of Bateson and Saunders (6) we may call such characters *allelomorphs*. A *heterozygote* is formed by the union of a pair of opposite allelomorphic gametes (sexual cells), a *homozygote* by the union of gametes in which the allelomorphs are identical.

Bateson describes the immediate offspring of a cross as the filial generation F_1, subsequent generations being F_2, F_3, &c. The parents of the cross-bred plant belong to the generation P_1, its grandparents to P_2, and so on.

Mendel's discovery may be at once briefly stated, using these more modern terms. Having applied to certain varieties of peas the method of artificial cross-pollination with subsequent separate raising of all the offspring obtained, and that of recrossing with the parent forms, Mendel came to the conclusion that the male and female germ cells (or gametes) of a heterozygote contain the pure parental allelomorphs completely separated from one another, and that the segregation of characters takes place in such a manner that the

separate allelomorphs of the parents are represented in the gametes in all possible combinations in equal numbers, with the exception that the two allelomorphs of the same pair never occur together in the same gamete. To this principle Correns (11) has applied the term "Mendel's Law."

Thus if the parental allelomorphs be represented by A and A′ respectively, they will give rise to a heterozygote containing both allelomorphs—AA′; but the gametes of this will contain the pure parental allelomorphs A and A′, moreover 50 per cent. of the gametes will contain A but not A′, and 50 per cent. will contain A′ but not A. If we pay attention to two pairs of characters—A & A′, B & B′ (AB in one parent, A′B′ in the other), the heterozygote will contain AA′BB′. This will produce equal numbers of gametes: 25 per cent. AB, 25 per cent. AB′, 25 per cent. A′B and 25 per cent. A′B′; but there will be no gametes of the form AA′ or BB′.

It is found, therefore, on self-fertilizing a heterozygote formed by the union of two gametes which contain the allelomorphs A and A′ respectively (and whose own gametes are therefore 50 per cent. A, 50 per cent A′ in each sex), that offspring of the forms AA, AA′, A′A and A′A′ appear in equal numbers. If, on the other hand, the gametes of the heterozygote AA′ are crossed by the gametes of the pure parental form A′ (all gametes A′), the offspring will show the forms AA′ and A′A′ in equal numbers. In the particular cases studied by Mendel AA, AA′ and A′A were similar in appearance, so that in the first of the above cases the proportion in which the offspring appeared was apparently 3 A : 1A′ or 75 : 25; and in the second case 1A : 1A′ or 50 : 50. These characteristic proportions are sometimes spoken of as Mendelian ratios.

We may now pass on to consider the experimental evidence upon which the above conclusions are based.

(1) *Mendelian Monohybrids.*

These are heterozygotes formed by the union of gametes in which the allelomorphs of a single pair only are considered.

In Mendel's cases such heterozygotes exhibit only one of the pair of allelomorphic characters, and this is said to be *dominant*, the other allelomorph being *recessive*. A dominant allelomorph is thus one which is "so preponderant that it is difficult or quite impossible to detect the other in the hybrid"* (from its external appearance).

By self-fertilization of the hybrid generation F_1 is obtained F_2, the first generation bred from the hybrids. In F_2 the recessive character appears in one out of every four of the offspring, the remaining three still exhibiting the dominant character. In F_3 and in all subsequent generations these "extracted recessives" breed true, and the dominant character, so far as is known, never reappears among their self-fertilized offspring. The dominant forms of F_2 are proved on examination of F_3 to have been of two types. One out of every three of them (the extracted dominant) breeds true, and continues to do so in subsequent generations, whilst the two remaining dominants give in F_3 a mixed offspring consisting of dominants and recessives in the same proportion as before 3 : 1. And these on examination show the same constitution as in the previous generation.

We thus have, for the zygotes in each generation :—

P	(dominant character)	A	×	a	(recessive character)	
F_1		Aa				
		(heterozygote looking like A)				
F_2	AA	Aa		aA		aa
	(extracted dominant)	(heterozygotes, but looking like AA : on self-fertilization they each give)				(extracted recessive)
F_3	AA	AA	Aa	aA	aa	aa
		(extracted dominant)			(extracted recessive)	
F_4	AA	AA	and so on		aa	aa
	and so on	and so on			and so on	and so on
	breeding true	breeding true			breeding true	breeding true

* The term hybrid was used by Mendel to denote the offspring of cross-fertilization between members of different groups of plants, no matter whether the latter are described by systematists as species or varieties. De Vries points out (70) that this usage is historically correct.

F_2 may also be more concisely written A + 2 A a + a, avoiding an unnecessary repetition of letters. This expression is the formula for F_2 of a Mendelian monohybrid.

Example I.—Sutton's Telegraph Pea, with green or partly green cotyledons, rarely becoming dull yellow in weathered pods, was crossed with a small smooth-seeded native pea, having bright yellow cotyledons. From 17 successful pollinations 50 seeds were produced, the cotyledons of all of which were completely yellow. 41 of these seeds gave rise to plants which produced altogether 646 seeds (F_2), of which 488 had completely yellow cotyledons and 158 had green cotyledons, the majority being strong bright green, but a few showing slightly yellowish patches and thus resembling the parent form Telegraph. The yellow and green seeds were thus in the proportion 3·09 : 1.

A considerable number of these seeds were sown, but only 44 yellow and 11 green seeds produced plants. The latter gave rise to 295 seeds, 291 of them bright green or partly yellowish and 4 quite yellow, but paler than the offspring of yellow seeds. Pure bred Telegraph plants grown at the same time produced a similar lot of seeds as regards colour, but these included a somewhat larger proportion entirely dull yellow. This was probably due to their having been exposed in the pods rather longer.

Of the 44 plants derived from yellow seeds, 16 gave rise to yellow seeds only, viz., to 1,013 yellow seeds. 28 plants produced 1,152 seeds, both green and yellow, 877 being of the latter and 275 of the former colour or 3·19 : 1.

In a further generation a somewhat larger number of offspring was obtained, and the previous result again confirmed. The seeds of six plants (which had yielded both yellow and green seeds in F_3) were sown and gave rise to the following offspring :—

Forty-seven green seeds gave rise to plants which bore 1,325 green seeds only (F_4).

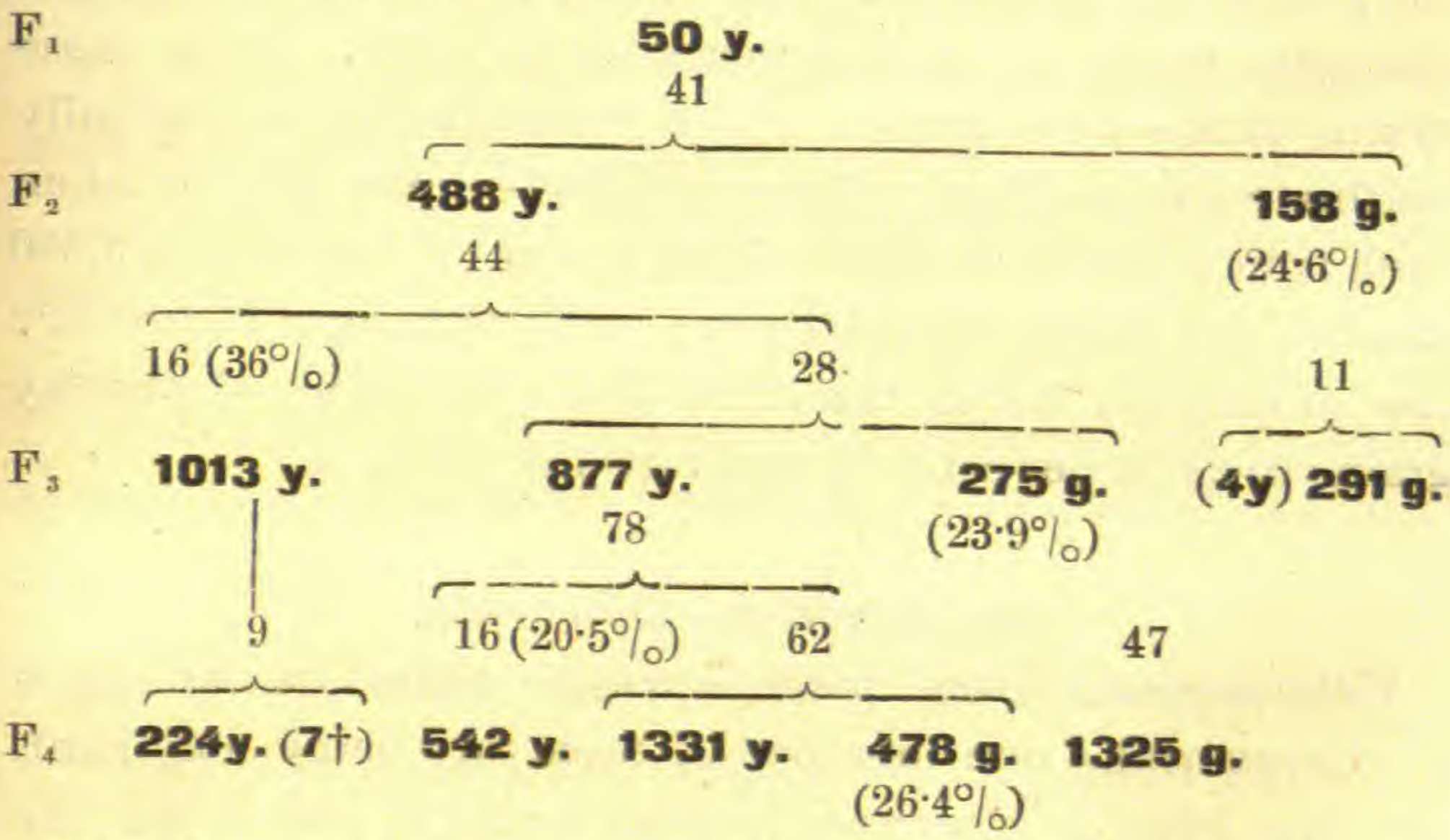
Sixteen plants from yellow seeds gave rise to 542 yellow seeds only.

Sixty-two plants from yellow seeds produced 1,809 seeds, of which 1,331 were yellow and 478 green, or 2·78 : 1. Each of these plants produced both green and yellow seeds.

A considerable number of seeds in this generation were damaged by insects or fungus. Every perfectly developed seed of the series was clearly recognizable as yellow or green without removal of the testa. Such seeds only were counted.

The proportion of heterozygotes to extracted dominants in F_3 — 62 : 16, or 3·9 : 1—deviates widely from Mendelian expectation (2 : 1). Such a difference illustrates well the necessity of growing a considerable number of plants for determinations of this kind.

The following table* gives a diagrammatic representation of the course of this experiment :—



The above case agrees in the closest way possible with one of Mendel's, who himself used a variety in which in the seeds of many plants "the green colour of the albumen

* This arrangement is used by Correns (11).

† Showed a slight tinge of green almost certainly due to imperfect ripening, the seeds appeared to be fully developed, but were not properly hard.

(cotyledons) was less developed and at first may easily be overlooked." The cause of the partial disappearance of the green coloration, as Mendel states, has no connection with the hybrid character of the plants, as it likewise occurs in the parental variety. These observations are fully borne out by the case of the pea Telegraph. They apply in an even more marked degree to the variety Telephone (Sutton's). The point is worth notice on account of Weldon's criticism (76) of Mendel's work, in which stress is laid upon the exceptional behaviour of Telephone.

Example II.—Larger figures were obtained in the case of a cross between two races of Indian corn (Zea Mais), "Black Mexican" and "Boone County White." The former is characterized by a sugar endosperm and wrinkled grain, and the latter by a starchy endosperm and indented grain. The sugar corn was used as the pollen parent, and the form of the grains (F_1) on the indent parent was unchanged, the sugar character being completely recessive as xenia. From these grains plants were grown, which were allowed to mutually pollinate one another. There resulted—upon 18 cobs taken each from a separate plant—7,075 grains (F_2), of which 5,310 showed the starch character and 1,765 the sugar character: the proportion being therefore 75·06 per cent. of starchy grains to 24·94 per cent. of sugar grains, or 3 : 1.

(2) *Mendelian Dihybrids.*

Heterozygotes from parents which differ in two pairs of allelomorphs, one member of each pair being dominant. For the sake of clearness we may write A and a for the allelomorphs of one pair, B and b for those of the other. (The parents show, *e.g.*, AB and ab respectively.) A and B are dominant, a and b recessive; F_1 the cross-bred generation exhibits AB to the exclusion of ab, but in reality includes AaBb.

In F_2 the visible combinations AB, Ab, aB, ab, appear in the proportion :—9 : 3 : 3 : 1.

(We have here, be it noted, two entirely new combinations of characters, viz., Ab and aB, not seen in the parent forms).

On examining a further generation F_3 the offspring of the 9 AB plants of F_2 are found on the average to be as follows :—

The offspring of 4 plants include 9AB, 3Ab, 3aB, 1ab.
" 2 " 3AB, 1Ab.
" 2 " 3AB, 1aB.
" 1 " AB exclusively.

The 3Ab plants (F_2) produce the following offspring :—

The offspring of 2 such plants include 3Ab and 1ab.
" 1 " Ab only.

The 3aB plants produce the following offspring :—

The offspring of 2 plants include 3aB, and 1ab.
" 1 " aB only.

And, finally, the ab plants produce nothing but ab.

The sixteen plants of F_2 are thus shown by their offspring to be of the following kinds :—

One each of the pure forms : AB, Ab, aB, and ab, which breed true.

Four heterozygotes in respect of both pairs of characters ; these give in F_3 the same series as the original heterozygotes of F_1 (AaBb) gave in F_2 ; they are, therefore, of the same form—4 AaBb.

Also the following four sets of two plants each : —

2AB giving AB and Ab ; these we may write 2ABb.
2AB " AB " aB ; " " " 2AaB.
2Ab " Ab " ab ; " " " 2Aab.
2aB " aB " ab ; " " " 2aBb.

Altogether, therefore, AB+Ab+aB+ab+2ABb+2aBb+2AaB+2Aab+4AaBb, which is the result of combining the formulæ — (A + 2Aa + a), (B + 2Bb + b) each of them characteristic of F_2 of a monohybrid. The relation of the

sixteen terms may also be shown by the following arrangement:—

$$\left.\begin{matrix}4\ A\\8\ Aa\\4\ a\end{matrix}\right\}\text{combined with}\left\{\begin{matrix}1\ B+2\ Bb+1\ b.\\2\ B+4\ Bb+2\ b.\\1\ B+2\ Bb+1\ b.\end{matrix}\right.$$

or

$$AB+2ABb+Ab.$$
$$2AaB+4AaBb+2Aab.$$
$$aB+2aBb+ab.$$

We see that each pair of allelomorphs behaves independently of the other and follows the same rule as that for monohybrids.*

Example III.a.—Sutton's Telephone Pea, cotyledons usually much wrinkled and showing various tints of green which tend to become partly or wholly yellow in weathered pods,† was crossed with pollen from Ringleader, a smooth-yellow-seeded variety. Twelve pods were obtained containing 42 seeds all completely yellow and smooth or very slightly dimpled in form. From these seeds were obtained 33 plants, which fruited, giving rise to 428 seeds, of which—

224 were yellow and smooth or slightly dimpled ;
87 were green and smooth or slightly dimpled ;
81 were yellow and irregularly wrinkled ;
26 were green and irregularly wrinkled ;

or in the proportion 9 : 3·5 : 3·25 : 1·04.

From the reciprocal cross—Ringleader × Telephone—only 4 smooth yellow seeds were obtained in two pods. Three plants arising from these yielded in F_3 smooth yellow 22, smooth green 8, wrinkled yellow 6, wrinkled green 0.

Example III.b.—Sutton's Telephone was crossed by pollen from the ordinary native Pea grown in Ceylon, having smooth nearly spherical seeds and bright yellow cotyledons. Eleven of the pods resulting from the cross contained only yellow, nearly smooth seeds, 25 in number ; but one such

* No account of gametes is taken in the above description, which deals simply with zygotes (plants).

† As far as my experience goes some tinge of green can always be detected in seeds gathered immediately they are ripe.

pod produced two fully green seeds with smooth surfaces. One of these seeds germinated and produced a plant which bore only eight seeds, all of which were green ; five of these were smooth, one wrinkled, and two small and irregular. In F_3 only one of the smooth seeds germinated, and the plant yielded 50 seeds, all nearly smooth and green. This case is plainly exceptional, and agrees with similar exceptions seen by Tschermak (58), whose explanation—an unexpected false hybridism in respect of yellow—may hold in this case as well ; but the evidence is meagre.

Of the 25 yellow seeds of F_1, 20 produced plants bearing 205 seeds :—sm. y. 109, sm. g. 43, wr. y. 40, wr. g. 13, or in the proportion 9 : 3·55 : 3·3 : 1·07.

The reciprocal cross yielded in F_1, 20 seeds all smooth and yellow. 14 plants in F_2 produced :—sm. y. 110, sm. g. 44, wr. y. 28, wr. g. 14.

The offspring of yellow seeds in all four cases (*III.a* and *III.b.*) were therefore as follows in F_2:—sm. y. 465, sm. g. 182, wr. y. 155, wr. g. 53 ; the proportion being 9 : 3·52 : 3 : 1·02.

The excess of smooth green seeds over theoretical expectation is distinct in every case, but considering the small total number of plants examined this is possibly fortuitous.

In counting the seeds for the above estimations, green and yellow seeds were almost always clearly distinguishable, the colour of the cotyledons being recognizable through the semi-transparent testa. There was, however, sometimes a slight doubt in the discrimination of smooth and wrinkled seeds, both of which categories show considerable variation in external form.* But a further generation showed that the amount of actual error was not very great. Thus 4 seeds out of 174 appeared to have been wrongly sampled in this respect.

Taking all four cases together, and writing A = smooth, a = wrinkled, B = yellow, and b = green, the result shown in the following table was obtained in F_3, self-fertilization being allowed to take place.

* Gregory (39) has shown that in such cases there is still a very clear distinction between the starch grains of the two types.

Parents F_2.		Constitution as shown by Offspring in F_3.									
No.	Form		AaBb	AaB	Aab	ABb	aBb	AB	Ab	aB	ab
95	AB	expected ...	42	21	—	21	—	10·5	—	—	—
		found ...	43	18	1	19	—	13	—	1	—
33	Ab	expected ...	—	—	22	—	—	—	11	—	—
		found ...	1	—	24	—	—	—	8	—	—
36	aB	expected ...	—	—	—	—	24	—	—	12	—
		found ...	1	1	—	—	24	—	—	9	1
10	ab	expected ...	—	—	—	—	—	—	—	—	10
		found ...	—	—	—	—	—	—	1	—	9
(176)	Total ...	expected ...	44	22	22	22	22	11	11	11	11
174		found ...	45	19	24	19	24	13	9	10	10

It will be seen that there are seven cases, either of unconformability or of error, viz.:—

	A seed sown as		gave rise to		where the expectation was	
1.		sm. y.		sm. and wr. green		yellow
2.		sm. y.		wr. y. only		smooth
3.		sm. g.		all four types		green only
4.		wr. y.		do.		wrinkled only
5.		wr. y.		sm. and wr. green		wr. y. (and g.)
6.		wr. y.		wr. green		yellow
7.		wr. g.		sm. green		wrinkled only

In cases 2, 4, 5, and 7 the most likely supposition is that round and wrinkled were not truly distinguished in sampling, whilst in cases 1, 5, and 6 we may suppose that a truly green seed had turned yellow on exposure after the manner of the Telephone parent.*

Case 3 remains, and in this single case I am disposed to think that a mistake was made in taking up the plant, and that this was really the offspring of a yellow seed.

(3) *Tri-Polyhybrids.*

Other pairs of characters in peas are found to behave in the same way. Mendel worked with seven pairs, viz.:—

(1) The shape of the ripe seed, whether smooth; or angular and wrinkled.

(2) The colour of the seed albumen (cotyledons), whether yellow; or of a more or less intense green tint.

(3) Coloured testa, flowers and leaf axils; allelomorphic as a group to white in all three cases.

(4) Pods, whether simply inflated; or soft and constricted between the seeds, the parchment layer being undeveloped in the latter case.

(5) Colour of unripe pods, whether green; or yellow.

(6) Position of flowers, whether axial; or terminal.

(7) Length of axis, whether tall; or short.

Examples of cases 1 and 2 have already been described. I have also been able to examine cases 3, 4, and 7, and obtained results agreeing closely with those of Mendel and other observers. Mendel found all possible combinations of the

* In the case of crosses with other varieties, in which the green colour of the cotyledons is more constant, this form of irregularity is not obtained.

seven pairs of characters according to the formula (A + 2Aa + a) (B + 2 Bb + b) (C + 2 Cc + c) &c.

In the case of the parchment layer of the pod, I found the heterozygotes from a cross between Sutton's French Sugar Pea and my native yellow variety to show a slight approach to the recessive character, the stiff parchment layer being to some extent wanting from certain areas of the pod. The appearance, however, was much nearer to that of the dominant, and from a little distance such pods appeared fully inflated.

(4) *The Theory of Purity of the Gametes.*

Mendel's explanation of his facts with regard to peas is as follows :—He supposes the pollen grains and ovules, or, as we should now say, the germ cells of the hybrid plants (heterozygotes), to contain each of them only one member of every pair of allelomorphs, and that with this limitation all possible combinations of the various allelomorphs occur in the gametes in equal numbers. Then, if the male and female gametes meet simply according to the laws of chance, we shall obtain the observed proportion of offspring showing the various characters. This supposition explains the facts, and no other hypothesis has so far been advanced which does so. This is the essential part of Mendel's discovery, and it is to this principle that the term "Mendel's Law" was applied by Correns in 1900.

Thus in the case of a monohybrid, A × a, the heterozygote Aa (F_1) produces gametes A and a. These combine in all possible ways, AA, Aa, aA, aa, with the result AA + 2Aa + aa, or A + 2Aa + a.

In the case of a dihybrid, ABab, the gametes AB, Ab, aB, and ab, arise in F_1. And these form the combinations ABAB + AbAb + aBaB + abab + 2ABAb + 2ABaB + 2ABab + 2AbaB + 2Abab + 2aBab, or (omitting duplications) AB + Ab + aB + ab + 2AaB + 2AbB + 2Aab + 2aBb + 4AaBb = (A + 2Aa × a) (B + 2Bb + b), and so on for more complicated cases.

We can test the proportions of the different forms of gametes produced by a heterozygote by crossing it—as Mendel did—by a pure recessive. Thus Aa (gametes A and a) crossed by a will give Aa+aa, appearing under the forms A and a in equal numbers, if the theory is correct.

Example IV.—A number of white grains of Flint corn (Zea Mays)—of doubtful ancestry as regards colour characters—were sown near similar yellow and blue grains, and produced plants which yielded (F_1) some 90 per cent. of white grains and 10 per cent. or less of scattered blue and yellow grains. The latter are doubtless cases of xenia due to cross pollination from the surrounding plants.

A number of these yellow grains were sown in a plot in which pollination was effected by plants produced from the white grains of the same cobs. The latter proved to be true extracted recessives, since considerably less than 1 per 1,000 of the whole number of grains produced by them (F_2) were yellow or blue, and these are to be accounted for by the escape of pollen from the cross-bred plants grown in the same plot. The tassels were carefully removed from all the plants on this plot (other than the white-grained recessives) previous to the opening of the male flowers, but a little pollen appears to have escaped from one or two plants; not enough, however, to have had any appreciable effect upon the numbers here considered. Nine plants, offspring of yellow grains, produced the following (F_2) :—

Plant.	1	2	3	4	5	6	7	8	9	Total.
White grains ...	202	223	256	222	280	222	211	173	193	1,982
Yellow grains ...	286	217	216	201	244	207	249	166	177	1,963
Blue grains ...	—	—	1	—	—	—	6	3	—	10

The blue grains are to be regarded as the result of accidental xenia. Taking all the plants together the result is 50·1 per cent. of white and 49·7 per cent. of yellow, out of a total of nearly 4,000 grains.

The accuracy of the sampling can be tested by growing another generation (F_3) and again pollinating by the recessive. The yellow grains should all be heterozygotes and again produce 50 per cent. of yellow grains and 50 per cent. of white, whilst white grains should produce nothing but white. 78 white and 126 yellow grains were sown. These were taken from the finest cob, No. 5, which had yielded 46·6 per cent. of yellow grains. The recessive form used in this case was a white Dent variety—"Boone County White."

From the white grains 59 plants produced fruit, and 44 of them produced exclusively white grains (F_3). The remaining 15 cobs showed white grains with the following exceptions :—

1 cob showed	2 blue grains	
6 cobs had each	1 yellow grain ...	... 6
6 „ „	2 yellow grains...	... 12
1 „ „	3 „ „ ...	... 3
1 „ „	6 „ „ ...	... 6
	Total ...	27

All the plants upon which these yellow grains appeared grew close together near one end of a row, and it seems clear that some "yellow" pollen had escaped from a plant in the next row but one. The purity of the extracted recessives is therefore fully established.

Of the offspring of yellow grains of the same generation (F_2) one cob was gathered from each of 96 plants. One of these cobs showed 32 blue grains, in addition to 253 yellow and 205 white grains ; and the first mentioned are doubtless the result of a previous accidental cross by blue. The remaining 95 cobs showed, without exception, yellow and white grains only (F_3) in the proportion approximately of

50: 50 in each cob. The actual percentages were as follows:—

Percentage of Yellow Grains.		Plants.	Percentage of Yellow Grains.		Plants.
43	...	1	50	...	20
44	...	1	51	...	12
45	...	3	52	...	9
46	...	3	53	...	9
47	...	5	54	...	6
48	...	11	55	...	—
49	...	14	56	...	1

The curve resulting from these figures is somewhat irregular, owing to the small number of cobs examined. Nevertheless it shows some resemblance to a normal curve of variability. By Galton's method its probable error is approximately 1·6. The question arises whether this amount of probable error depends on anything besides the size of the samples taken, viz., the number of grains in the cobs; a number which varied from 271 to 862, the average being 560. Now according to figures quoted by de Vries (70) from Rodewald, the probable error of a number of random samples taken from a mixture of two things in equal numbers is:—

1·69 when the samples include 400 individuals each
1·52 „ „ 500 „
1·38 „ „ 600 „

For samples of 560, therefore, the probable error is about 1·43, but in the present case the samples are not all equal; and as the smaller samples give rise to a proportionately greater error, the theoretical value cannot be very far from 1·6, which is the value got by experiment in the present case. The statement therefore appears justified that the difference from exact equality of yellow and white grains observed in any particular cob depends simply upon the size of the sample which such a cob represents, or in other words is strictly a matter of chance. For the case, therefore, of the female germ cells of a particular variety of maize, it is shown that there is a segregation of the allelomorphic characters yellow and white in equal numbers; the result of

the experiment being thus in the closest agreement with Mendel's chief deduction from his experiments with peas.

Example V.—The blue colour of the aleurone layer, appearing in certain strains of Indian corn, seemed at first sight to afford an exception to the law of segregation of allelomorphs in equal numbers.* This blue colour appeared in certain members of the above strain of flint corn in varying degrees of intensity. The present experiment was made with blue xenia grains appearing in the same way as the original yellow grains used in Example IV. A number of these blue grains were sown upon the same plot as the yellow grains in question, and pollination was, therefore, effected from the same extracted recessives, viz., white flint. Twelve resulting cobs showed the following proportion of blue and non-blue (W) grains :—

No.	B.	W.	Total.	Per Cent. B.
1	156	244	400	39
2	118	311	429	27·5
3	108	302	410	26·4
4	143	440	583	24·6
5	74	234	308	24
6	78	256	334	23·4
7	88	293	381	23·1
8	125	425	550	22·7
9	86	308	394	21·8
10	73	262	335	21·8
11	87	356	443	19·7
12	70	286	356	19·6

Altogether 3,717 white grains and 1,206 blue, or 24·5 per cent. of the latter. It appears, therefore, that if "blue"† were fully dominant, the gametes of the heterozygote must have been formed in the proportion 3 white to 1 blue, instead of in equal numbers. If, on the other hand, there is really segregation of the characters in equal numbers in the gametes, some of the white grains must be heterozygotes, since these must then make up half the total number of grains, and in

Cf. also Correns (15).

† *I.e.*, the appearance of a visible blue colour of any intensity.

this case there must be failure of dominance of blue in the case of some 50 per cent. of the heterozygotes.

The point can be tested by sowing the white grains and once more pollinating by the recessive, *i.e.*, white. Blue and white grains from cob No. 5, which contained 76 per cent. of white grains, were sown separately, and pollination was effected by a white dent form.

If Mendel's Law of segregation of allelomorphs in equal numbers holds good, the expectation is that 50 out of 76 of the white grains will prove themselves to be pure white homozygotes, whilst the remaining 26 will be heterozygotes; and we may expect the blue colour to appear among the offspring of the latter.

The actual offspring of the white grains was as follows (a single cob being gathered from each plant) :—

23 cobs with white grains exclusively.

4 cobs with from one to four blue grains and the remainder white.

10 cobs with from 1·7 to 25·7 per cent. of blue grains, *i.e.*, 12 or more in each cob.

Assuming that the four cobs with from 1 to 4 blue grains are cases of accidental xenia (as is perhaps most probable, since 1 to 6 blue grains appeared upon some 10 per cent. of the white dent cobs in the next row), we get 73 per cent., or 55·5 out of 76 as the proportion of white grains which were homozygotes in the previous generation, the expectation being 50 out of 76. The remaining grains were heterozygotes which showed the white character. In view of the small number of plants examined the result is in reasonably close agreement with Mendelian expectation.

The offspring of blue grains pollinated by the recessive showed a similar proportion of blue grains to that in the previous generation. Altogether 4,034 blue and 10,300 white grains were counted, or 28·1 per cent. of the former. We must suppose that exactly the same phenomenon is here repeated.

(5) *Mendel's Paper on Hieracium.*

Mendel himself showed in a later paper (translation Bateson (2)) that the results which he obtained in the case of seven pairs of characters in peas are not universally applicable. As the result of experiments in crossing different forms of the genus Hieracium he came to the following conclusions:—

The characters of the hybrids were, as a rule, more or less intermediate between those of their parents, although in some cases there was partial dominance. Hybrids arising from the same cross were not always identical in appearance. In further generations, which resulted from self-fertilized hybrids, the pure parental characters did not appear, but the offspring agreed in appearance both with each other and with the hybrid plant from which they were derived.

In cases such as this it seems clear that the simple form of Mendel's Law is not followed.

II.—RECENT CONFIRMATORY OBSERVATIONS AND CRITICISMS.

There has already been occasion to allude to the simultaneous confirmation of Mendel's observations afforded in 1900 by the publication of the work of de Vries, Correns, and Tschermak. Among other observations in the same direction may be mentioned those of Spillman (41) with wheat, Hurst with orchids (40), and Emerson (34) with kidney beans. Biffen (8) has confirmed many of Spillman's results, and his discovery that in the case of wheat susceptibility to, and immunity from, disease behave as allelomorphic characters and obey Mendel's Law, the former being dominant, is of special interest from a practical point of view.

Miss Saunders (6) found a Mendelian behaviour in Lychnis, Atropa, Datura, and in a considerable number of cases in crosses between hairy and glabrous races of Matthiola, but in some of the latter certain exceptional or

more complicated phenomena were observed. And the same was the case in the poultry crosses studied by Bateson (6).

Mendelian ratios have been observed in the case of certain crosses between different races of mice by Cuénot (24) and Darbishire (27). Here again phenomena other than those seen by Mendel in peas appear in certain instances to complicate the result. Bateson (5) has summed up the information existing as regards colour-heredity in mice and rats, and has shown that Mendel's theory throws abundant light upon the earlier results of Crampe and von Guiata. The more recent results of Cuénot are discussed below.

De Vries in his earlier papers (*e.g.*, 67), was disposed to assert an almost universal scope for Mendel's Law and also for the law of dominance, except in cases of what he calls "false hybridism," a term which de Vries used in a wider sense than Millardet. But Correns (15) and Tschermak (59) have found exceptions to both laws in the inter-race hybrids which they have studied. These two authors have shown, however, that the law of segregation of characters in the gametes in equal numbers has a very wide scope.

Tschermak (59) finds no part of Mendel's discovery to apply universally even to peas. Some of this writer's earlier criticisms have, however, since been explained away, especially those which had reference to the phenomenon of segregation of characters. Tschermak found blending instead of dominance in the case of a considerable number of pairs of characters, including some of those for which Mendel described a regular occurrence of dominance in his own experiments. But he found blending to be more common in vegetative than in cotyledon characters.

Weldon (76) has criticized Mendel's original work. He cited a number of exceptions to dominance, but failed to notice sufficiently the importance of Mendel's Law; and Mendel's own demonstration of this principle by re-crossing with the recessive form.

Weldon found that the figures obtained by Mendel in his experiments were such as might fully be expected if the theoretical explanation which that author gave to them is correct. Weldon was able to select from a sample of the pea Telephone (Carter's) seeds which exhibited a complete range of colour from green to yellow, and of shape from wrinkled to smooth, and he states that if Mendel had used this pea his experiments would have failed. But Mendel himself particularly noted the difficulty as regards colour, and evidently did use a pea which behaved nearly like Telephone in this respect. I have repeated some of Mendel's experiments using Telephone* as the wrinkled green parent, and obtained a result closely in accordance with Mendel's own. Gregory (39) has shown, moreover, that in cases where a "round" and a "wrinkled" pea are difficult to distinguish by the external appearance, a glance at the starch grains as seen in a section of the cotyledon enables one to place the seed in its proper group at once.

Bateson (2) in defence of Mendel pointed out that the phenomenon of dominance is of quite subsidiary importance to that of the segregation of characters in the gametes. He showed that exceptions to dominance may occur in the categories which Mendel used, but that they have not been observed in a large enough number of cases to affect the main result. Various explanations may be offered of such exceptions, and they still need further study. Very many of them are doubtless simply due to error. Bateson pointed out the clear agreement with Mendel's theory of several independent observations cited by Weldon as exceptional.

Yule (79) has pointed out that the law of ancestral heredity (in a wide sense as he himself defines it) will hold good for the dominant character in a population breeding at random and following Mendel's Law for the particular pair

* From Sutton; but showing the same phenomenon. My original sample, now three years old, includes a large majority of fully yellow seeds, though at first these were less than 1 per cent. The change is largely, if not entirely, determined by the action of light.

of characters concerned. On the other hand, two parents showing the recessive character can produce nothing but recessive offspring in the simple Mendelian case.

Pearson (54) has worked out more completely a "generalized theory of the pure gamete" in cases where dominance is wanting, and an indefinite number of pairs of allelomorphs are concerned.* On this theory Pearson finds a value of one-third for parental correlation (in the case of bi-sexual reproduction without preferential mating), a value identical with that obtained by Galton in his original investigations upon the inheritance of stature (37).

Pearson finds that the statements: firstly, that the average value of parental correlation deduced from recent biometric observations upon all kinds of material appears to be from ·45 to ·5; secondly, that this correlation appears to vary slightly from character to character; and thirdly, from species to species, are inconsistent with the theory of the pure gamete; which throws the "Mendelian" back into the position of the biometrician of 1885.†

We have seen, however, that in certain cases the simple form of Mendel's theory has been proved to hold good, a fact of which Pearson takes no notice. On the other hand, not even a "Mendelian" supposed, even in 1900, that Mendel's Law held good for all characters in all species. But Pearson ignores the whole mass of non-biometric work of the last four years with its examples of irregular dominance and latency of characters. These factors, as well as the effect of conditions upon post-germinal development, are entirely indeterminate in the cases for which biometrical determinations of parental correlation have been made. It seems

* Presumably in determining a single measurable external characteristic, since otherwise the results would not be comparable with those for stature.

† Pearson here seems to overlook the fact that he himself, no longer ago than 1900, found theoretical reasons for using the value ·3 to represent the intensity of parental correlation; a figure still further removed from the "cluster point of existing measurements" than the value $\frac{1}{3}$. (See Grammar of Science, Ed. II., p. 459).

likely that these factors, to say nothing of possible cases of false hybridism and other non-Mendelian phenomena, would have some effect upon the values of parental correlation. Moreover the value ·45 — ·5 is arrived at from the average of a number of cases which show a very much wider range.

It seems, therefore, unjustifiable to apply the average result of biometric computations as a criterion for testing experimental observations upon the behaviour of the gametic representatives of definite characters in definite cases.

On the other hand, if the applicability of Mendel's Law continues to be extended in future at the same rate as it has been during the past few years, it may become necessary to examine whether definite reasons cannot be discovered to account for the wide deviation in certain cases of the observed value of parental correlation from the value ·33.

On the whole, it seems clear that in the law of ancestral heredity we have a foreshadowing of the more precise and definite law of Mendel.

III.—THE SHAPE AND COLOUR OF THE SEEDS OF PEAS.

In recent years a considerable number of "exceptions to Mendel's Law" have been cited with respect to these characters. One such exception, indeed, was known to Mendel himself, namely, the existence of a correlation between a coloured testa, coloured flowers, and purple spots in the axils of the leaves. In Mendel's experiments none of these characters ever made its appearance, except in association with the other two. In such a case as this we may suppose with Correns (15) that the different external manifestations depend, in part, upon a single internal "Anlage." On the other hand, Tschermak has described races in which certain of these characters appear without the others (63).

Correns himself was the first (11) to note an exceptional case, in which the colour of the testa behaves in a different manner from that which Mendel described. In his cross

between "grüne späte Erfurter Folgererbse" with a colourless testa and "purpur-violettschotigen Kneifel-erbse" with an orange-red to brown testa, Correns found, in the first generation and often in the same pod, seeds with an almost colourless testa and seeds with a fully orange-red testa. Violet spots also made their appearance.

The appearance of violet spots upon the testa in this way has also been noticed by Tschermak (59); but the former observation has not been confirmed and may rest upon a misunderstanding. Bateson (2) has pointed out that the result may have been due to conditions; and I have myself found the testa of Sutton's French sugar pea to change from gray to orange-brown upon exposure, so that these colours cannot be distinguished as separate plant characters.

With regard to seed shape Tschermak (61) obtained some remarkable results in the case of crosses between Pisum arvense (red flowers) and P. sativum (white flowers). In the first example described the former had "slightly wrinkled" seeds, which may conveniently be called "dimpled," the latter had smooth seeds. No change was produced in the shape of the seeds as the direct result of crossing; smooth "female" crossed by dimpled "male" and dimpled "female" crossed by smooth "male" gave rise in each case to seeds identical in appearance with those of the maternal variety. The resulting plants (F_1) had all of them coloured flowers, and produced exclusively dimpled seeds with a coloured testa. Thus coloured flowers, coloured testa, and dimpled seeds were always associated; and Tschermak regards this as indicating a correlation between a vegetative character and a sexual one, namely, between coloured flowers and testa on the one hand, and the character of the ovum from which dimpled cotyledons arose on the other. And upon this conception he bases important theoretical conclusions.

But there is another possible explanation. Correns has found in many cases that the shape of the grains of Zea Mays depends solely upon that of the pericarp, by which

the form of the endosperm is passively moulded. It appears possible, therefore, as Correns points out, that in the present case the dimpled form of the cotyledons may be impressed upon them by the testa.

There are indeed certain difficulties in the way of accepting this view. The endosperm of a grain of maize is quite fluid at a time when the external form of the grain is already clearly distinguishable, but the same is by no means true of the cotyledons of a pea. Tschermak cites as a further difficulty the appearance of dimpled seeds upon plants of the first generation from a cross between a race of Pisum arvense having smooth seeds and a smooth-seeded race of P. sativum ; an example of the appearance of a new (or atavistic) character on crossing. But it does not appear that this observation has any very direct bearing upon the point at issue.

Gregory (39) has shown that the starch grains of the cotyledons of a dimpled pea resemble those of a smooth pea, and differ widely from the smaller starch grains of a truly wrinkled variety ; and this renders it likely that the shape of a wrinkled pea may depend on something other than the cotyledons, *i.e.* upon the testa. On the whole, therefore, the view of Correns appears to be the more probable.

The following example illustrates several interesting points with regard to seed characters. In speaking of these it is very necessary to bear in mind that a seed includes portions contributed from two separate generations. Thus in seeds born on a first cross plant (F_1) the testa belongs to the maternal generation, but the cotyledons to the next generation (F_2). So that on the hypothesis here adopted the shape of a dimpled seed is a character belonging to one generation, whilst that of a wrinkled seed belongs to another.

Example VI.—Sutton's French Sugar pea ("male" parent) was used to pollinate a native pea with smooth yellow seeds. The former plant had coloured flowers with a red standard and purple wings ; and there were purple spots in the axils of the leaves. The testa in freshly ripe seeds was almost always

of a greenish-grey colour, more or less flecked with purple spots; the grey colour showed, however, a tendency to become first orange and then brown on exposure. The seeds were strongly dimpled (starch grains of the round type); they were large and of a characteristic somewhat flattened form. The pods were very wide, and were constricted between the seeds, the parchment layer being undeveloped.

The "female" parent had smooth spherical seeds, with a nearly transparent testa. The flowers were white and the axils green; the pods were inflated and small (narrow).

The seeds immediately resulting from the cross were indistinguishable from the ordinary spherical seeds of the native pea. The cross-bred plants (F_1) had coloured flowers and axils, and the testas were coloured like those of the "male" parent. The seeds were intermediate in size and some were of a somewhat square shape, unlike that of either parent, whilst others showed a nearer approach to the flattened form of French sugar seeds. All were distinctly indented. The pods were inflated, but showed some signs of a reduced development of the parchment layer, especially towards the base (inflated pod almost completely dominant). The width of the pods was intermediate between those of the two parents.

In (F_2) the following groups of plants were to be distinguished :—

(*a*) Pods inflated; seeds indented; testa grey, with purple spots	39
(*b*) Pods inflated; seeds indented; testa grey, without purple spots	11
(*c*) Pods inflated; seeds smooth or nearly; testa colourless	12
(*d*) Pods soft; seeds indented; testa grey, with purple spots	11
(*e*) Pods soft; seeds indented; testa grey, without purple spots	5
(*f*) Pods soft; seeds smooth or nearly; testa colourless	8

The ratio between the number of plants with inflated pods and the number of plants with soft pods, was thus 62 : 24 or 2·6 : 1.

The plants with smooth colourless testa had white flowers and no pigmentation in the axils. All the other plants showed the red-purple colour in these two regions. The ratio between plants with coloured flowers and those with white was 66 : 20 or 3·3 : 1.

The plants with coloured flowers fell into two groups according to the colour of the testa. In both groups the grey colour was nearly the same, but one group showed in addition a flecking of well-marked purple spots, seen best in unripe seeds; in the other group these spots were absent or only represented by a few very faint blueish dots. Among the plants having coloured flowers the ratio between those with purple spots on the testa and those without was 50 : 16 or 3·1 : 1.

It appeared further that flattened seeds of the type characteristic of "French sugar" were associated with wide pods and cubical or spherical seeds with narrow pods; but the shape of the seeds and width of the pods varied so much in F_2 that this relation was difficult to ascertain exactly. It was quite clear that the dimpled character was associated with a coloured testa, whilst smooth seeds had always colourless testas. Coloured seeds with purple spots contained in distinctly wide pods in which a parchment layer was absent, exactly resembled the typical seeds of French sugar; whilst white-coated seeds in narrow pods closely resemble the normal seeds of the native yellow pea, but were usually larger. Certain examples of both these forms came true to seed in F_3. Nutrition also clearly plays a part in determining the shape of these seeds: starved seeds are usually smaller, flatter, and more dimpled than those upon strong and well-nourished plants.

The above will serve to give an idea of the large number of factors upon which the shape of a pea seed can be shown to depend, apart from the cotyledon characters of strict wrinkling or smoothness. To return to the question of colour. It has been shown that the ratio of total coloured

seeds to white approaches 3 : 1 ; and further that among the coloured seeds the ratio of those with purple spots to those without also approaches 3 : 1. The total proportion, therefore, would appear to be 9 : 3 : 4. (A ratio also found by Tschermak (63) to exist in several similar cases.)

At first sight this does not appear to be a Mendelian ratio, but written beneath the proportion for a Mendelian di-hybrid case the agreement is clear; thus :

9 : 3 : 3 : 1
9 : 3 : 4

Now suppose the French sugar pea to include two allelomorphs : A giving a testa coloured greenish-grey like the common field pea ; and B giving purple spots when A is present, *but ineffective when* A *is absent.* For the white-coated pea we may write ab (absence of the greenish-grey colour and of purple spots).

AB × ab gives—

F_1 ABab

(Gametes : AB ; Ab ; aB ; ab.)

F_2 AB + 2ABa + 2ABb + 4ABab + Ab + 2Aab + Ba + 2Bab + ab

This obviously gives the required proportion. In F_3 we should expect to find—

1 constant purple	AB
2 purples giving purple and field-coloured	2ABb
2 purples giving purple and white ...	ABa
4 purples giving purple, white and field-coloured	4ABab
1 constant field coloured ...	Ab
2 field-coloured giving f. coloured and white	2Aab
4 constant white ...	...Ba + 2Bab + ab

Twenty to forty seeds were sown from each of the following F_2 plants :—

29 with purple-spotted testas ...	(p)
8 with field-coloured testas ..	(f)
7 with colourless testas ...	(w)

All the offspring of (w) plants produced white flowers only. Of the offspring of (p) plants, eight families produced coloured flowers only, and twenty-one families included plants with white and plants with coloured flowers. Among the offspring of (f) plants four families produced coloured flowers only, four families included both types.

The seeds of the offspring of the above (F_2) plants were also examined, namely, those of 803 (F_3) plants in all.

(*a*) Offspring of (p) plants :—

The offspring of 15 plants included 165 (p), 55 (f), 71 (w).
" 5 " 77 (p), 26 (f).
" 6 " 88 (p), 26 (w).
" 3 " 55 (p) only.

(*b*) Offspring of (f) plants :—

The offspring of 4 plants included 66 (f), 19 (w).
" 4 " 56 (f) only.

(*c*) Offspring of (w) plants :—

The offspring of 7 plants included (w) only, altogether 99 plants.

These figures will be seen to be in very close agreement with the theoretical explanation already given.

Of the above 44 (F_2) plants, 33 had inflated pods and 11 had constricted pods. The offspring of the latter in F_3 included 179 plants all with constricted pods.

Of the offspring of (F_2) plants with inflated pods twenty families included plants of both forms, namely, 295 plants with inflated and 77 with constricted pods; or 3·9 : 1, Thirteen families included plants with inflated pods only, viz , 252 such plants.

The difference of the ratio 3·9 : 1, from that of 3 : 1, considerably exceeds the probable error for a sample of 372 individuals. A considerable number of plants in this generation ripened no pods at all owing to the bad weather, and it seems reasonable to suppose that the soft pods were

more affected in this way than those which were protected by a stiff parchment layer.

Example VII.—Native pea No. 2 crossed with "Sutton's Satisfaction." The former has coloured flowers and axils and very small smooth seeds. The testa has a greenish grey colour with fine purple dots, and in addition a marbling or mottling of fairly extensive brown patches, like those exhibited by the English variety "Maple." Satisfaction has white flowers, nearly colourless testa and large wrinkled seeds. Satisfaction was used both as the "male" and as the "female" parent. In the former case there was no change in the appearance of the seeds borne upon the native pea. In the latter nearly smooth seeds were obtained, which in other respects resembled those of Satisfaction.

F_1 from both crosses showed red flowers and axils, and seeds coloured like the native pea, but these were slightly wrinkled (dimpled).

Let us work out the expectation for colour of testa in F_2 on the analogy of the previous Example (*VI*).

Let A represent the coloured (greenish) testa, B the purple spotting, C the "maple" marking.* For the colourless testa write abc.

F_1—ABCabc produces the gametes ABC, ABc, AbC, Abc, aBC, aBc, abC, abc. If we expand the expression (A+2Aa+a) (B+2Bb+b) (C+2Cc+c), and follow the supposition that both B and C can only appear when A is present, we shall expect in F_2:—

27 plants with maple, spotted, coloured testa ... (m.p.f.)
9 plants with purple spots but no maple marks (p.f.)
9 plants with maple marks but no purple spots (m.f.)
3 plants with plain-coloured testa ... (f.)
16 plants with colourless testa ... ... (w.)

* These three colours are situated in three separate parts of the testa and are apparently quite distinct in nature.

Only 25 plants were raised in F_2, viz., 11 (m.p.f.), 6 (p.f.), (m.f.), 2 (f.), 4 (w).

But in F_3 3 plants from seeds showing (m.p.f.) in F_2 had the following offspring :—

No. 2	...	18	(m.p.f.)	...	3	(m.f.)	...	8	(p.f.)	...	1	(f.)	...	14 (w.)
No. 7	...	48	„	...	8	„	...	7	„	...	5	„	...	20 „
No. 8	..	16	„	...	9	„	...	1	„	...	3	„	...	3 „
Total ...		82			20			21			9			37

A proportion which closely approaches that which is expected on the above hypothesis.

The final test of the hypothesis will be to make artificial crosses between, *e.g.* (f) plants and (w) plants. From certain of these crosses all the original types should be obtained.* This experiment has not yet been caried out.

IV.—THE VIEWS OF DE VRIES.

De Vries has extended the operation of Mendel's Law to a large number of characters belonging to plants of widely separated natural orders. In his first paper upon the law of segregation of hybrid characters (67) de Vries propounded, as a general rule, that the hybrid always shows one only of a pair of antagonistic characters, and this in all completeness. Dominance, he asserts, is always complete. But this is by no means the case, as Correns (11) has well pointed out, and as Mendel himself observed in many of the characters of peas. In the remainder of his discussion of this class of hybrids de Vries follows Mendel closely.

In a second paper de Vries grouped together Mendel's examples in Hieracium, the false hybrids of Millardet and a series of cases discovered by himself in crossing different forms of Oenothera and other species, as "false hybrids":

* *Cf.* Cuénot's experiments described below.

and distinguished them as a group from the "true hybrids" which follow Mendel's Law. The group in question is characterized as follows:—The first generation of "false hybrids" may be uniform or di- or poly-morphic. As a rule they breed true; but they may show "splitting." Such "splitting" when it occurs is not into equal but into unequal parts.

This classification is distinctly unsatisfactory, and it is not repeated in de Vries' later papers.

De Vries has also studied the behaviour of a number of very variable characters on crossing, and concludes that these also obey Mendel's Law in fundamentals. In the case of crosses between tricotyledonous "half—" and "mid-races" he shows with a high degree of probability that Mendel's Law is followed in this case too, in spite of the existence of transgressive variability.

De Vries believes that by the aid of Mendel's Law he has solved the problem of the difference between species and varieties, or rather, of that between specific characters and varietal characters. According to the mutation theory, varietal characters arise by the "retrogressive" or by the "degressive" method of mutation, and follow Mendel's Law;* specific characters which arise by progressive mutations do not. Thus, in terms of his theory of intracellular pangenesis, de Vries believes that the pairs of characters which on crossing obey Mendel's Law are always represented by the same pangen in different states, active and latent respectively in the most usual case. Characters which have arisen progressively do not follow Mendel's Law, but obey the law of unisexual crossing; that is to say, they produce blended progeny which breed true. This being the case, the long-established view that varieties are perfectly fertile on crossing, whereas species when crossed show a diminution

* In such a case the phylogenetically older character is represented by the active pangen and is dominant. Bateson and Saunders, however (6), have pointed out exceptions to this rule.

of fertility, is shown to be a foreshadowing of the distinction between Mendelian and unisexual crossing; and forms which differ only by such characters as obey Mendel's Law when crossed are fertile together. Forms, on the other hand, which differ by true specific distinctions exhibit infertility which increases with the number of such differences up to complete sterility.

Correns (22) has criticized these views of de Vries. He finds that de Vries' supposition—Mendel's Law holds good for varietal characters, whereas species-characters on crossing yield constant hybrid-characters—does not hold generally good. Correns has described cases in Zea Mays in which hybrids in respect of varietal characters give constant progeny. On the other hand, certain "species-" characters, for example, some of those which Bateson has examined in the case of poultry, have been shown to follow Mendel's Law.

In opposition to de Vries' view of the existence of an unpaired character in the case of unisexual- (species-) hybrids, Correns believes that the rudiment of a corresponding character exists in the other parent form; since the "progressive" character does not really pass over unmodified in the unisexual cross, but is reduced to half its former value. Correns believes that a progressive mutation takes place by the modification of a pangen already existing, not by the formation of a completely new one. He would, therefore, speak of a pair of "Anlagen" in this case also.

De Vries regards a "retrogressive" mutation as taking place simply by a process of becoming latent (*i.e.*, inactive), of a pangen. But Mendelian hybrids not infrequently show characters intermediate between those of their parents, as Correns has clearly shown; hence in this case the "recessive" allelomorph has a distinct effect, and is not entirely latent. Here again Correns would speak of a pair of "Anlagen." So also Bateson, who uses the term "pair of allelomorphs."

V.—THE OBSERVATIONS OF CORRENS ON MAIZE AND OTHER PLANTS.

Correns (15) distinguishes the following types of behaviour in cross-bred plants :—

Type.	Vegetative Development.	Formation of Gametes.
I.—Pisum type	Heterodynamous	Schizogonous
II.— —	Heterodynamous	Homoogonous
III.—Zea type	Homodynamous	Schizogonous
1V.—Hieracium type	Homodynamous	Homoogonous

In the case of heterodynamous vegetative development there is dominance or nearly so of one of the characters concerned (Correns uses the term "paarling"=allemorph). In the homodynamous case there is blending of characters, a phenomenon particularly well seen in crosses between races of maize having differently coloured endosperms or different shapes of grain. In the former example we are concerned with a special case, namely, that of xenia. But Correns has also shown that in the case of several races of plants with differently coloured flowers, the apparently heterodynamous heterozygote has really a colour almost exactly intermediate between those of the parents; a fact not readily distinguishable by the eye alone owing to the operation of Weber's Law. For example, in the case of the hybrid between Hyoscyamus niger and H. n. pallidus, de Vries describes the colour of the former plant as dominant, whereas the colour of the flowers of the offspring is really intermediate, or even somewhat nearer to that of H. pallidus.

Heterodynamous pairs of characters are only a limiting case of homodynamous pairs; and Correns suggests that the former term should be used when the offspring show more than 75 per cent. of the character of one parent.

Millardet's false hybrids constitute, according to Correns, another limiting case (dichodynamous) of homodynamous characters. In the series leading up to these, the mutual

relation of the characters in the particular (poikilodynamous) pairs varies greatly, whilst the number of intermediate forms becomes reduced.*

The formation of the gametes is described by Correns as schizogonous when it takes place according to Mendel's Law. In the homoogonous method of development there is no separation of allelomorphs in this process. Unlike the different modes of vegetative development, the schizogonous and homoogonous methods of formation of the germ cells are regarded by Correns as being sharply distinct.

Good examples of the "mosaic" development of the heterozygote are to be found in maize-crosses, especially in crosses between forms with a blue and with a white aleurone layer respectively. Webber (73) has suggested that such cases might be accounted for by parthenogenesis of both the nuclei which usually coalesce to give rise to the endosperm, the patches of colour being derived from the two. Correns pointed out that the appearance of a pale blue aleurone layer with darker patches as the result of the cross blue by white is inexplicable on this hypothesis.

Bateson and Saunders (6) suggested, on the other hand, that the pied condition might be due, not to dominance failing sometimes and succeeding sometimes, but to the existence in the mosaic of islands of the recessive character in the paired or unresolved state (the phenomenon then not being described in terms of dominance at all). But this suggestion also fails to explain the same observation. The fact itself I have been able to confirm in the case of a cross between "Black Mexican" sugar corn and "Boone county White" dent corn.

In maize Correns finds the power of development of an "Anlage" to vary greatly, depending upon the individuality of particular germ cells, plants or races, as well as in

* Giard points out (80) that this view is quite opposed to that which Millardet himself held upon the subject. Millardet regarded his cases of false hybridism as being due to parthenogenesis of the male or of the female pronucleus.

the case of schizogonous characters upon the mode of origin of the particular allelomorph—whether arising in a homozygote or in a heterozygote.

In certain cases there is greater or less correlation between different sets of allelomorphs. In such cases, as Bateson and Saunders point out, Correns' terms "halb-identisch" and "conjugirt" are already well enough expressed by the terms "in perfect" and "in imperfect correlation."

VI.—LATENCY OF CHARACTERS.

I have already had occasion to account for the absence of a character—the presence of purple spots (on the testa in peas)—in certain individuals in which it should have appeared according to the simplest form of Mendel's theory for dihybrids. The explanation tentatively put forward was that this character was unable to manifest itself except in the presence of another character, or rather group of correlated characters including the greenish grey colour of the testa and the dimpled form of the seeds. This assumption having been made, it was shown that the example was in perfect accordance with Mendel's Law.

There is evidence, however, that this explanation may cover a considerable number of supposed exceptions. Thus Tschermak has described (63) a series of cases which show considerable resemblance to the above, but in which a new or atavistic form appears in F_1. Before describing Tschermak's cases an example of this kind of reversion may be given.

Example VIII.—I crossed Barr's dwarf kidney bean "Green Haricot" with pollen from "Canadian Wonder." The former plant has a pale green testa and pale greenish-white flowers, and the pods are green.

Canadian Wonder has deep crimson seeds and pale lilac flowers, and the pods are also green in colour.

The hybrid plants had perfectly black seed coats. The flowers were of a fairly deep crimson colour, like that of the

male parent much intensified. The pods showed spots and flecks of purple on a green basis.

Now a tall form of Phaseolus vulgaris grown by natives in Ceylon shows just these same characters of flowers, seed, and pod-colour, and this variety has a distinctly primitive and relatively unimproved appearance. It therefore seems likely that this was a true case of atavism on crossing in the strictest sense. Unfortunately all the offspring of the cross-bred plants were killed by drought before the flowers appeared, and I have not yet been able to repeat the experiment.

In one of the crosses described by Tschermak a race of Pisum arvense with "rose-coloured" flowers crossed by certain white-flowered races of Pisum sativum yielded in F_1 plants with exclusively "red" flowers, like those of the ordinary Pisum arvense.

In F_2. Tschermak found the proportion red : rose : white to be 239 : 75 : 83 : and in several other cases of similar crosses the ratio 9 : 3 : 4 was approached ; *i.e.*, coloured : white — 3 : 1 according to the Mendelian expectation ; and also among the coloured forms ; reversionary : coloured parental — 3 : 1.

Tschermak supposed the red colour to have existed as a latent rudiment in the rose-flowered parent, and that it was rendered evident on crossing ; and he applied to the phenomenon the term Cryptohybridism. The character which thus suddenly appears he described as cryptomeric. Similarly Tschermak crossed a race of Pisum arvense having no purple spots on the yellowish green testa with a white-coated race of Pisum sativum. In F_1 purple spots appeared in all the offspring. In F_2 appeared : purple spotted seeds, coloured seeds without purple spots, and white seeds ; doubtless in the same proportion. This series is identical with the offspring of the cross purple sugar pea by native yellow described above (p. 331), and there can be little doubt that a similar explanation in terms of gametes can be applied to it.*

*I received Tschermak's Paper in February just as these plants (F_2) were being gathered in.

On crossing A (B) (B being latent) with ab* we get :—

F_1 ABab. (B latent having become B active).

And the further account is identical in the two cases.

Tschermak also described a number of more complicated cases of a similar nature, but in his preliminary paper largely confined himself to demonstrating the existence of cryptomeric characters in plants. He pointed out that extracted Mendelian dominants and recessives require testing for traces of the opposite parental character. Thus we may hope, on crossing with a properly chosen race, to demonstrate the latency of the character purple spots in some of the white forms in the case already described.

Among examples of "Kryptomerie" in existing literature, Tschermak points out that a number of the spontaneous Oenothera mutants studied by de Vries were constant when inbred ; but on crossing showed a partial atavism. De Vries further upholds a very far-reaching Cryptomerism, namely, the inclusion of all the varieties of a species one within the other.

The special importance of Tschermak's contribution is, as he himself points out, the establishment of the fact that certain races and characters exist, which show atavism in a definite and regular way, following Mendel's Law in the majority of cases examined.

Cuénot (24) has already carried an investigation similar to this one a step further in the case of animals. This writer has worked out a series of cases of latency of colour characters in races of mice in a very ingenious fashion. Cuénot's hypothesis is nearly identical with the one suggested above. He supposes that the colours yellow (J), grey (G), or black (N) can only make their appearance when the same zygote includes a perfectly independent colour bearing character (C), which is allelomorphic to and dominant over the albino character (A). According to Cuénot's scheme all

* It appears unlikely that in this case the purple spotting was introduced by the recessive parent.

albino mice contain some colour in a latent condition; those with which he worked were represented by the following "formulæ" of heredity":—

Homozygotes AG; AN; AJ.
Heteorozygotes AG AN; AG AJ: AN AJ.

In the visible expression of the colours (when C is present) yellow is dominant over grey and over black, and grey is dominant over black. This being the case, Cuénot finds that Mendel's Law is rigidly followed in the formation of the gametes.

Cuénot gives the following example, being one of three possible methods by which all three colours yellow, gray, and black, as well as albino, can appear in the offspring of a single pair:—

Parents: AG (alb). AN (alb) CN (black) AJ (alb)
F_1 AG. AN (albinos) CN AJ (yellow)
Gametes AG AN CN AJ CJ AN

F_2	AG CN ... gray		4 albinos
	AN CN ... black		2 yellow
	AG AJ	albinos	1 black
	AG AN		1 gray
	AN AJ		
	AN AN		
	CJ AG	yellow	
	CJ AN		

The actual numbers obtained in F_2 were—

81 albinos, 34 yellow, 20 black, 16 gray, the expectation being—
76 : 38 : 19 : 19

These observations of Cuénot's indicate a very important step in advance, for they show that an individual, apparently recessive in character, may contain a dominant allelomorph in the latent state; and that this may fail to appear even on crossing different strains of recessives (a process frequently accompanied by the appearance of a previously latent character). Yet, at the same time, Mendel's Law may be strictly

followed in the formation of the gametes. And we are led to perceive that many apparent exceptions to Mendel's Law will require very careful study before it can be definitely stated that they follow any other method of gamete formation.

VII.—CORRELATION.

The cases so far cited of phenomena which extend beyond the limits of Mendel's original observations have all had relation to dominance, or to the visible expression of the characters in zygotic organisms. An important series of real exceptions to Mendel's Law, as to the behaviour of the germinal representatives of characters during the process of formation of the gametes, is afforded by cases of correlation. One such case at least was already known to Mendel, for in his own experiments coloured flowers, purple spots in the axils of the leaves, and coloured seed coats always appeared together on the same plants.

For such a case of correlation as that between coloured flowers and coloured axils Correns uses the term "semi-independent" (halbselbstandig)—both characters depend upon the formation of anthocyan, but each has its own independent position. In the case of "conjugate" characters (conjugirt), two or more characters, belonging to separate categories and each conceived as possessing an "Anlage" of its own, remain together during the formation of the gametes.

Correns himself points out that these two forms of correlation are not always easy to distinguish; moreover, it is somewhat doubtful how far we are yet justified in describing the particular behaviour of "Anlagen."

The following case would no doubt be ranked by Correns as an example of conjugate characters:—

Example IX.—A clear case of correlation was observed between the time of flowering on the one hand and the colour of the flowers (axils and seed coats) on the other.

This occurred in the cross already described between the native yellow pea and French sugar pea, but was not noticed until F_3. In this generation a considerable number of plants was grown.

At the end of May, 1904, I observed the time of flowering of the offspring (F_3) of 26 plants (F_2) which were shown to be heterozygotes in respect of floral colour.

On 25th May flowers had appeared upon 34 purple-flowered and 29 white-flowered plants ; and on 30th May 107 purple- and 79 white-flowered plants were in blossom. Thus, on the former date, the proportion purple to white was 1·17 : 1, and on the latter 1·35 : 1, instead of the 3 : 1 of Mendelian expectation. Subsequently the proportion of purple-flowered plants increased until the final total stood at : 383 purple and 118 white, or a proportion of 3·25 : 1.

It is clear, therefore, that in this case earliness was correlated with the presence of white flowers, and lateness with the presence of purple flowers ; and the original white-flowered parent had been observed to come into blossom several days before the French sugar pea.

The case is of interest as showing clear correlation between a distinctly variable and indefinite character—time of flowering—and a perfectly definite and constant character—colour of the flowers. For I have never observed any flower which could be called intermediate in colour between these two classes. The purple flowers may show slight differences in tint, but these are hardly noticeable. The white flowers never, apparently, show any tinge of colour.

In certain crosses between races of Matthiola, Correns (13) found correlation carried to such an extent that the hybrids appeared to form only two kinds of gametes, containing all the characters of one and of the other parent respectively. For this kind of segregation Correns proposes the term "zygolytic" as opposed to the "seirolytic" method in which the germ plasm is segregated into its individual "Anlagen."

VIII.—DE VRIES' ANALYSIS OF FLORAL COLOURS.

In addition to his experiments with peas and with Hieracium, Mendel made crosses also between certain strains of Phaseolus, in order to test whether his conclusions held good with those plants as well. In the case of a certain cross between Phaseolus vulgaris and P. nanus he found the result to be in perfect agreement with those previously described for Pisum crosses.

Mendel next crossed Phaseolus nanus, which had white flowers and seeds, with pollen from P. multiflorus, the flowers of which were purple-red, whilst the seeds had purple spots on a peach-blood-red ground. The hybrid plants (F_1) resembled the pollen parent closely. In F_2 only 31 plants reached the flowering stage. These showed in certain other characters almost exactly the ratio 3 : 1 between dominant and recessive allelomorphs. Only 1 plant, however, showed white flowers and seeds, although eight were to be expected if the case was one of crossing between simple allelomorphic characters. The plants with coloured flowers showed a wide range of character in this respect, being of various grades of purple-red to pale violet, and the colour of the seed coat was no less varied. In the further generations only a small number of plants could be raised.

Mendel suggested that the small proportion of plants with white flowers could be explained by supposing the dominant colour of the flowers of Phaseolus multiflorus to be made up of two or more entirely independent colours, *e.g.*, A_1 and A_2. Then on crossing by a, we get ($A_1a + A_2a$); more properly written A_1A_2a, as Bateson points out (2). From the gametes A_1A_2, A_1a, A_2a, and a, there arise in F_2 the combinations : $(A_1 + 2A_1a + a)(A_2 + 2A_2a + a)$, or :

$1\ A_1\ A_2$	$2\ A_1a\ A_2$	$1\ A_2a$
$2\ A_1\ A_2a$	$4\ A_1a\ A_2a$	$2\ A_2aa$
$1\ A_1a$	$2\ A_1aa$	$1\ aa$

and Mendel suggested that each of these combinations denotes

a separate colour. The expectation is then of only 1 white among 16 individuals.

De Vries (69) describes a more definite case, and his description, though following that of Mendel, can be made somewhat clearer. We may, therefore, pass on to it at once. De Vries crossed Antirrhinum vulgaris having red flowers, by a variety the flowers of which were white. In F_1 all the plants had red flowers like the dominant parent. In F_2 the colour of the flowers on the different plants varied considerably, but de Vries was able to distinguish among 49 offspring of 1 cross the following proportion :—

51 per cent. red, 16 per cent. flesh-coloured, 31 per cent. "Delila," 2 per cent. white; and one of these red forms (a heterozygote) gave in F_3 :—58 per cent. red, 17 per cent. flesh, 20 per cent. Delila, 4 per cent. white, which approaches the proportion 56·25 : 18·75 : 18·75 : 6·25, or 9 : 3 : 3 : 1, characteristic of a Mendelian dihybrid.

De Vries explains this case by regarding red as a combination of flesh and Delila — F + D and white as the absence of either—W + W′.

Red × white gives FDWW′ (gametes FD, FW′, WD, WW′) giving the combinations—

(F + 2FW + F), (D + 2W′D + W′) whence the zygotes :—

FD + 2FDFW′ + FW′
2FDWD + 4FDWW′ + 2FW′WW′
WD + 2WDWW′ + WW′.

Each of the terms containing F and D is red, those containing F, but not D, are flesh ; D, but not F, Delila.

There result—

(a) 1 constant red ... ... FD
(b) 2 red which will give in F_3 red and flesh ... 2FDFW′
(c) 2 „ „ red and Delila ... 2FDWD
(d) 4 „ „ red and F, D, and W .... 4FDWW′
(e) 1 constant flesh ... ... FW′
(f) 2 flesh giving in F_3 flesh and white ... 2FW′ WW′
(g) 1 constant Delila ... ... WD′
(h) 2 Delila giving in F_3 Delila and white ... 2WDWW′
(i) 1 constant white ... ... WW′

De Vries' account is a little obscure, and he speaks in one place of "Constant Flesh + Delila × White" as a term in the series. He appears to mean FD WD., which can only be spoken of as Flesh + Delila × constant Delila or more properly Red × constant Delila. But I believe the above to be a fair account of his explanation.

In F_3 de Vries actually obtained evidence of the existence of all the terms (a)–(i) in F_2.

Bateson (3) has criticized this account and suggested as a more likely hypothesis that the gametes of the heterozygote R × W consist of R, D, F, and W in equal numbers. R being dominant to the other three members and W recessive to the first three. This would give the following terms in F_2:—

9 R, namely, 1RR, 2RF, 2RD, 2RW, 2FD
3 F, namely, 1FF, 2FW
3 D, namely, 1DD, 2DW
1 W, namely, 1WW.

This scheme plainly fits the facts equally well; and it will only be possible to learn which of the two methods of gamete-formation really took place, by a very extensive study of subsequent generations, or, as Mr. Bateson has himself pointed out to me, by crossing F_1 with the recessive on a large scale.

The above scheme also illustrates very clearly Bateson's view of a *compound allelomorph*, which is essentially opposed to the above view of a combination of colours in the flower held by Mendel and de Vries.

Bateson and Saunders (6) regard a compound character, when crossed with an allelomorph of simple recessive nature, as breaking up into simpler and possibly component elements. When similar elements of this kind meet in fertilization there is no further resolution, and a permanent new character thus arises by a process of analytical variation. The term hyp-allelomorph is used for the constituent elements of a compound allelomorph.

Hitherto no case of resolution of a compound allelomorph has been completely followed out; and it appears not impossible that many apparent cases of this kind may be shown to follow Mendel's Law, by the aid of the conception of latency, or by an extension of the view of de Vries. It is a serious objection to Bateson's view of the above case that upon this supposition the white parent contributes less than half the total characteristics of the offspring. An equal contribution from the two parents is of the essence of Mendel's theory. Judgment upon this point may, however, be reserved until further evidence is forthcoming.

CONCLUSION.

The preceding account is incomplete in many respects, but it may serve to give some idea of the kind of problems, upon which those experiments bear, which will be detailed in a following paper.

A particularly noticeable omission has been the absence of any adequate notice of the views expressed by Bateson and Saunders (6), who give, at the conclusion of their paper, a full discussion of the theoretical bearings of the Mendelian and post-Mendelian results. It is impossible to abstract their argument in any reasonable compass. And I would specially refer the reader to it for a disquisition upon the subject of false hybridism (Monolepsis of these authors) as well as upon the theoretical relation of the Mendelian theory to the problems of evolution.

The experiments, also, described by these authors, I have passed over almost in silence; partly because they relate to plants and animals of which I have no personal experience, but chiefly owing to their complexity, which renders necessary an examination of further generations before the results can be completely understood. A further account and discussion by the authors themselves may be looked forward to with interest.

Bateson and Saunders pointed out the probable analogy of the phenomenon of sex with that of Mendelian segregation. And Castle (9) has considered at some length the theory that the inheritance of sex among dicœcious animals and plants follows Mendelian principles. In the case of hermaphrodite animals and plants Castle believes that a mosaic inheritance of sex takes place ; and he discusses the bearing of a number of known facts upon these suppositions.

The exact time and method of separation of the germinal representatives (Anlagen) of a pair of allelomorphs is another point of great theoretical interest. Strasburger (56) supposes this process to occur during the visible reducing division which takes place in the nuclei of the embryo-sac- and pollen-mother cells. And this indeed appears to be the most obvious view. Correns (15), however, believes that he has found evidence to disprove this supposition in the behaviour of the colour of the pollen grains in the offspring of a cross between two races of Epilobium angustifolium. The pollen grains do not show segregation in respect of colour, and Correns consequently believes that the separation of the "Anlagen" must take place in the pollen grain itself.

There can be no doubt that Mendel's theory of the separation of the pure "Anlagen" of certain characters in the gametes of hybrids is one of the very greatest importance, both theoretically and in practice. Bateson and Saunders would extend this principle to the formation of the gametes in zygotes arising by normal fertilization. In this connection we may recall Weismann's view (75) that, the possible number of "Anlagen" contained in a gamete being limited, there must of necessity be a reduction in this number every time the gametes are formed in organisms which undergo normal fertilization. This is undoubtedly the case if we accept any theory of inheritance by definite germinal representatives. Mendel's discovery not only appears to render the acceptance of such a theory inevitable, but also shows that the reduction

in number of the "Anlagen" takes place in certain cases in a perfectly definite and simple fashion.

Reference has been made above to the four schemes of inheritance enunciated by Correns. Tschermak (60) has given an account of 64 such schemes in support of the objective reality of several of which he finds evidence in crosses between races of cereals. The distinctions between the greater number of these systems are concerned with differences in the vegetative development of the zygotic organism. Very few cases in which Mendelian segregation in the gametes does not take place have hitherto been worked out completely, although such undoubtedly occur.

Doubt has been expressed in certain quarters as to the sufficiency of the evidence of any case of Mendelian segregation so far published. But it appears to me to be impossible for any one, who has made definite experiments with certain characters in peas or in Indian corn, to doubt the validity of Mendel's explanation of the phenomena which he observed.

Finally I desire to express my thanks to those who have given me assistance during the course of the work herein partly described. I am particularly indebted to Mr. W. Bateson for a constant stream of information and advice most generously given. I am also greatly indebted to the staff of the Peradeniya institution, especially to the Director, Mr. J. C. Willis, on whose advice and by whose permission the work was undertaken; to Mr. Herbert Wright, who has aided me both personally and with the resources of the Experiment Station; and to Mr. H. F. Macmillan. I would also gratefully acknowledge the kindness of Mr. H. Webber of the U.S.A. Department of Agriculture, of the Director of the Calcutta Botanic Gardens, and of Mr. I. H. Burkill, from all of whom I have received supplies of seeds which have been made use of in the experiments.

SUMMARY.

In 1866 Gregor Mendel showed that, in the case of certain pairs of alternative characters in peas, the said characters, or

their germinal representatives, segregate in the germ cells of a cross-bred plant in such a manner that all possible combinations of the characters occur in equal numbers in the germ cells—the combination of the two characters of one pair in the same germ cell being impossible.

Mendel also showed in 1870, in the case of crosses between different forms of Hieracium, that the behaviour of certain characters cannot be described in the same simple fashion.

In the case of peas the particular characters which Mendel selected for observation showed the phenomenon of dominance. That is to say, one of each pair of parental characters was so preponderant that it was difficult or quite impossible to detect the other in the hybrid. In the case of other characters, however, Mendel observed intermediate forms in his hybrid peas. The hybrid Hieraciums were also more or less intermediate in appearance between their parents.

Since 1900 Mendel's Law of segregation has been shown to apply to a large number of characters in a variety of plants belonging to widely separated natural orders. In the case of a large number of such characters dominance has been found to occur, whilst in a further considerable number the hybrid forms (heterozygotes) show a more or less intermediate character. The same pair of characters (apparently) has, moreover, been found to show in some cases dominance in others blending.

In other cases again a number of further complications may be introduced.

A considerable group of these may be summed up under the head of latency of characters. Thus, when a character not visible in either of the parents makes its appearance in the offspring, we must suppose that this character, or the capacity for producing it, was present in a latent condition in one or both of the parents (Tschermak).

In the case of so-called "reversion on crossing" of which examples have been given, a latent character seems to be rendered visible by the act of crossing and appears in the

offspring of the cross. In other cases it seems necessary to suppose that some of the parental characters become latent in certain of the cross-bred offspring, owing it may be, to the inability of certain characters to appear, except in combination with certain others. On further crossing such characters may once more reappear. In such cases segregation may, and probably in many cases does, take place according to Mendel's Law.

In certain instances the phenomenon of correlation appears. In such cases certain groups of allelomorphs show a tendency to remain together in the formation of the gametes; such correlation may be complete or incomplete.

Examples occur in which each of a series of characters appears to dominate over the next with a definite system of valency (of Bateson ;=Werthigkeit of Tschermak).

In the cases of unisexual crossing described by de Vries, the hybrid shows in a reduced state a character present in one of its parents but absent in the other, and in this case segregation is said not to take place. In de Vries' Mutation crosses, finally, the first hybrid generation is polymorphic, and the different forms subsequently breed true, except for fresh mutations.

Other cases of greater complexity also without doubt occur, but the above include the majority of forms of crossing which have so far been definitely worked out.

Illustrations from Actual Experiments.

(1) Mendel's observations were confirmed for the categories smooth : wrinkled and green : yellow using Telephone and Telegraph crossed with a smooth yellow native pea. A doubtful exception appeared in the case of one cross. (*Examples I., III.*)

(2) Also for the allelomorphs coloured and white flowers, on a large scale in two cases; and for presence and absence of parchment layer in one case. (*Examples VI., VII.*)

(3) In the colour of the testa certain complications occur. These are described in terms of Mendel's theory by the aid of the hypothesis of latency. (*Examples VI., VII.*)

(4) The shape of the seeds of peas depends upon several factors, of which some account is given. (*Example VI.*)

(5) The time of flowering of hybrid peas showed in one instance a correlation with the colour of the flowers. (*Example IX.*)

(6) Some of the observations of Correns upon maize were confirmed. (*Examples II., IV., V.*) The process of re-crossing with the recessive was carried out on a considerable scale in one case, and Mendel's conclusion fully confirmed. (*Example IV.*) In the case of the allelomorphs blue and non-blue aleurone layer, Mendel's Law was shown to hold good in spite of great irregularity in the visible development of these characters. (*Example V.*)

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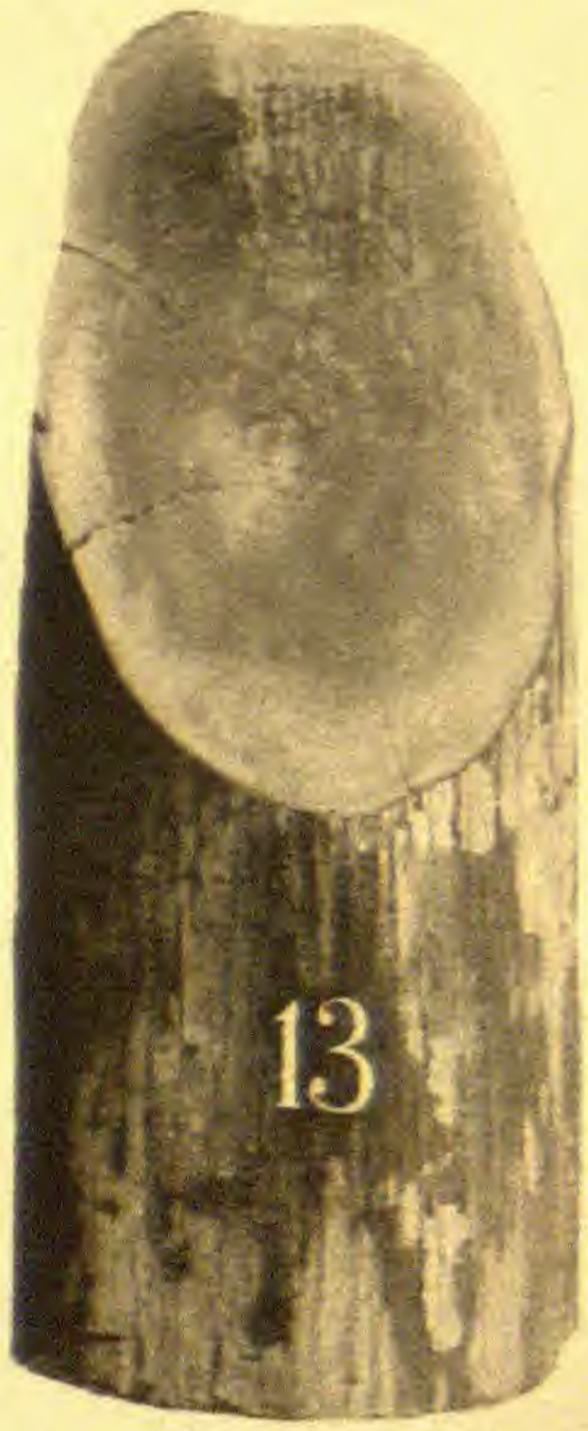
Peradeniya, July 16, 1904.

D. PRURIENS (1), D. HIRSUTA (2), D. MOONII (3), D. AFFINIS
D. MELANOXYLON (4), D. CHAMAEDENDRON (5), D. CILIATA (6).

D. SYLVATICA (7), D. OPPOSITIFOLIA (8), D. THWAITESII (9)



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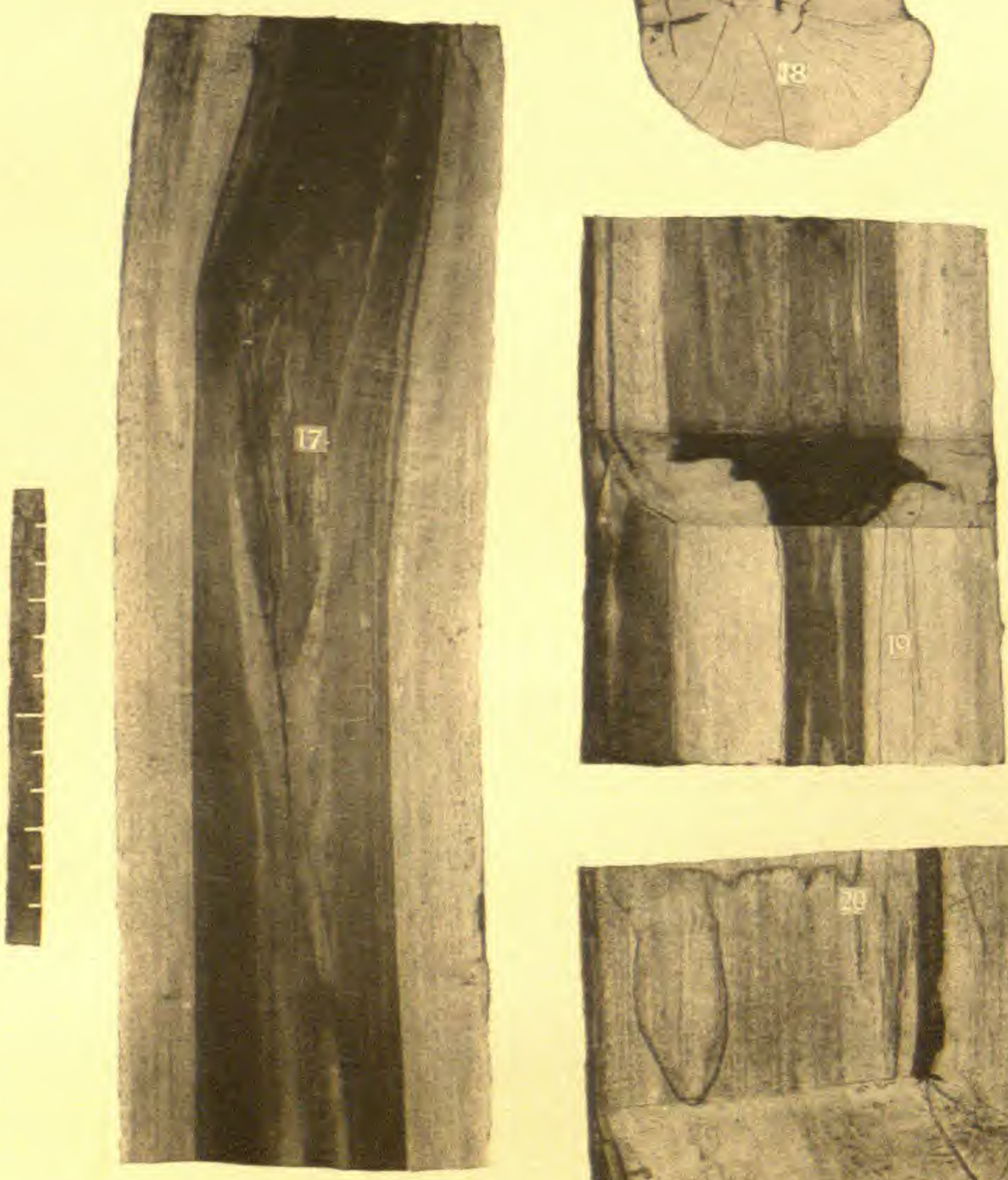

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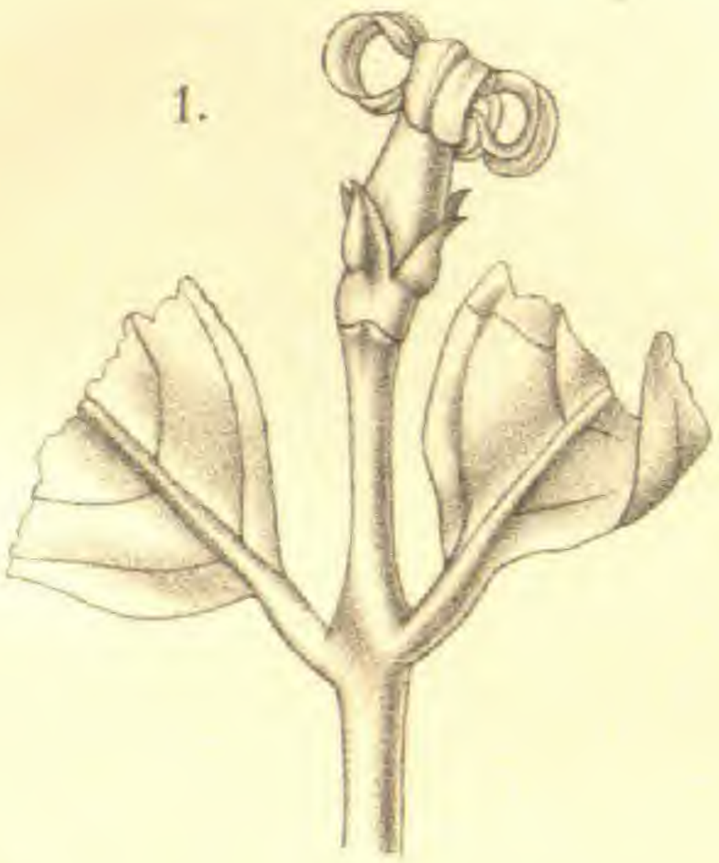

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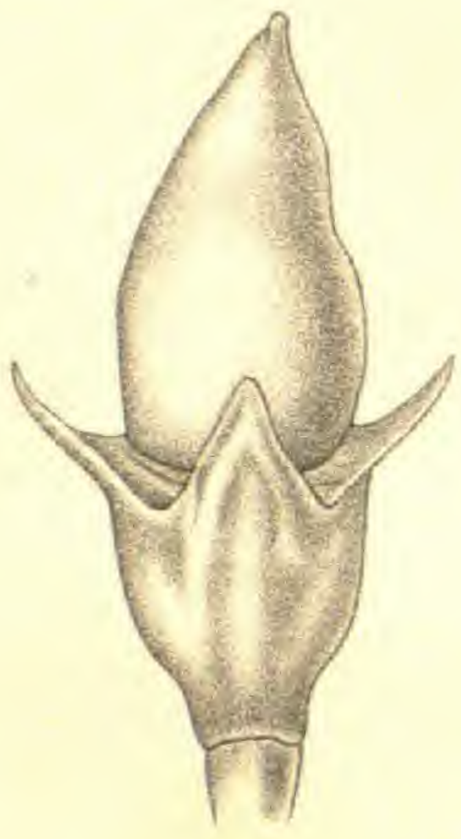

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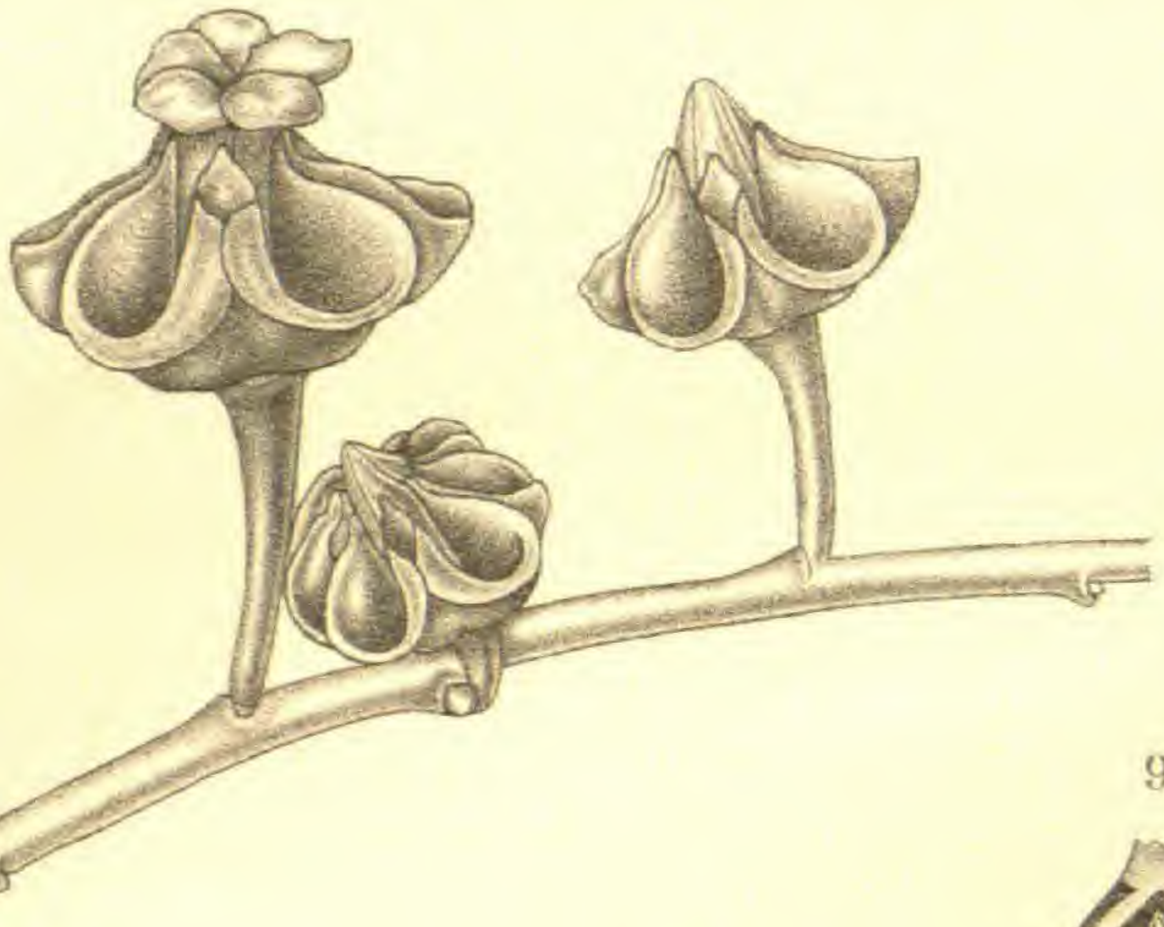

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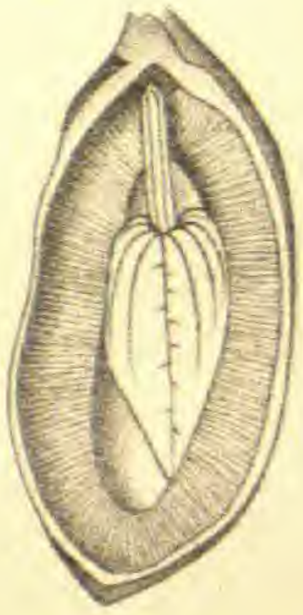

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D. OPPOSITIFOLIA, (1-4) D. QUAESITA (5-9).

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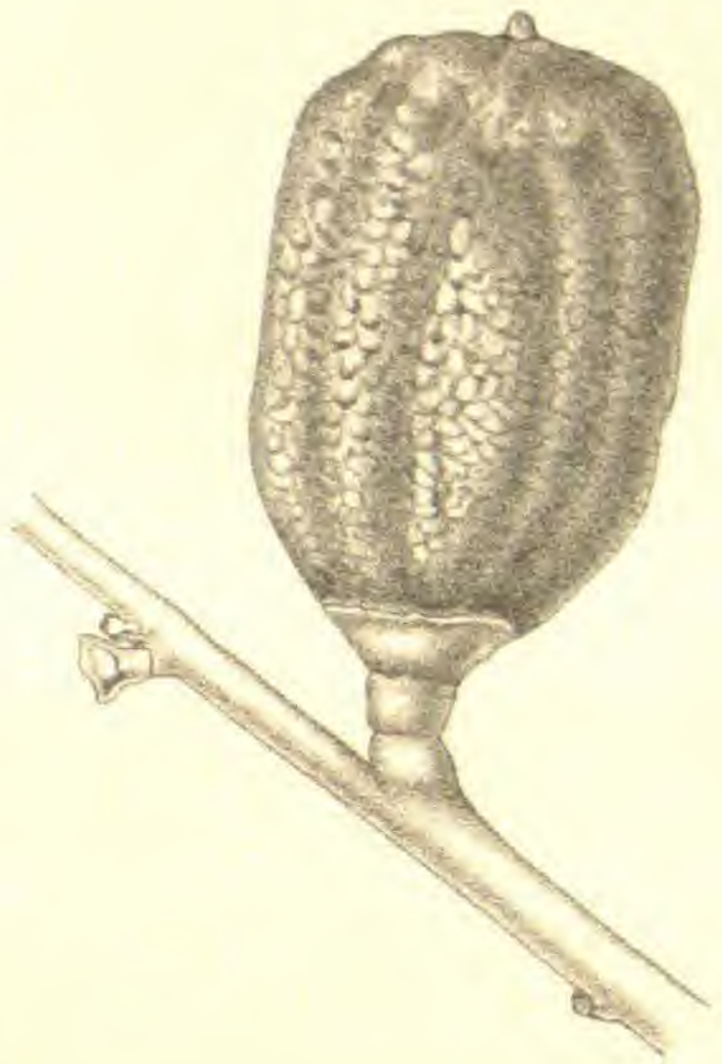

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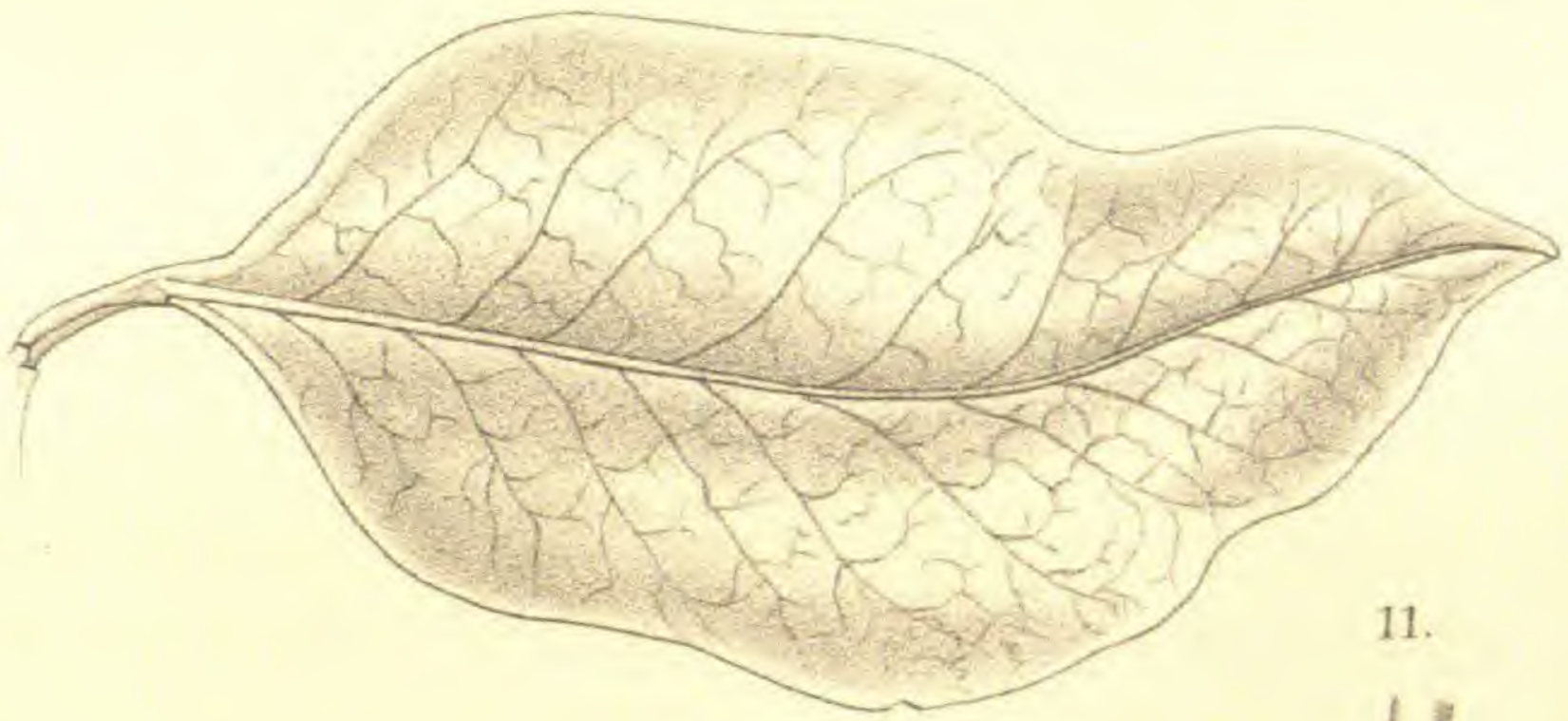

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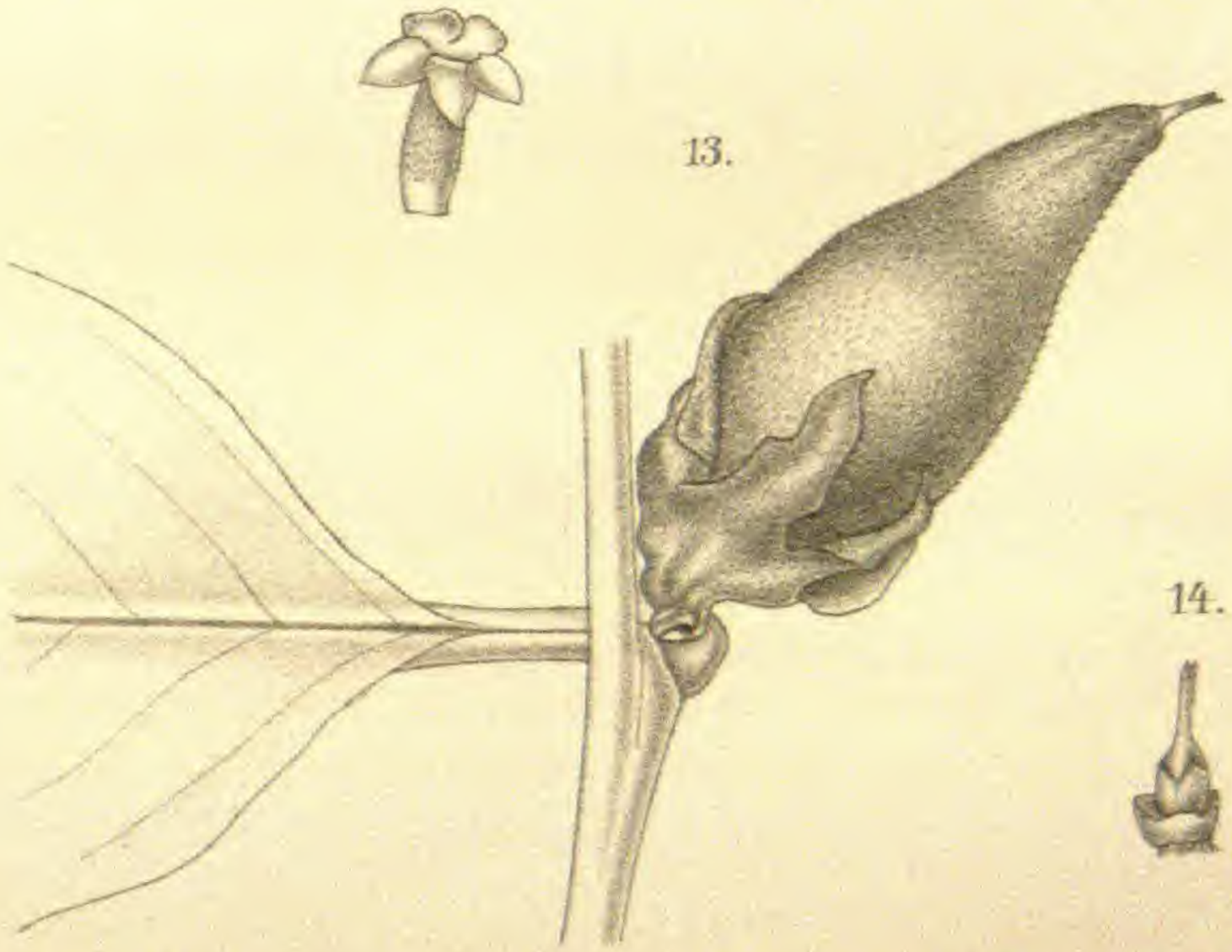

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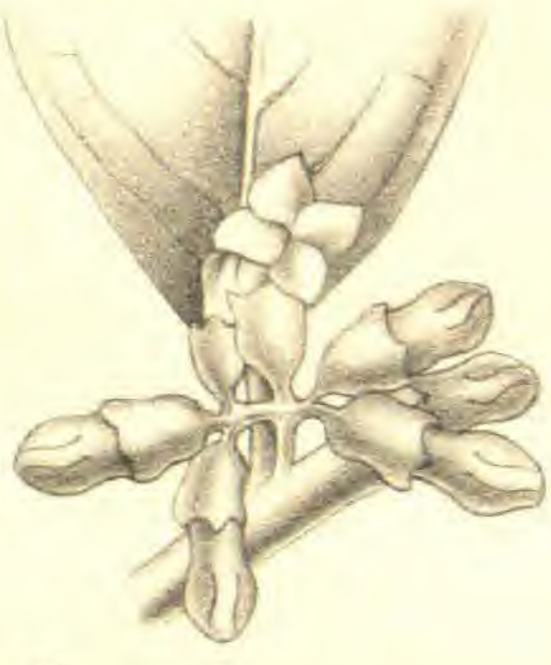
D. OOCARPA (1–7), D. ACUTA (8–14).



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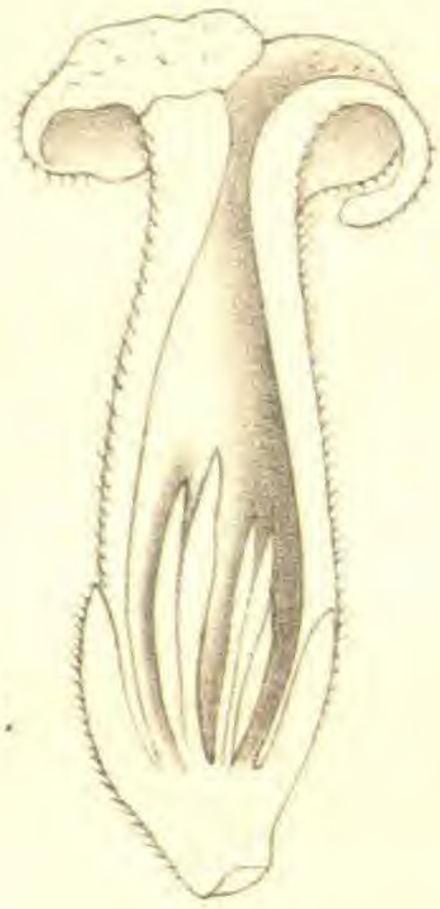

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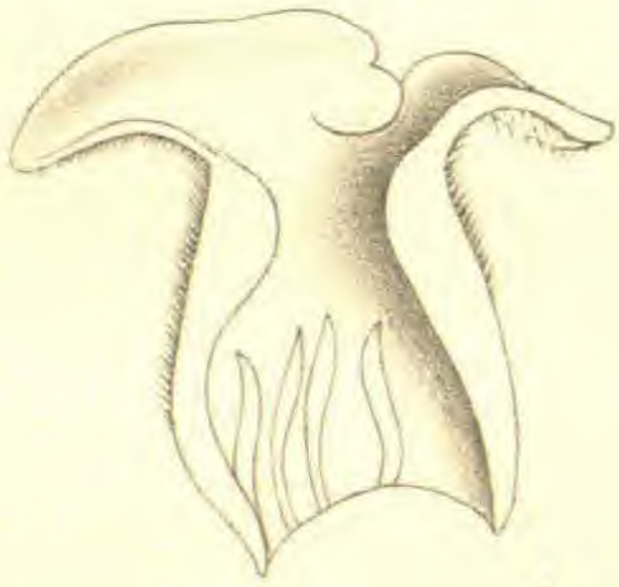

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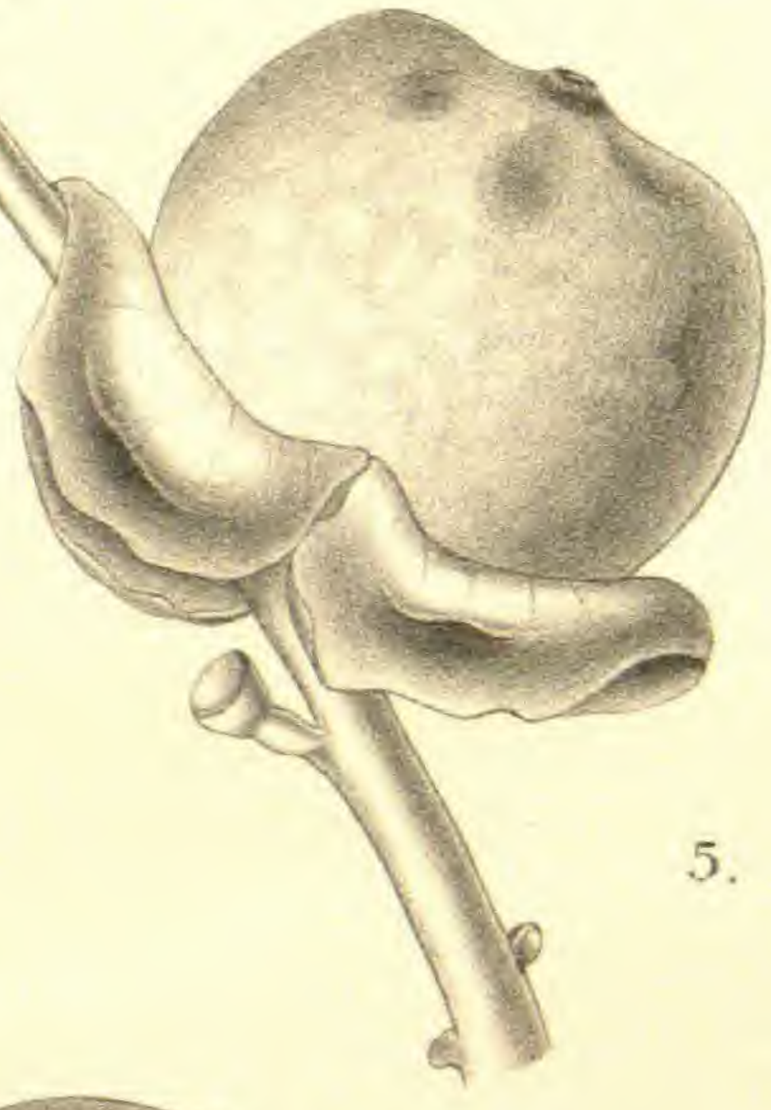

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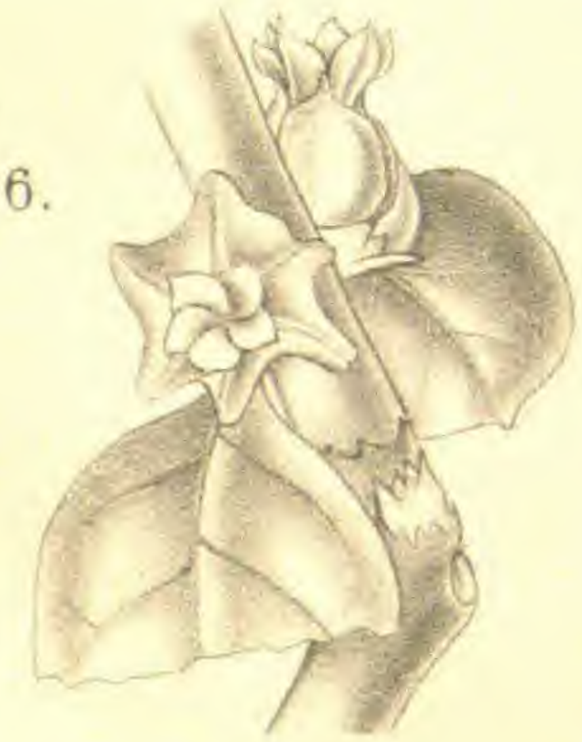

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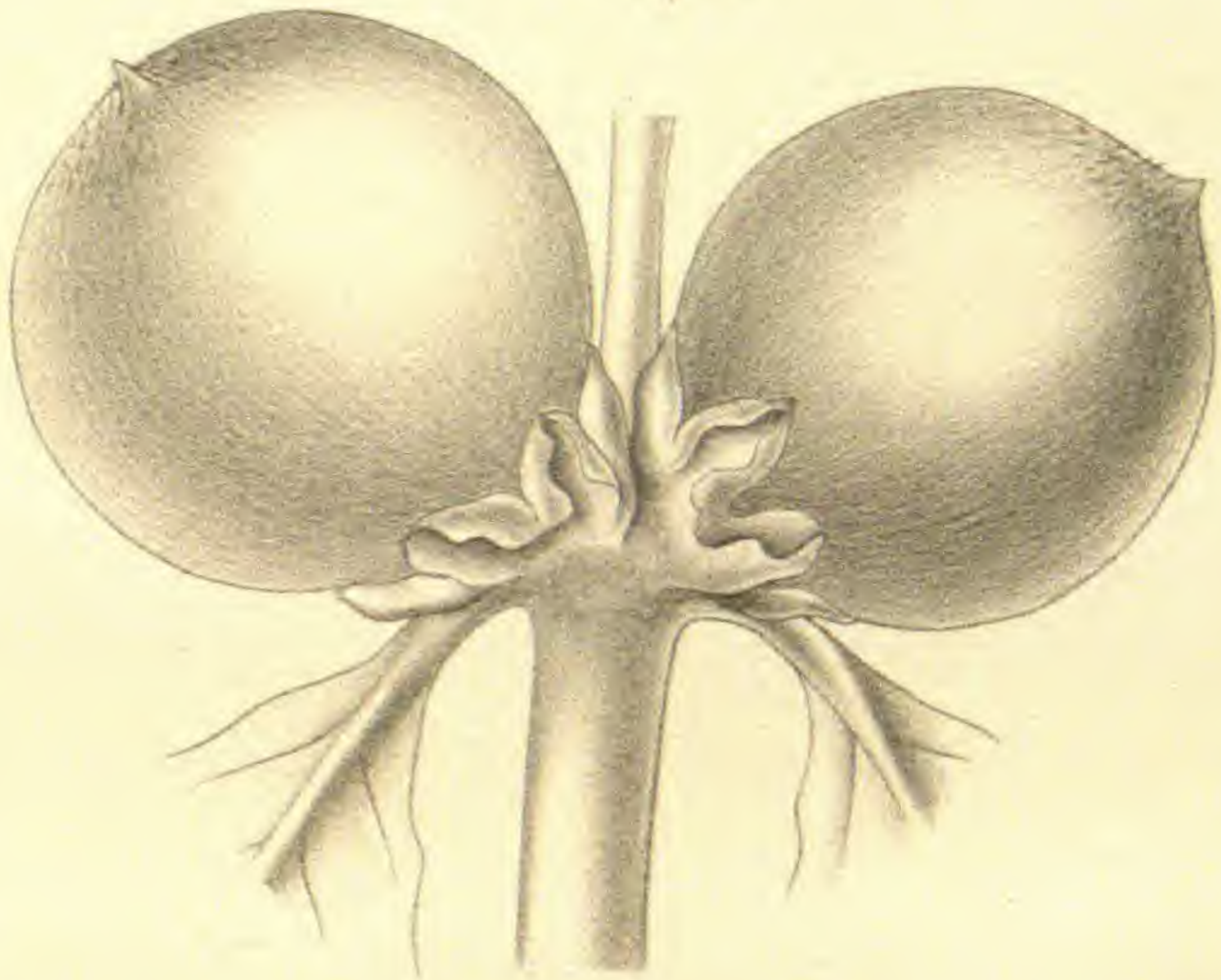

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D. CRUMENATA (1-5), D. MELANOXYLON (6-9).

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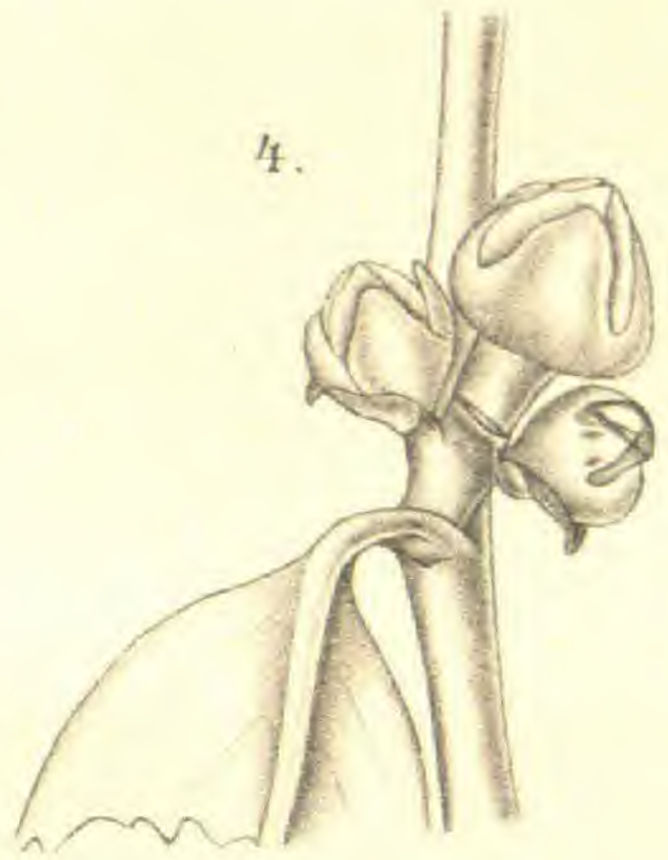

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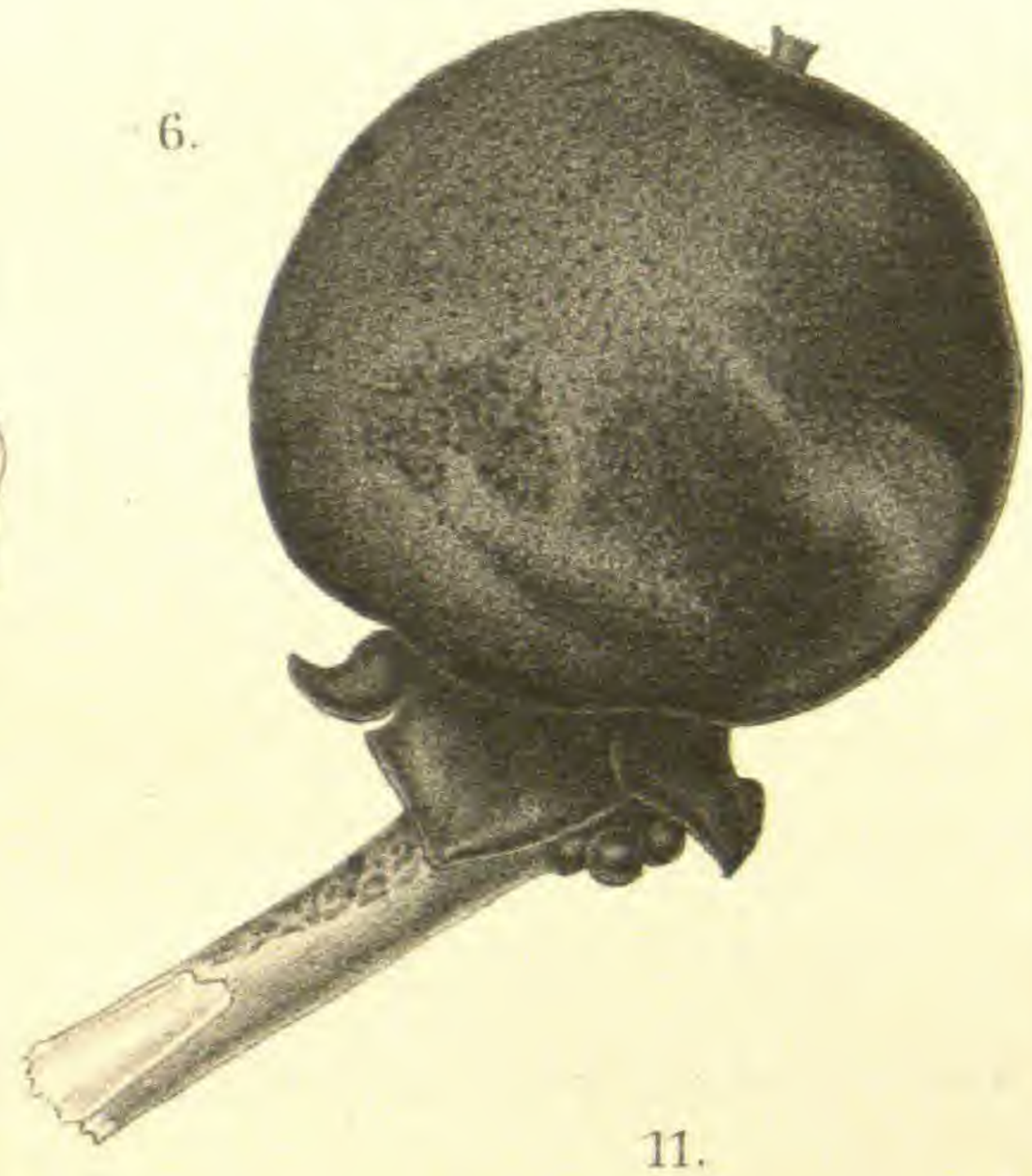

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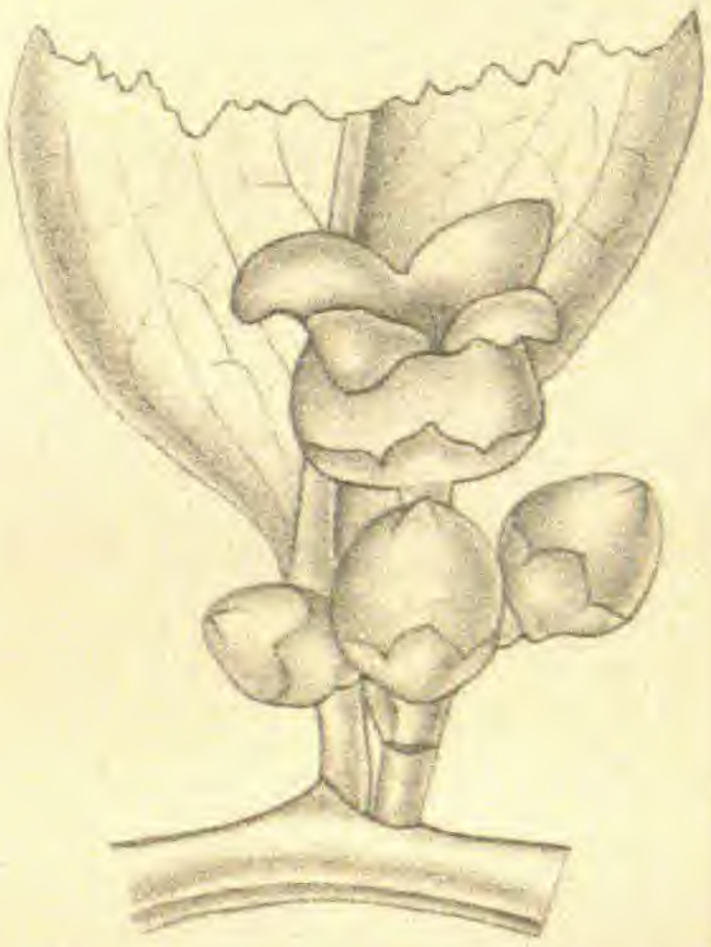

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D. EMBRYOPTERIS (1-12).

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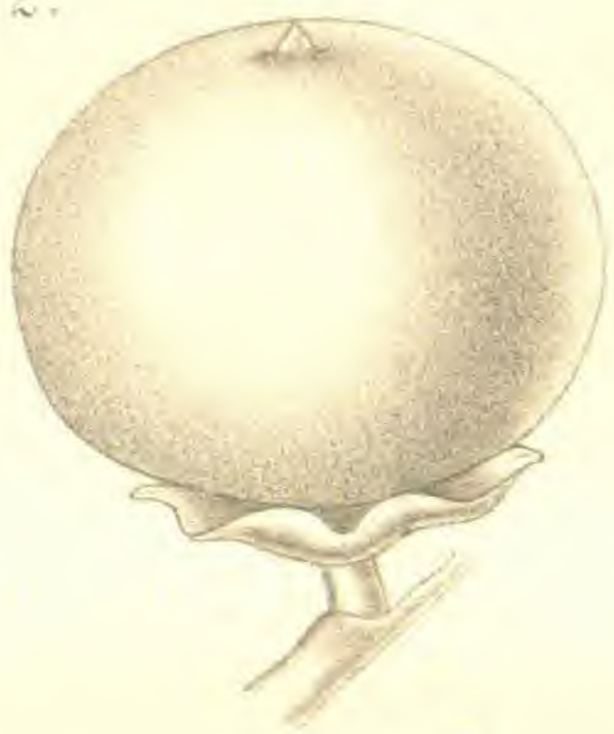

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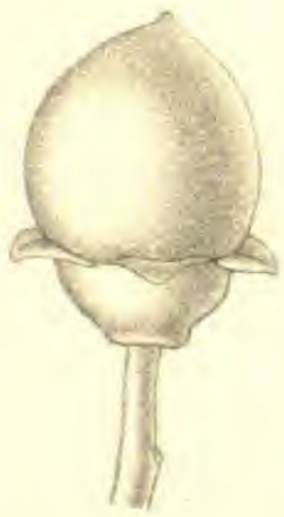

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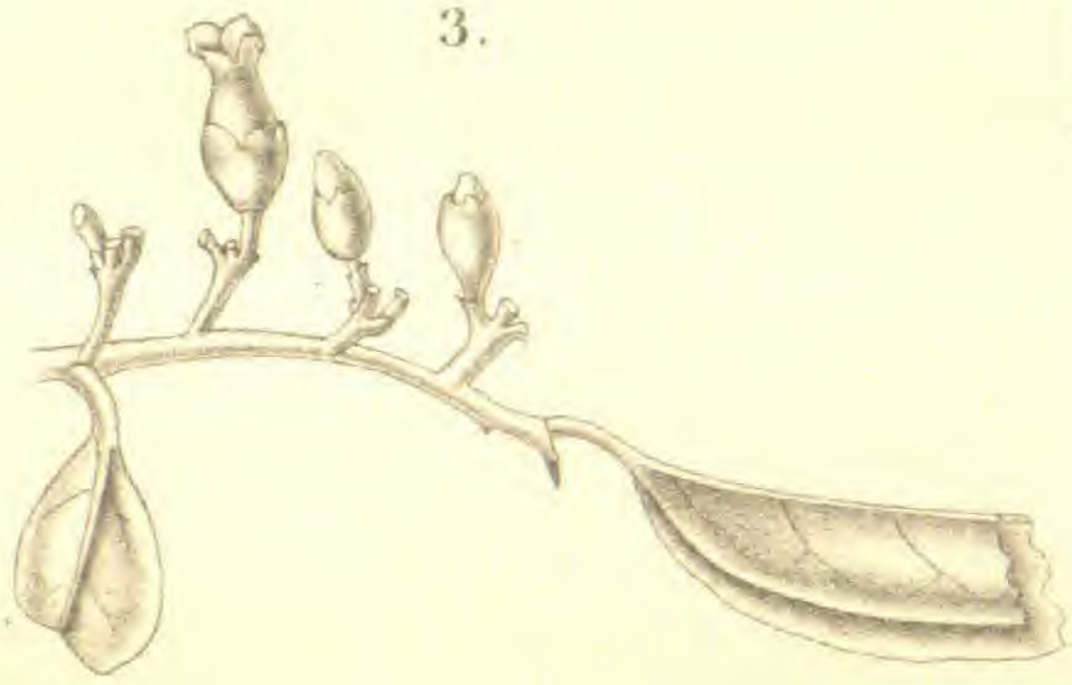

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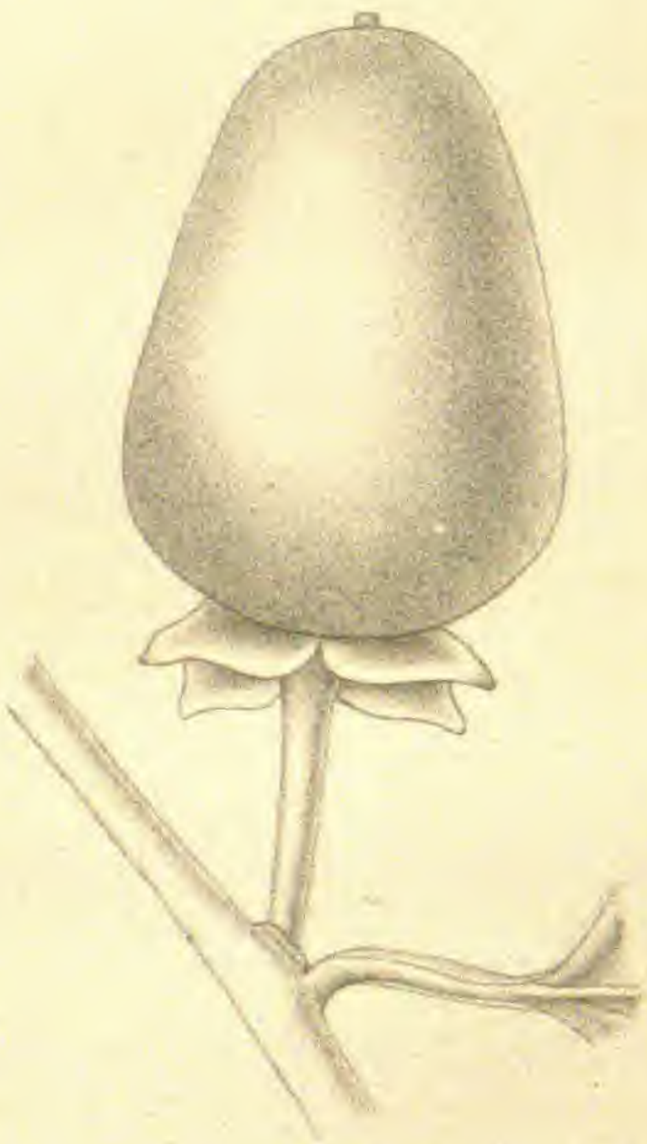

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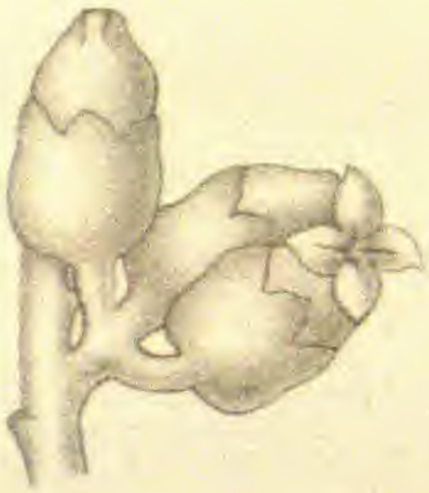

W. de Alwis et H.W. del. Imp. Aust. r. E. A. Funke Leipzig.

D. AFFINIS (1-6), D. TOPOSIA (7-10).

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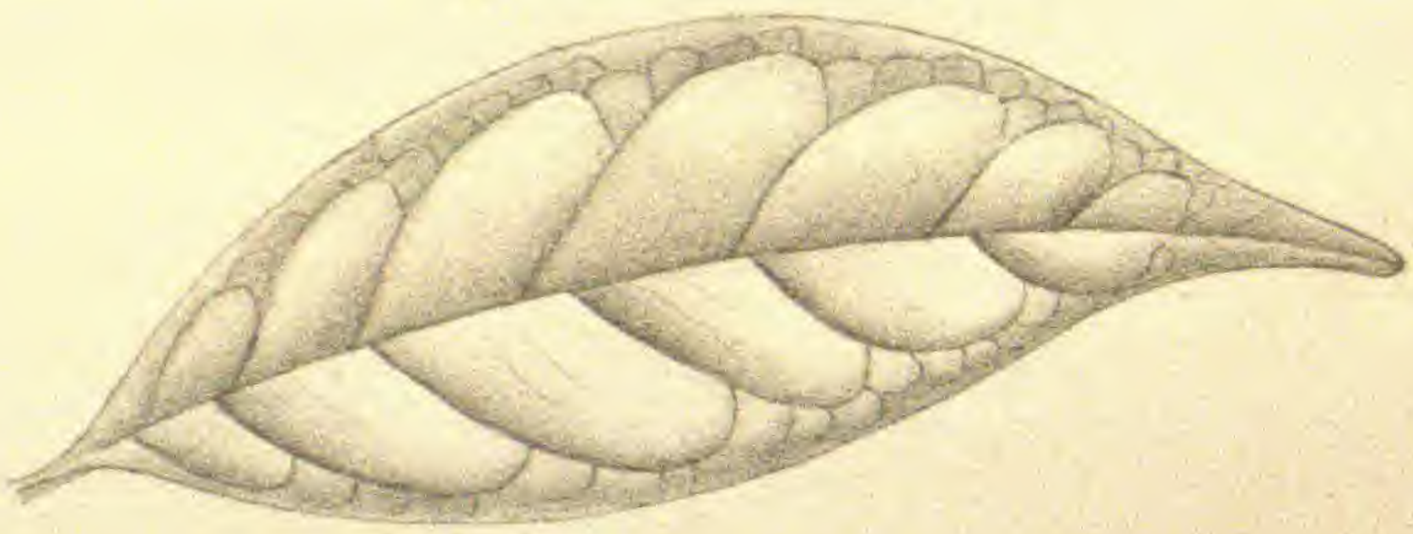
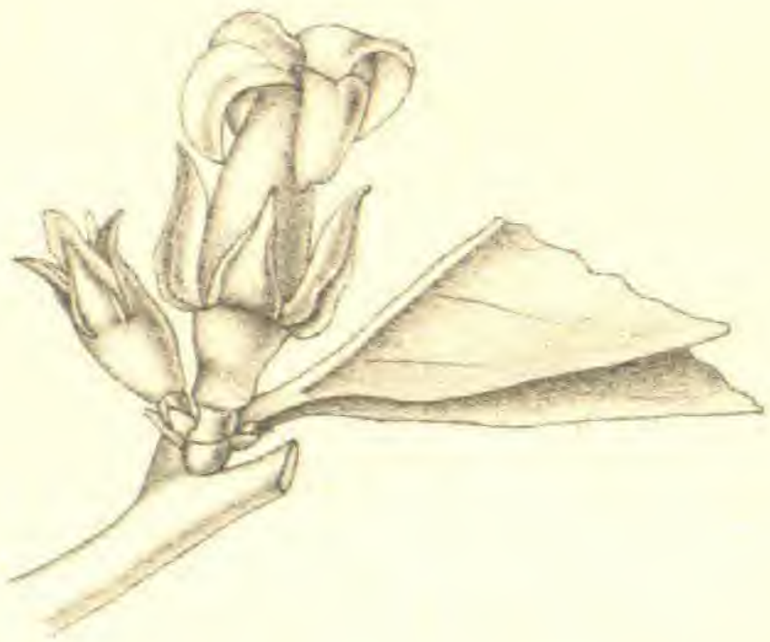


11.

W. de Alwis et H.W. del. Lith. Anst. v.E. A. Funke Leipzig.

D. SYLVATICA (1-9); D. ATTENUATA (10-15).

1.



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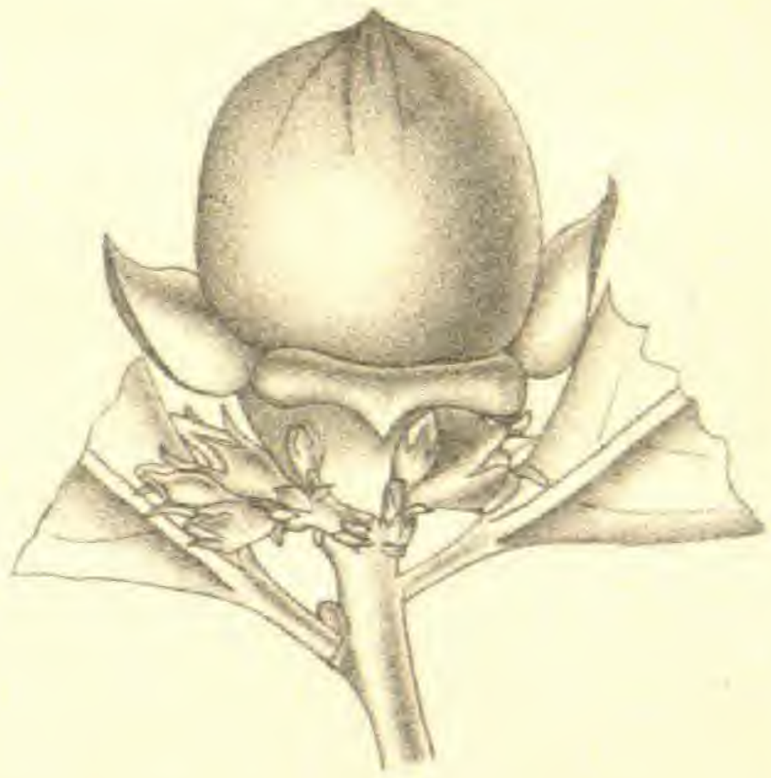

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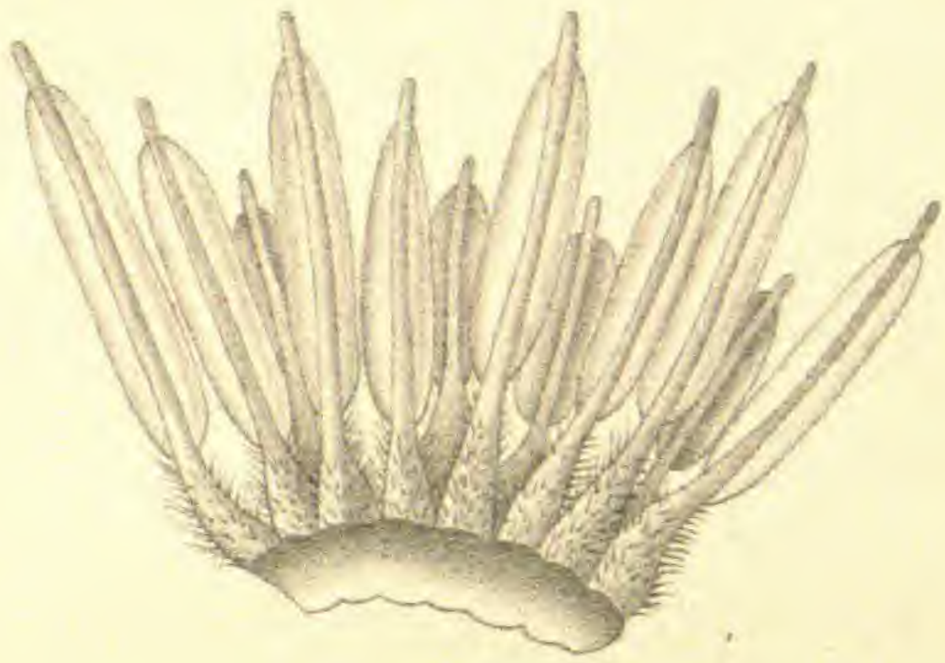

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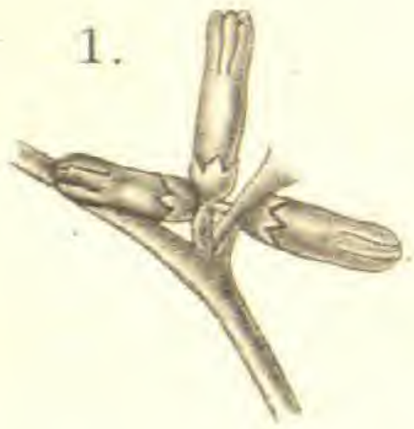
W. de Alwis et H.W. del.

Lith. Anst. v. F. A. Funke Leipzig

D. GARDNERI.

1.



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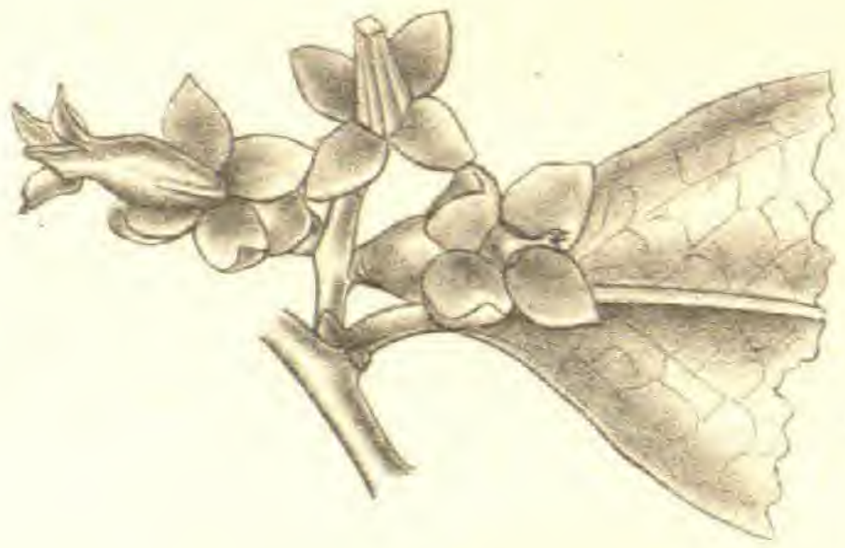

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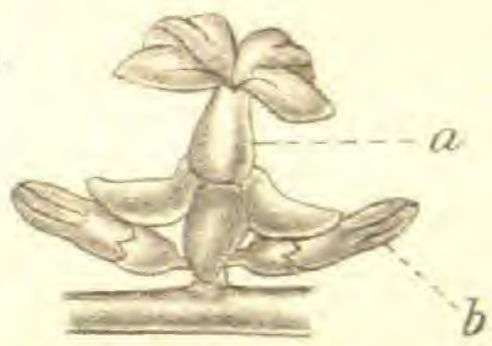

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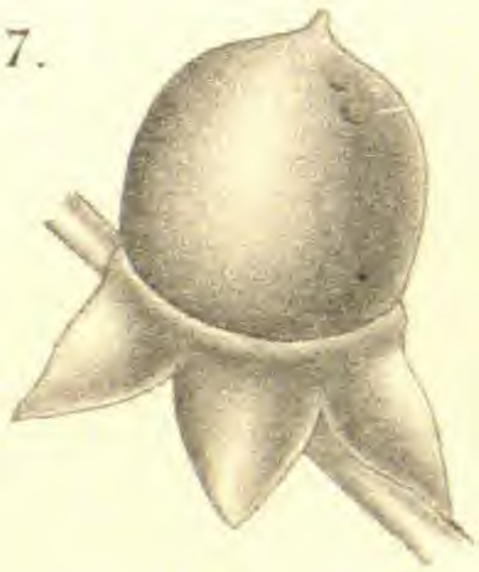

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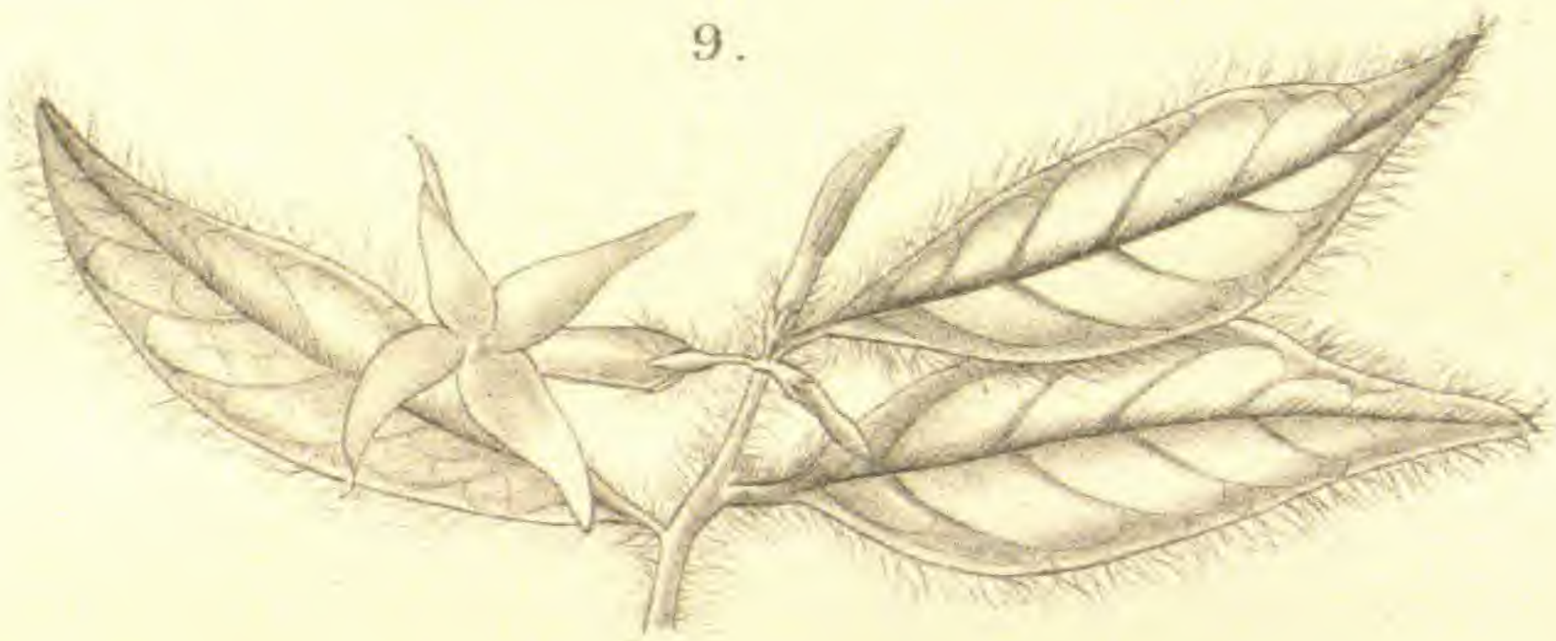

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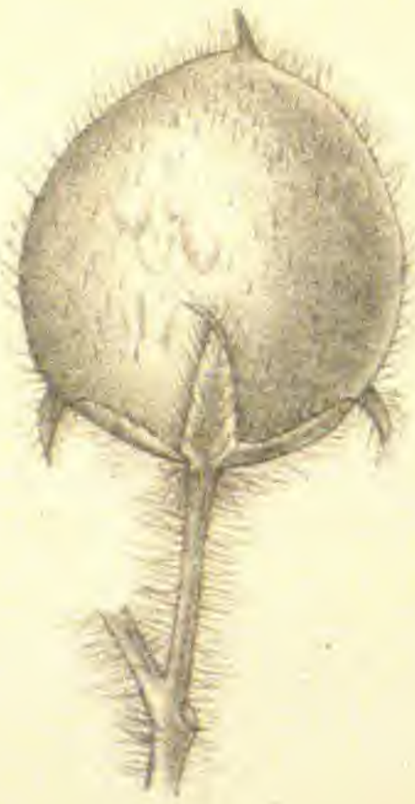
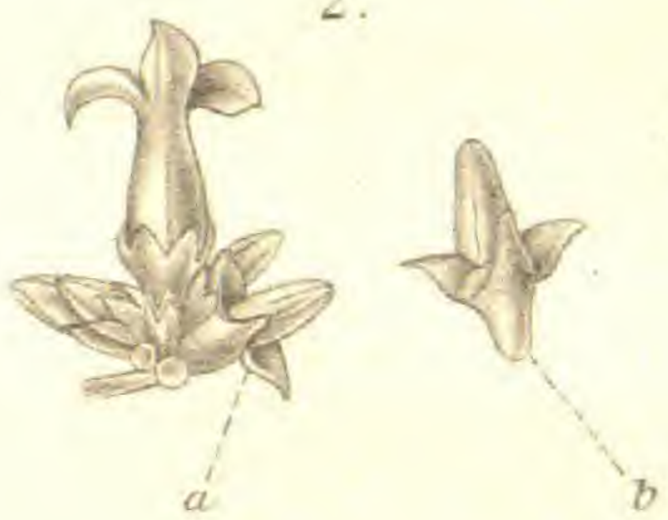


12.

W. de Alwis et H.W. del. Lith. Anst. v.E. A. Funke, Leipzig

D. EBENUM. (1-8), D. PRURIENS (9-12).

1.



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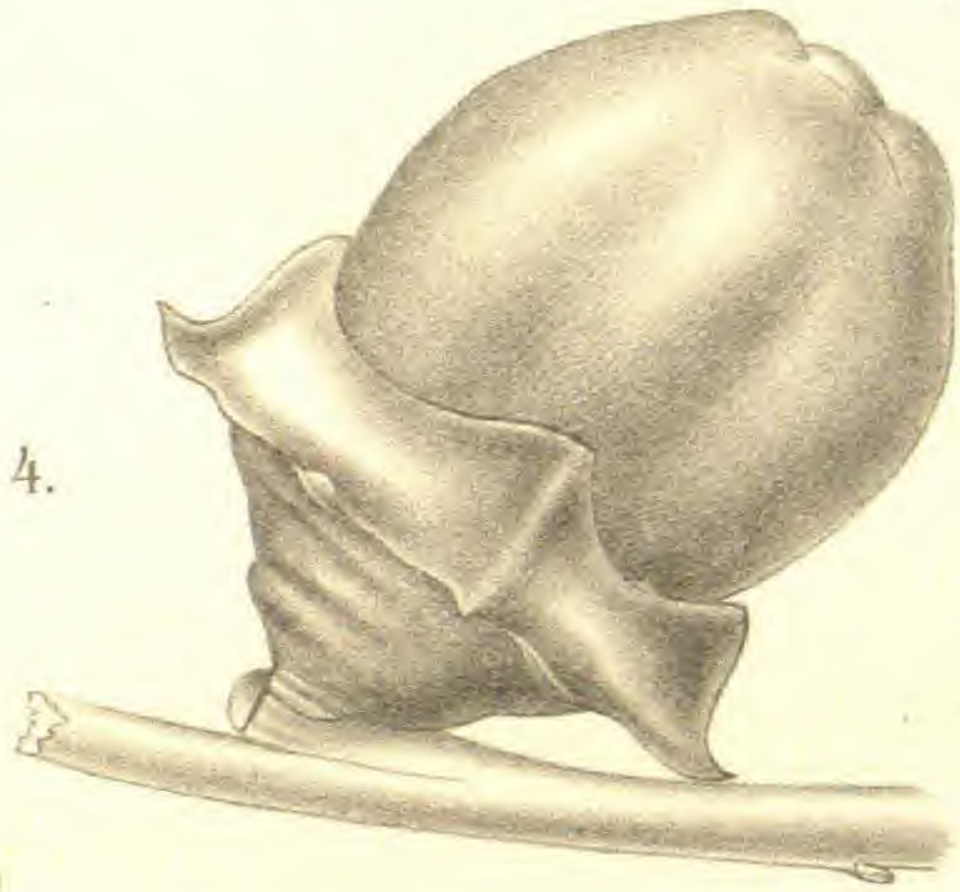

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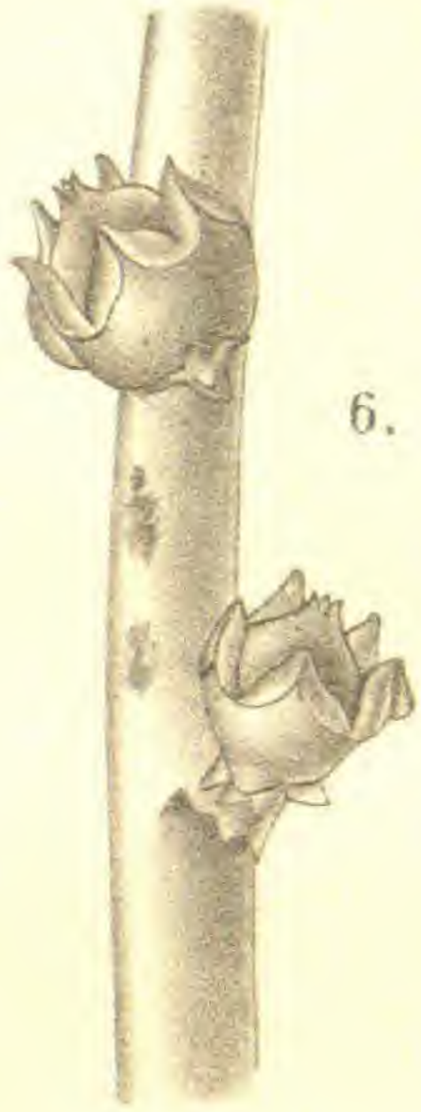

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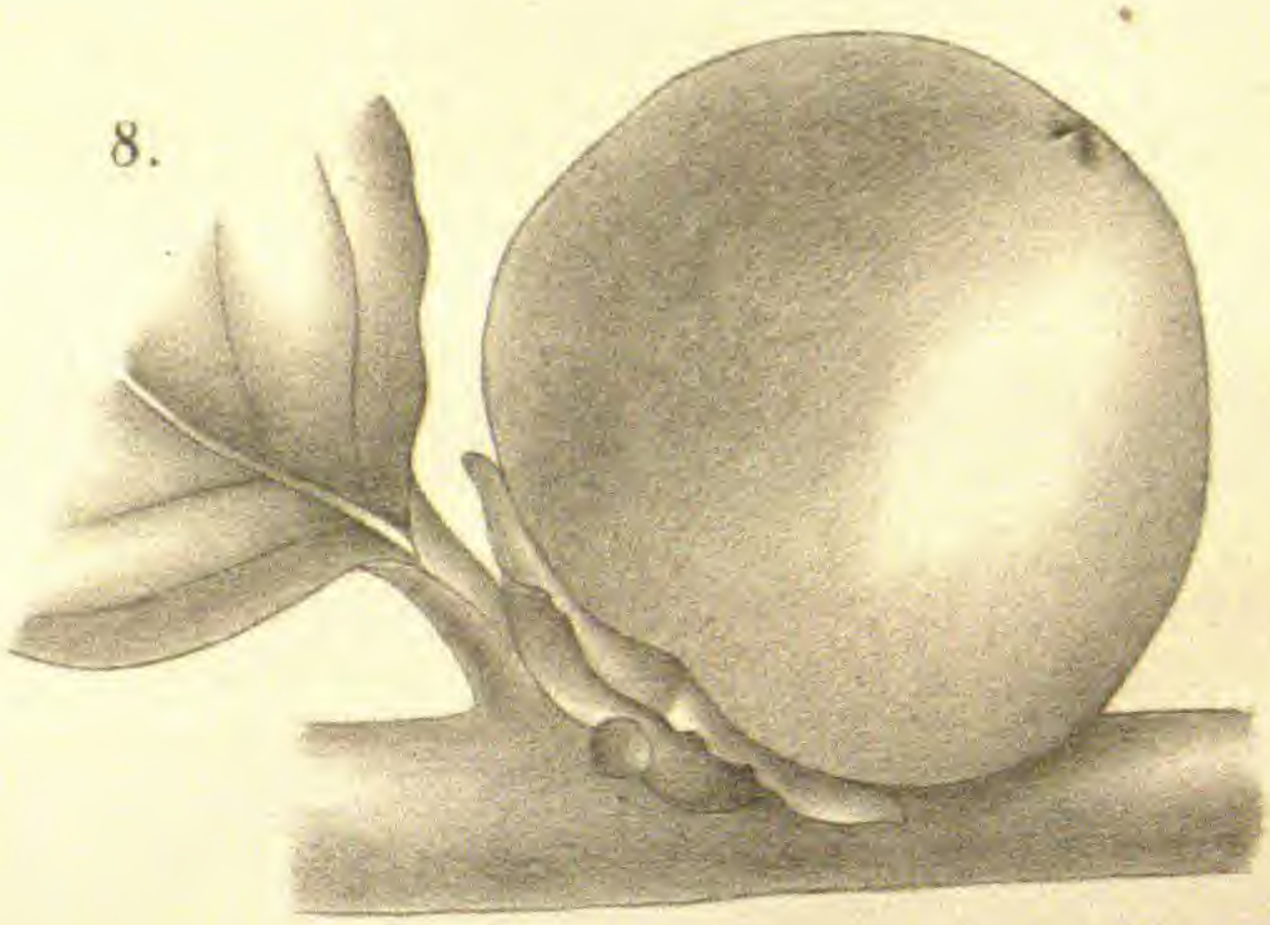

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W. de Alwis et H.W. del. Lith. Anst. v. F. A. Funke, Leipzig.

D. INSIGNIS (1-5). . D. MOONII (6-10).

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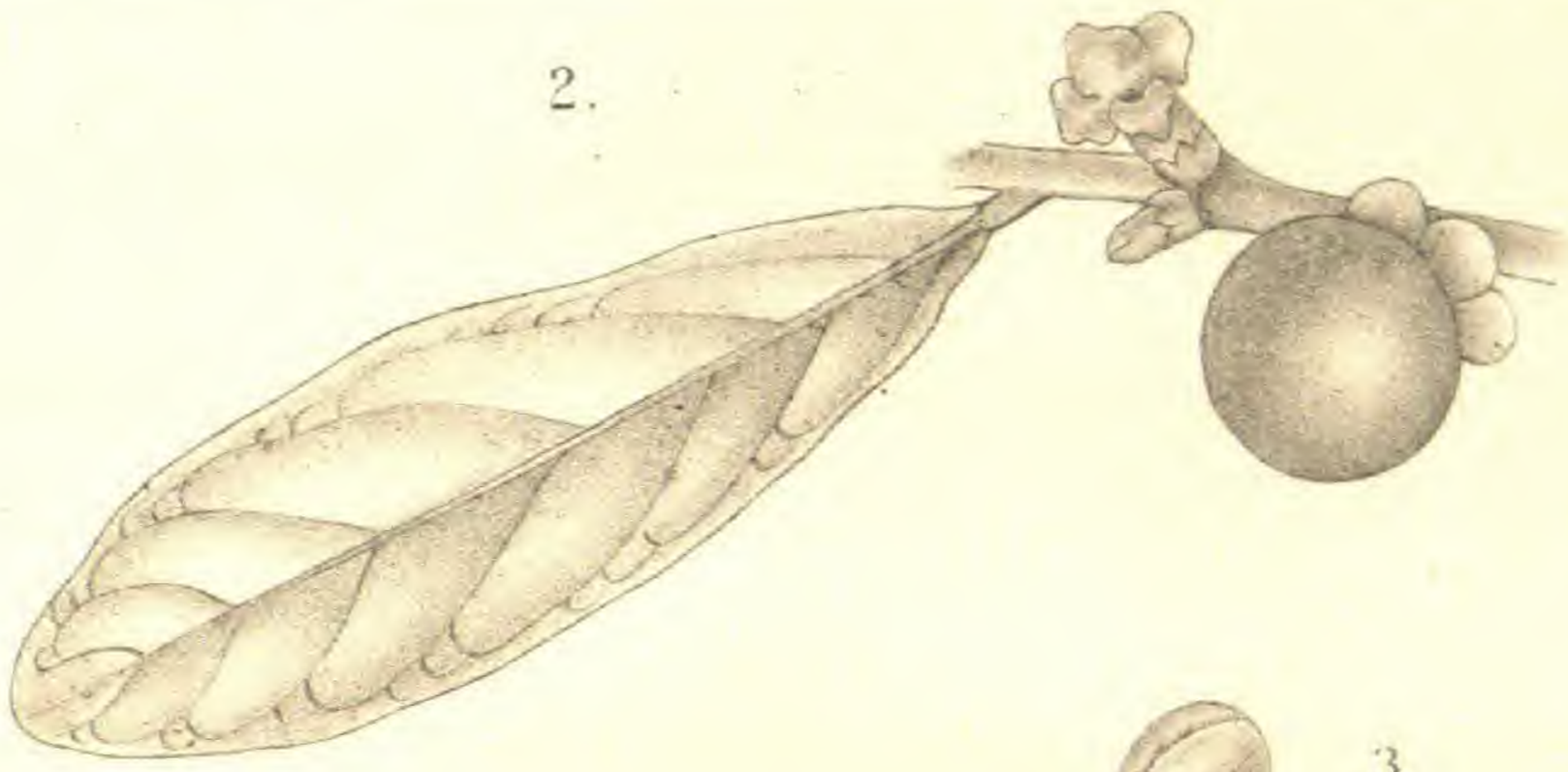

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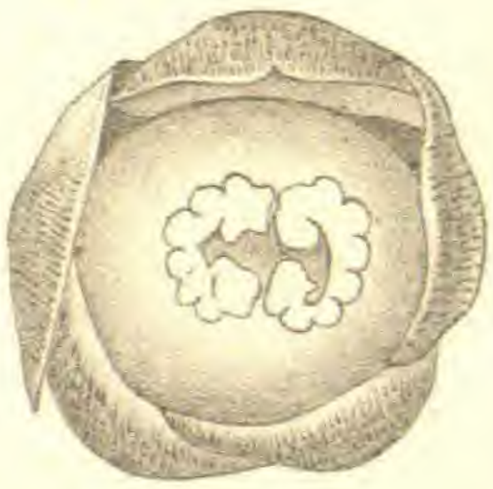

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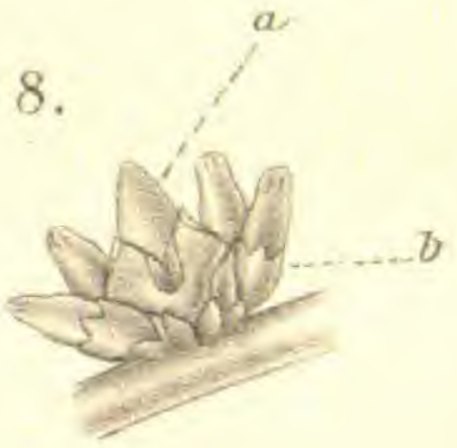

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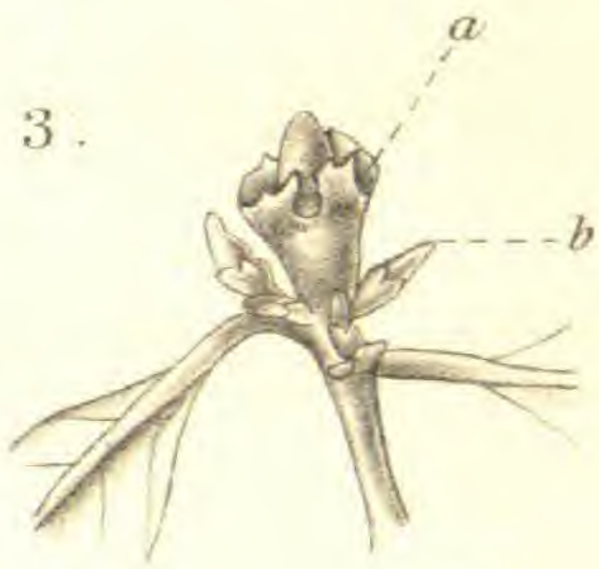
W. de Alwis et H. W. del.

Lith. Anst. v. E. A. Funke, Leipzig.

D. OVALIFOLIA (1-5). D. HIRSUTA (6-12).

1.

3.



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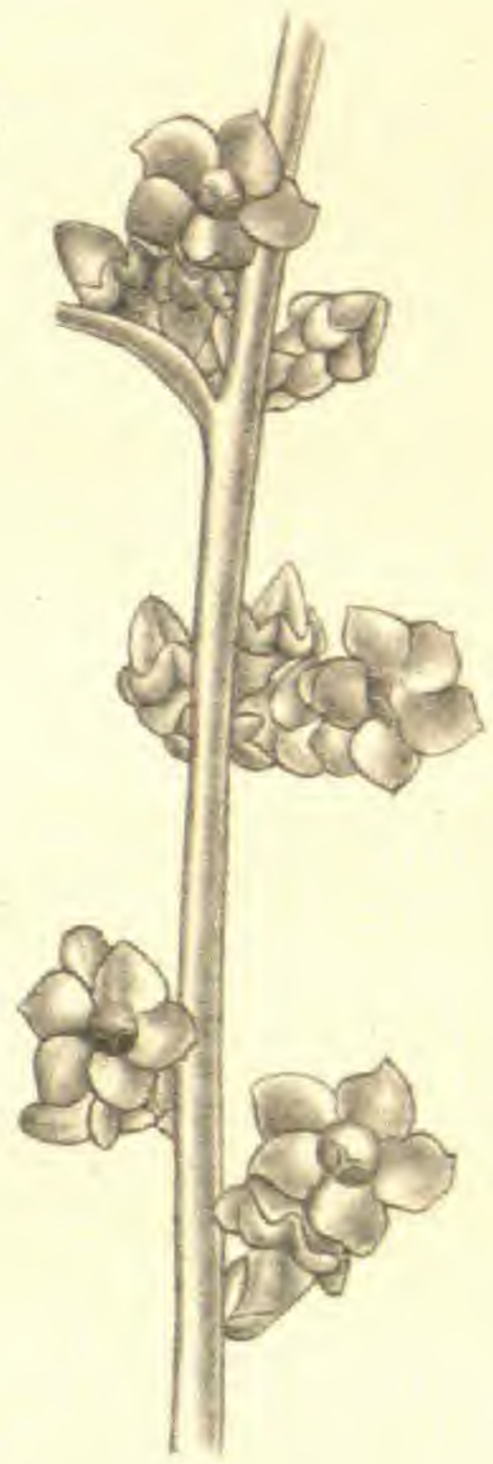

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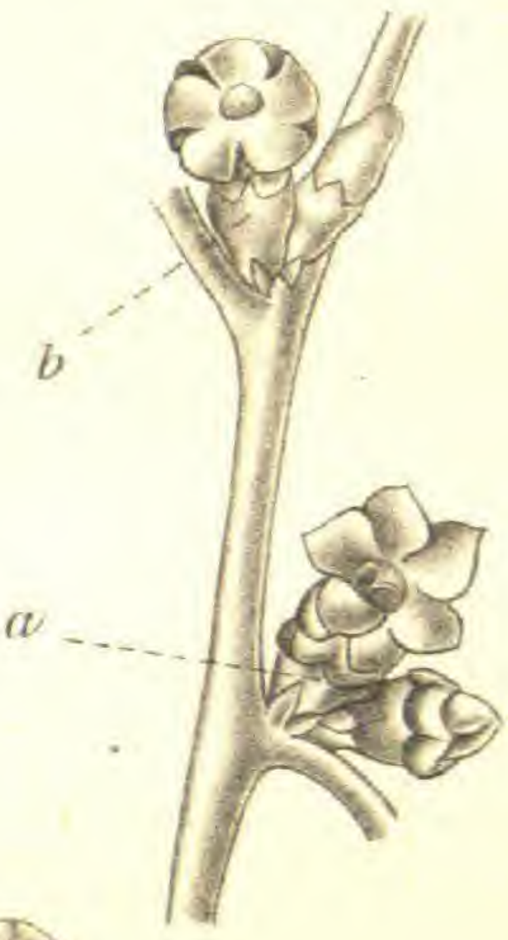

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Lith Anst. v. E. A. Funke, Leipzig.

W. de Alwis et H.W. del.

D. THWAITESII (1-6), D. MONTANA (7-10).

W. de Alwis et H. W. del. Lith. Anst. v. E. A. Funke, Leipzig.

D. INSIGNIS (1-3), D. TOPOSIA (4), D. SYLVATICA (5-6).

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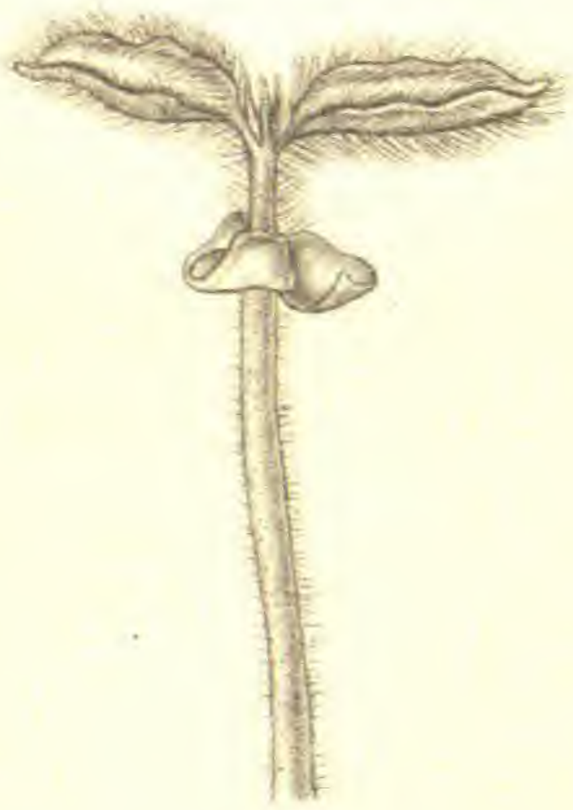

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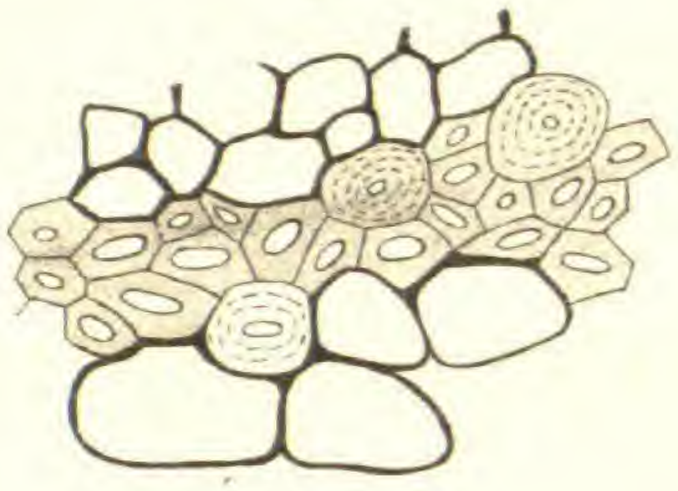
W. de Alwis et H.W. del.

Lith. Anst. v. E. A. Funke, Leipzig

D. PRURIENS (1–5), D. CRUMENATA (6).
D. EMBRYOPTERIS (7–9), D. EBENUM (8).

1.



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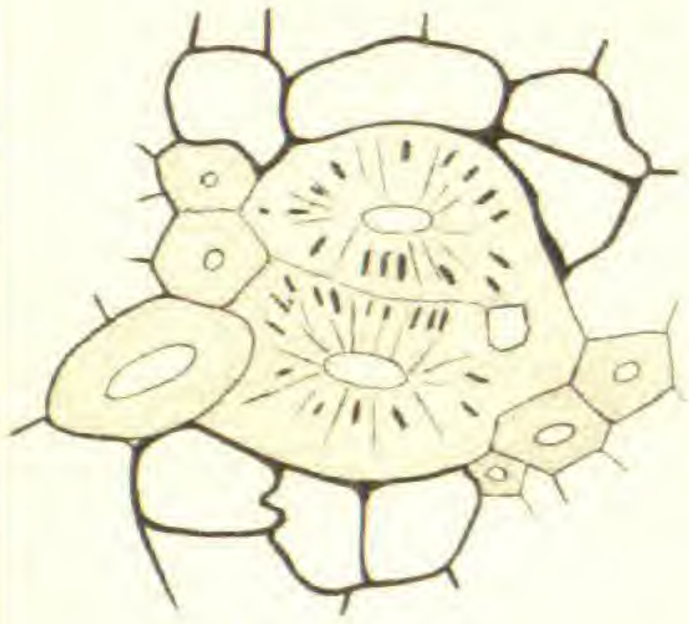

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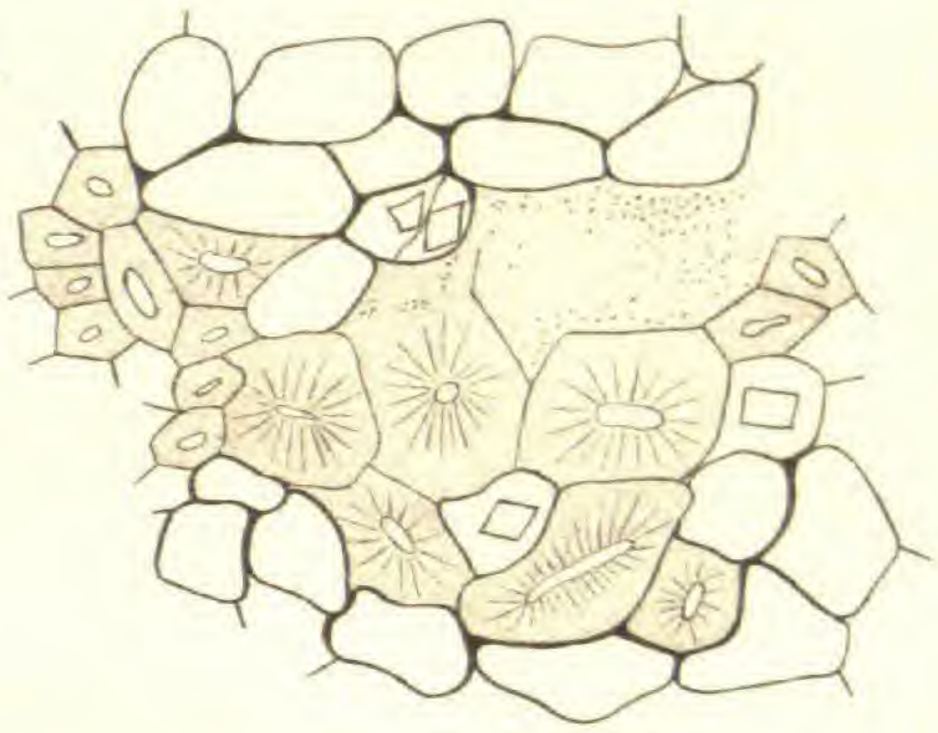

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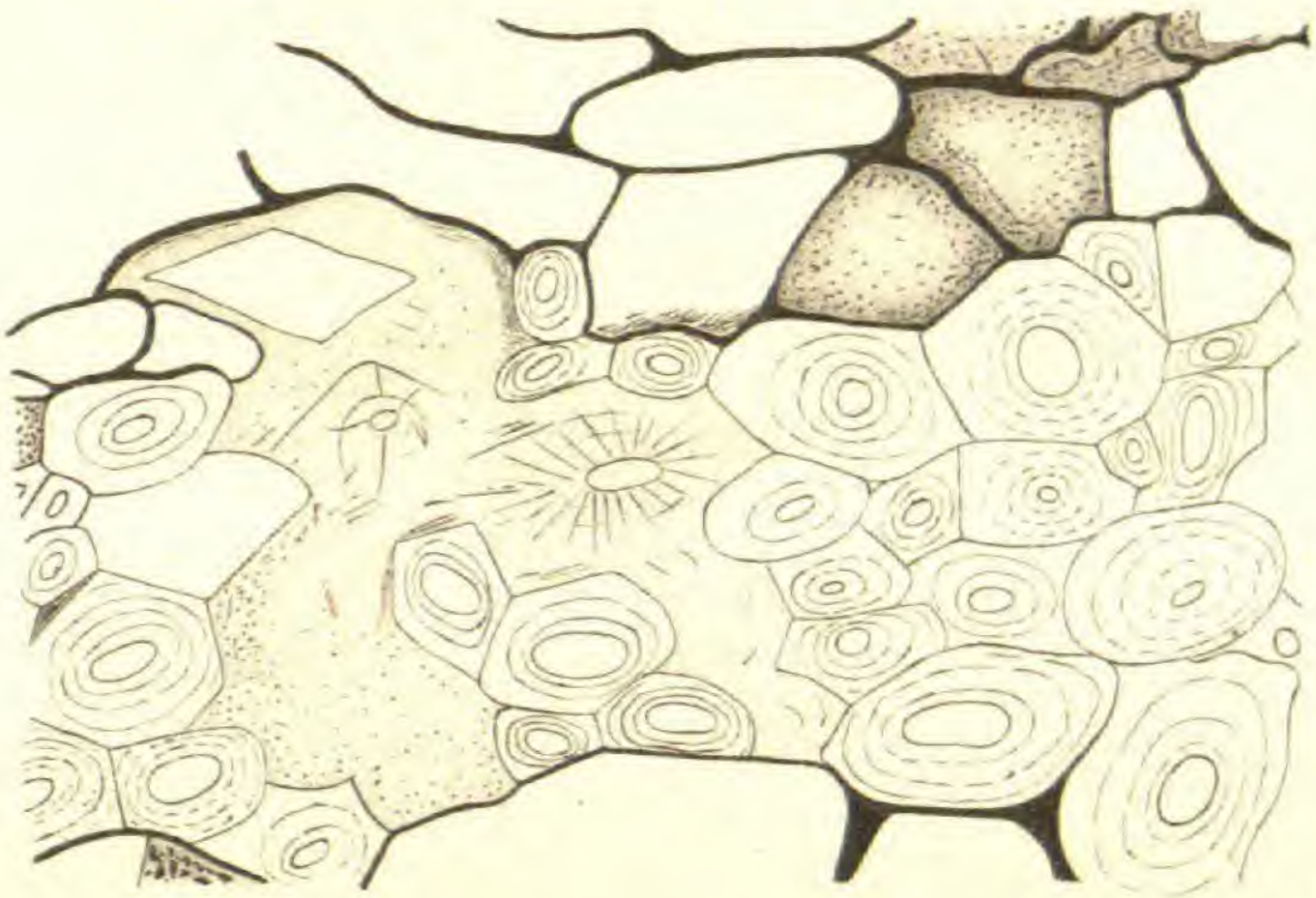

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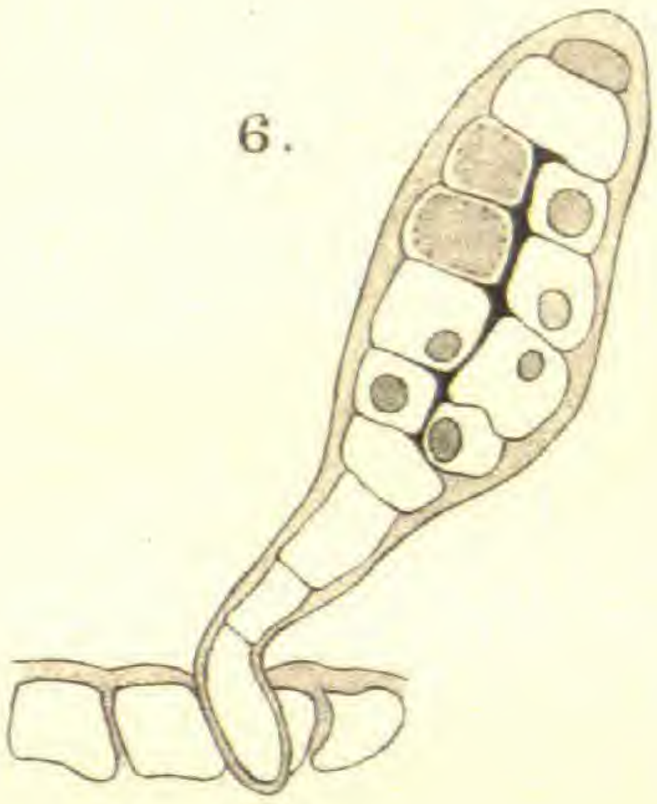

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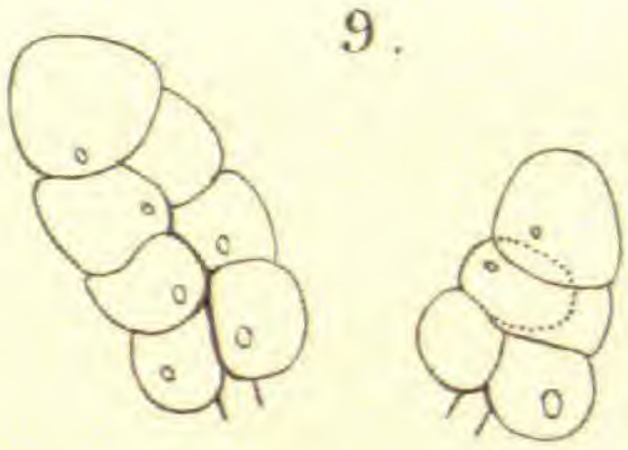

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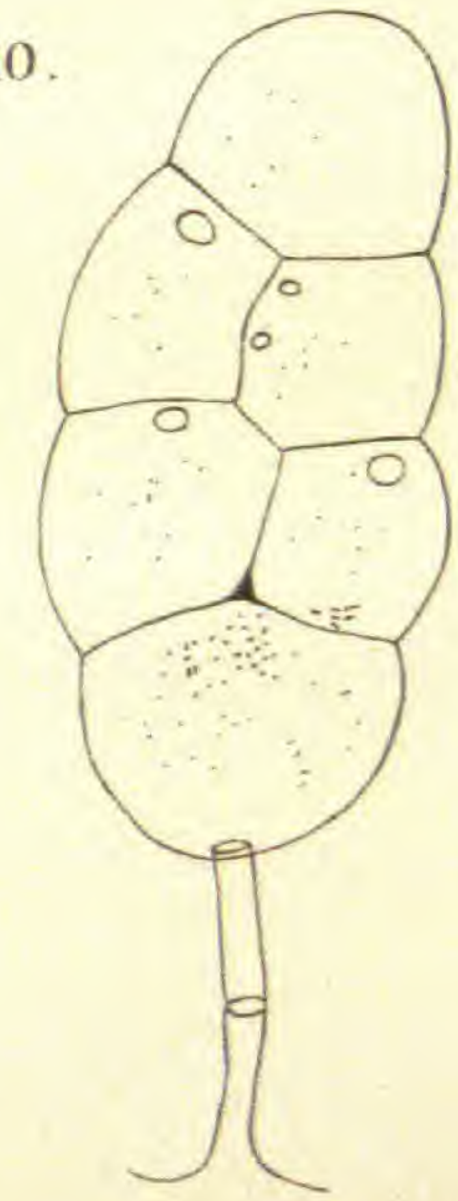

Herbert Wright del.

Lith. Anst. v. F. A. Funke, Leipzig.

D. EBENUM.

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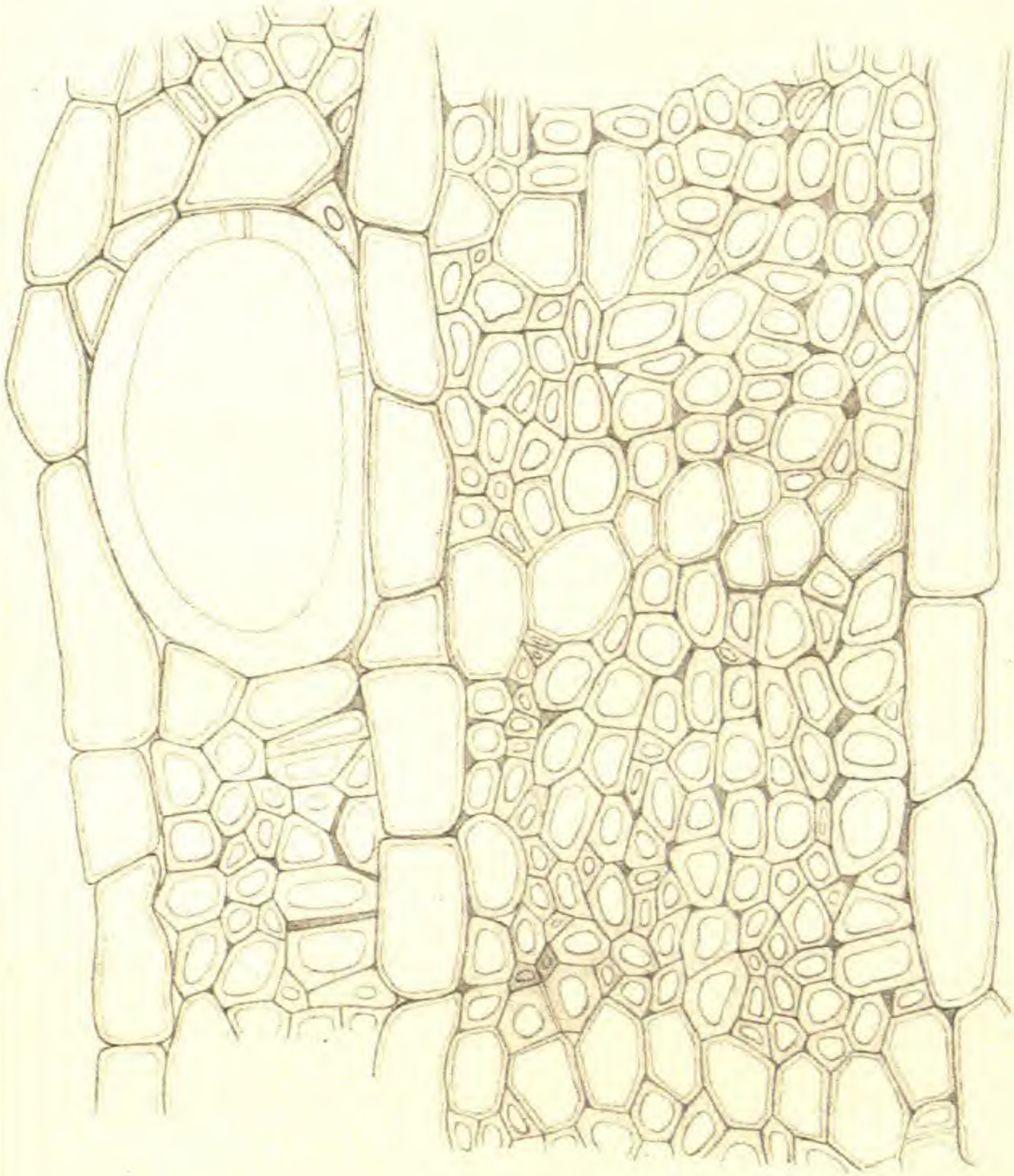

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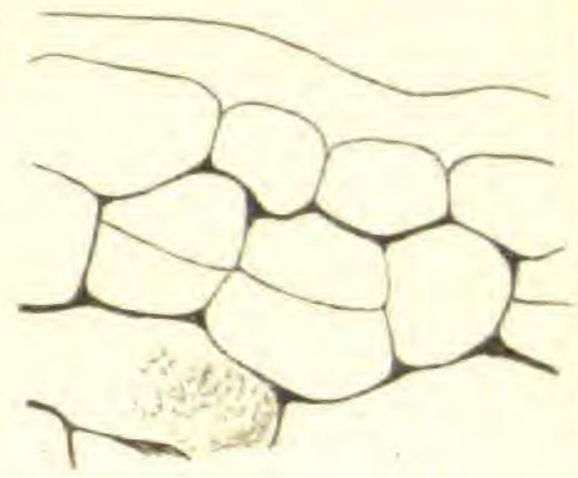

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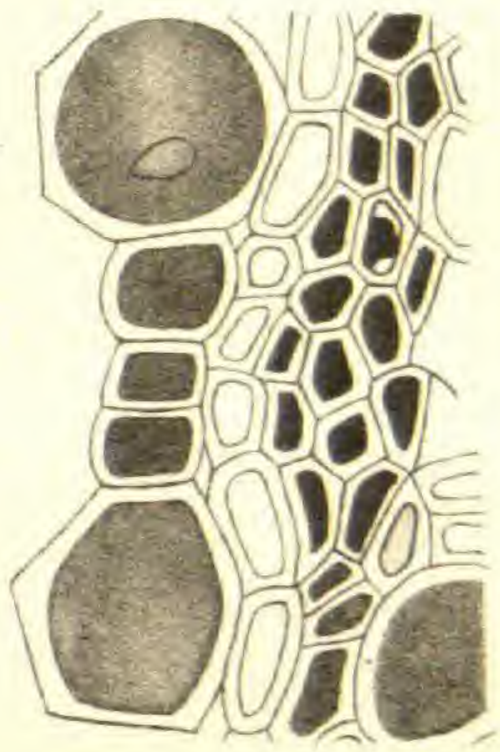

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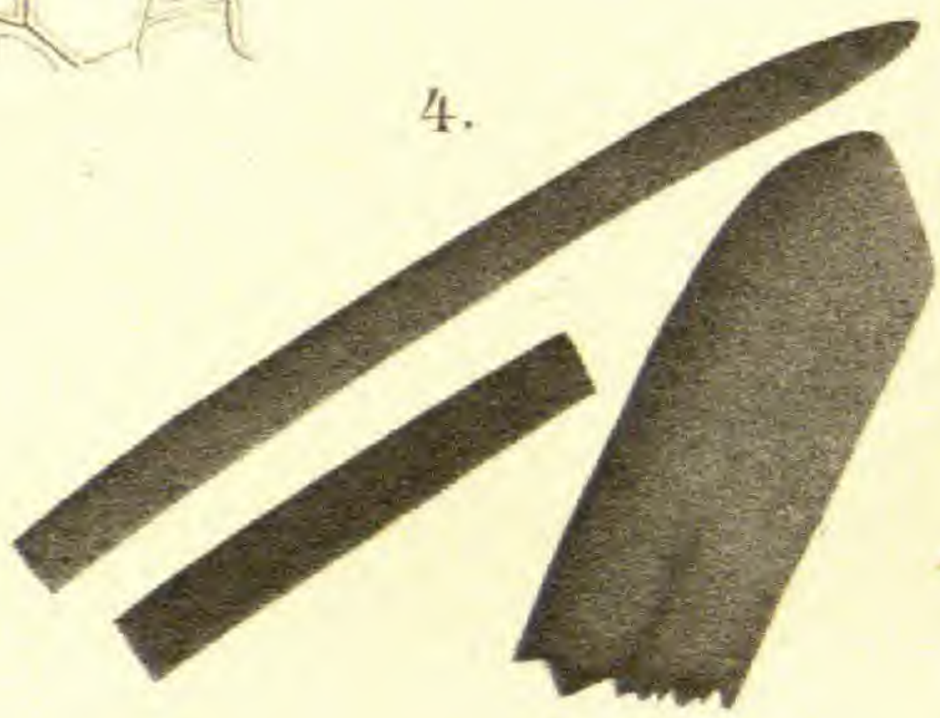

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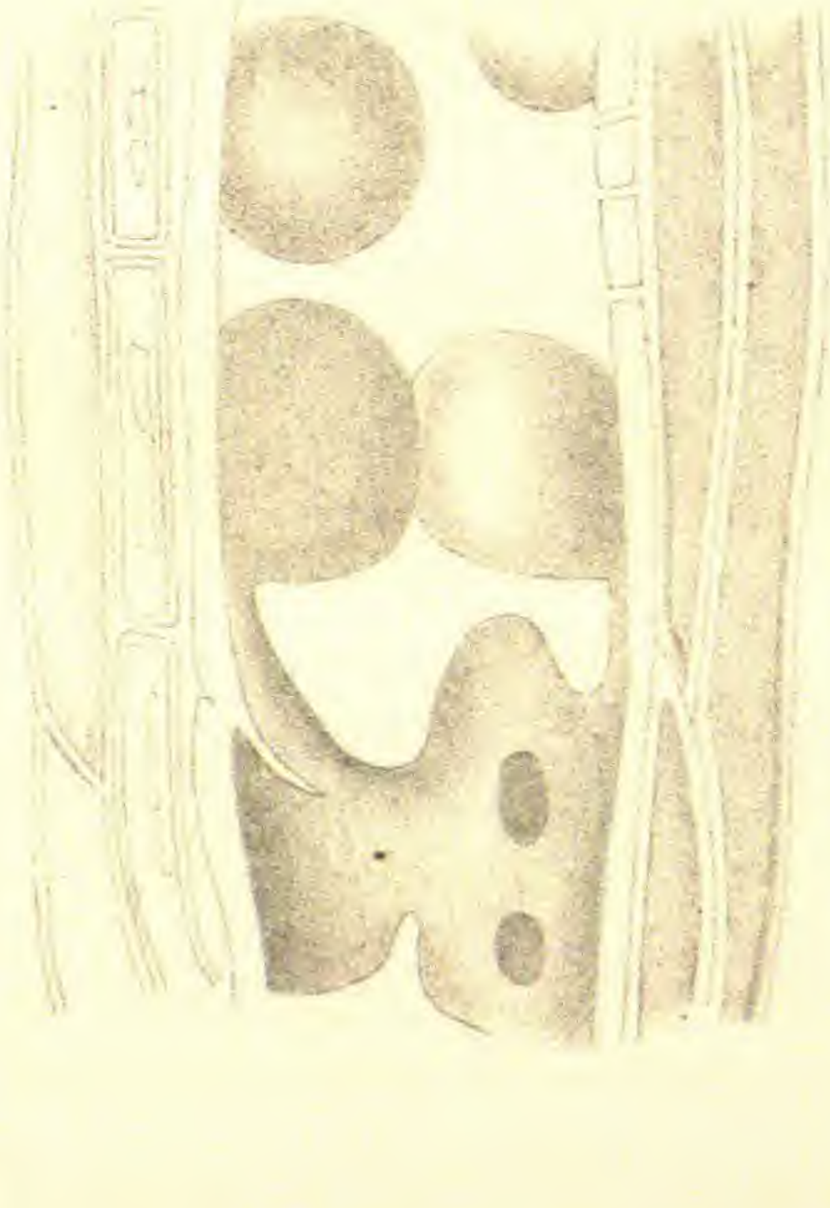

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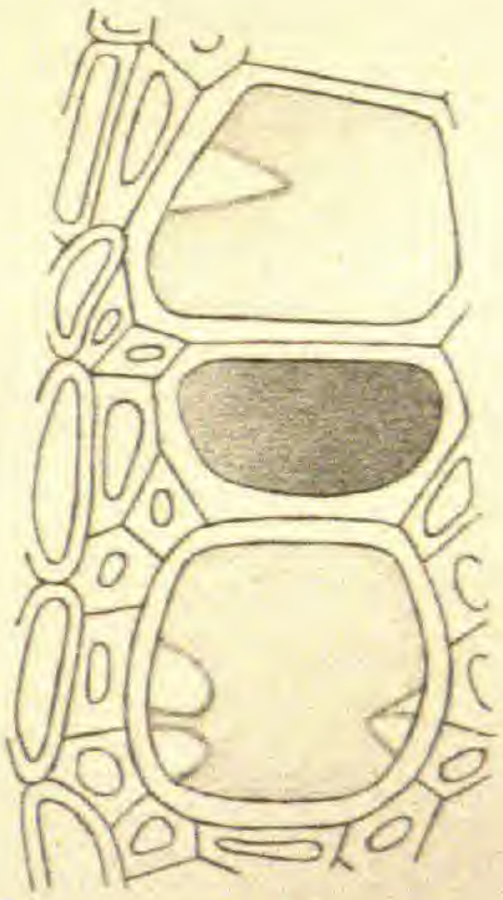
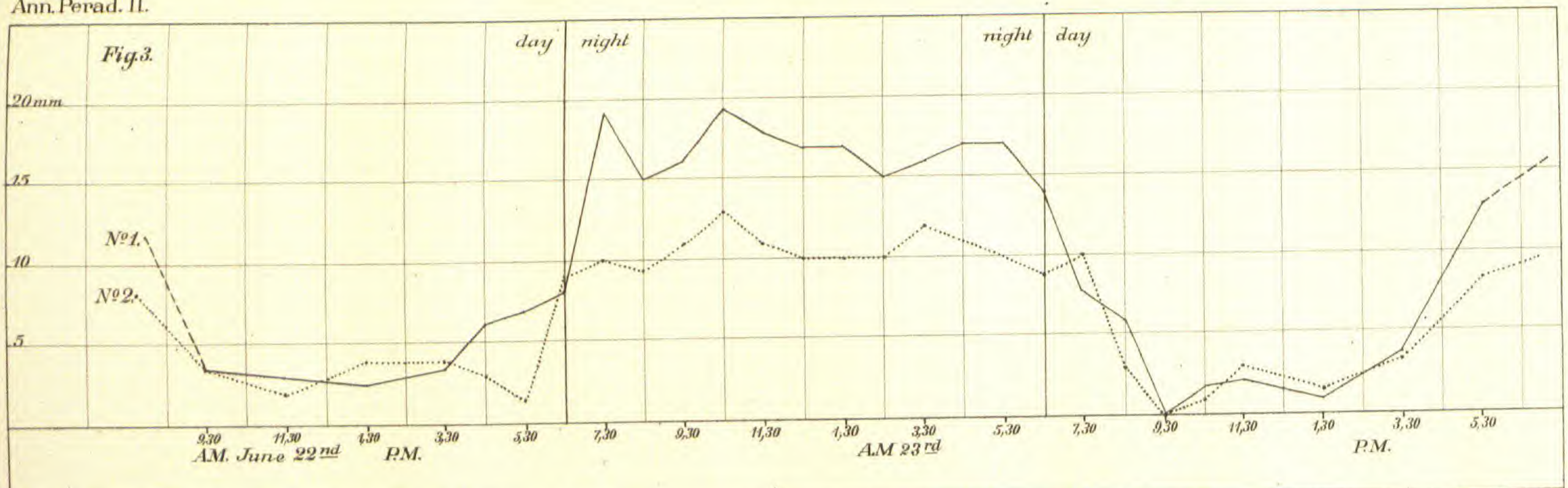
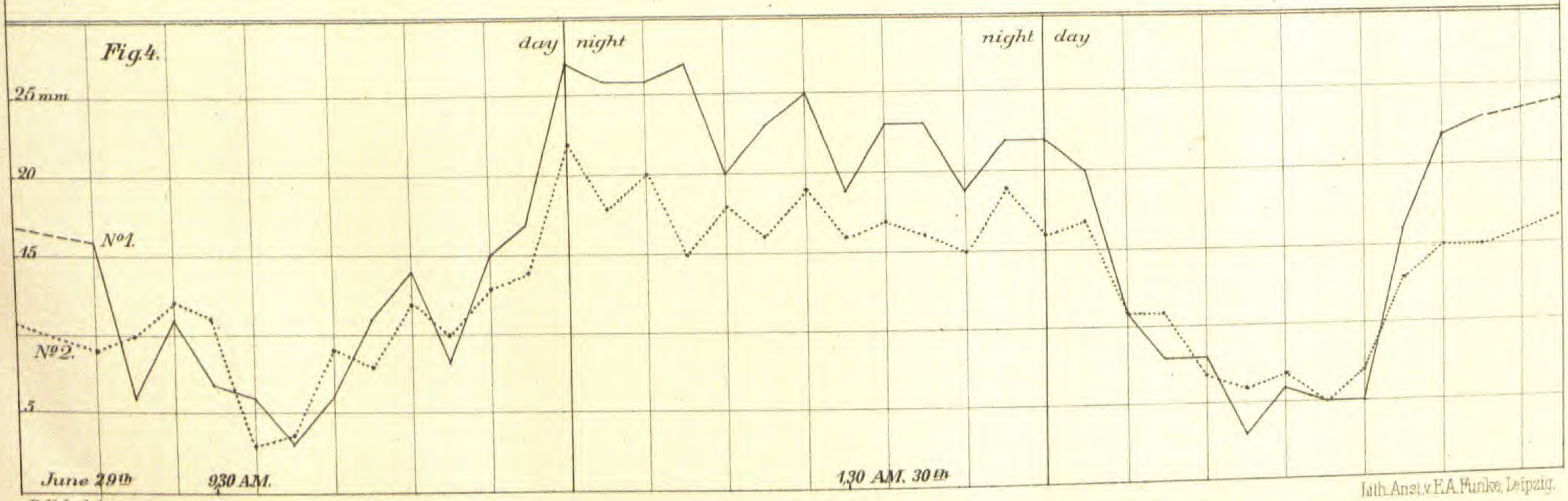


Herbert Wright del.

Lith Anst.v.E. A.Funke Leipzig.

D. EBENUM.





R.H.L. del.

Lith. Anst. v. F.A. Funke, Leipzig.

DENDROCALAMUS

Fig. 5.

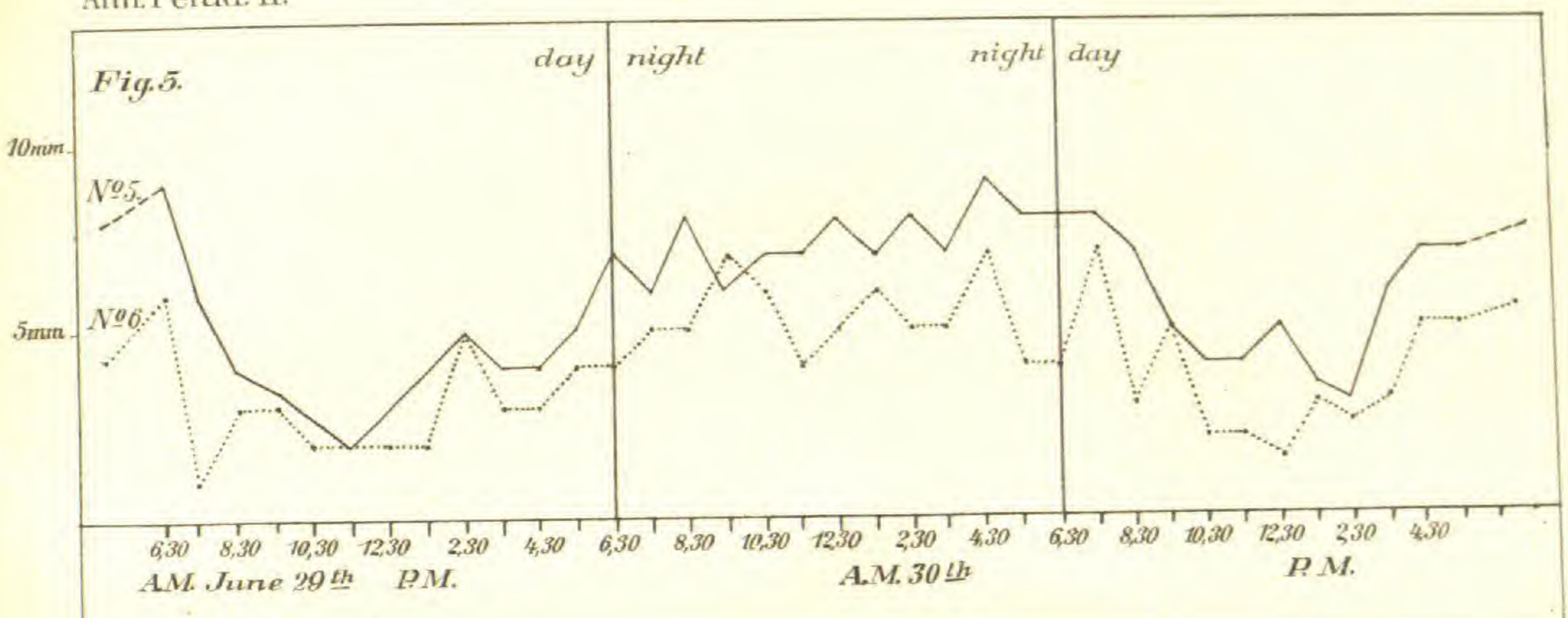


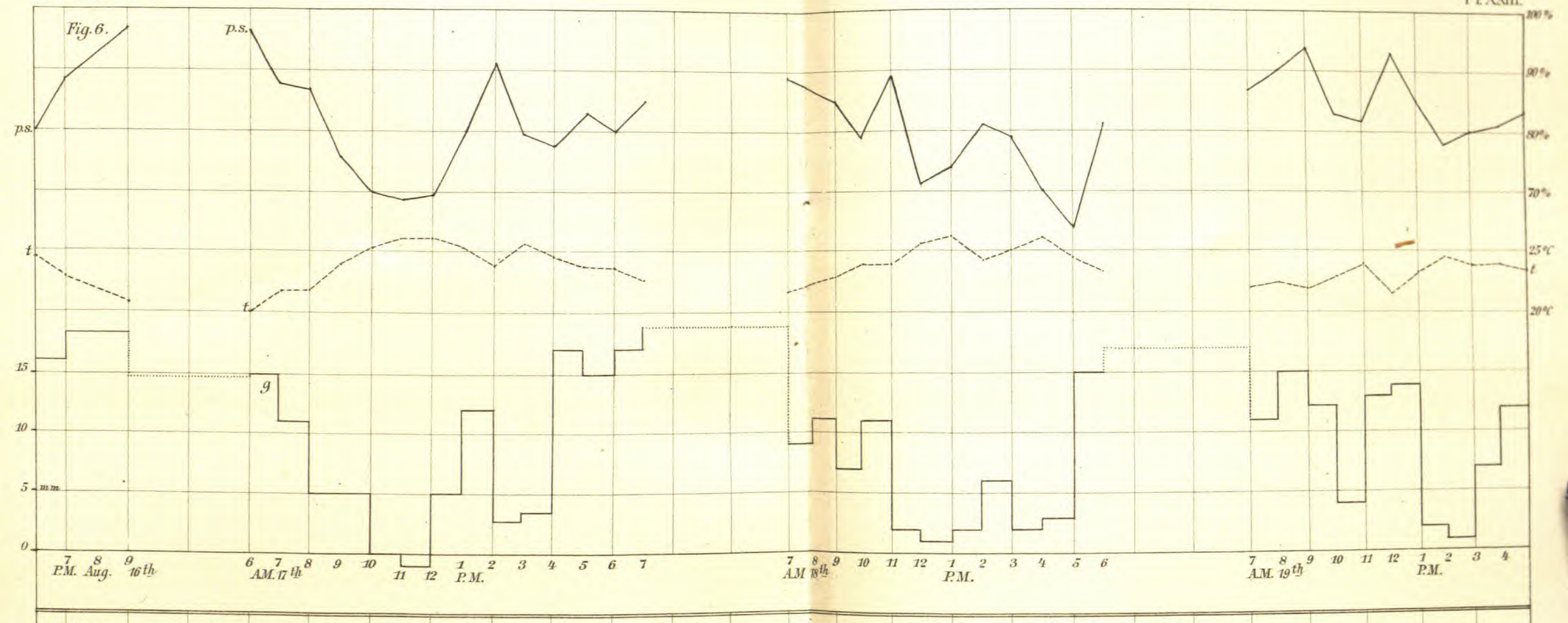
Fig. 2.

R.H.L. del.

Lith. Anst. v. E.A. Funke, Leipzig.

DENDROCALAMUS and GIGANTOCHLOA

Fig. 6.



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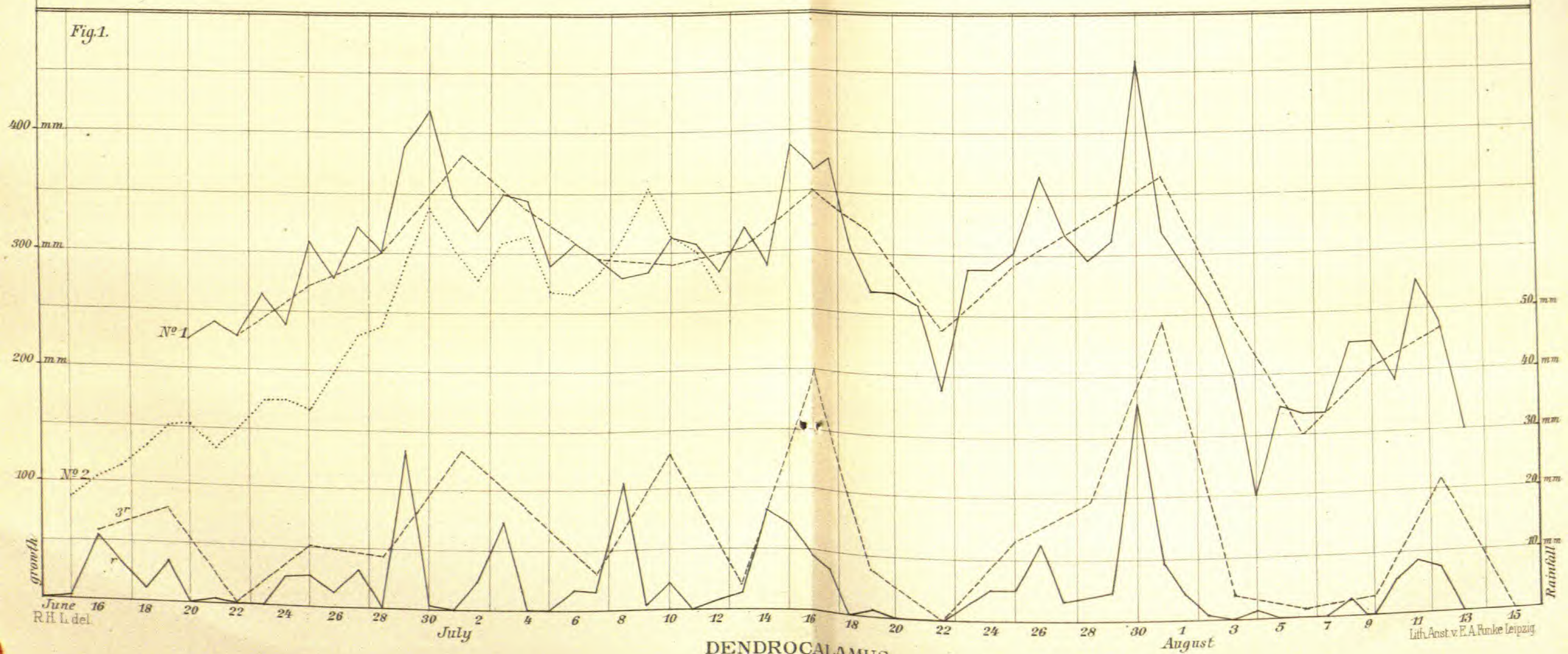

R.H.L. del.

Lith. Anst. v. E.A. Funke Leipzig.

DENDROCALAMUS.

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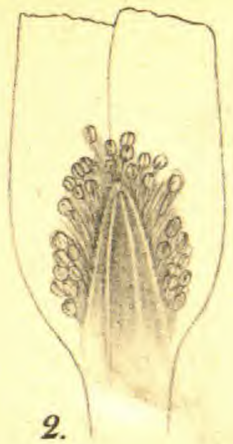
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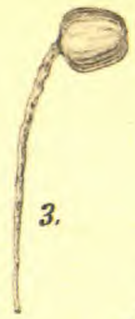
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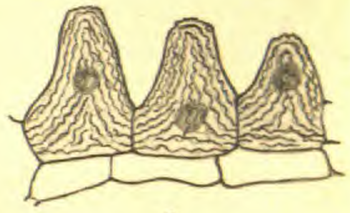
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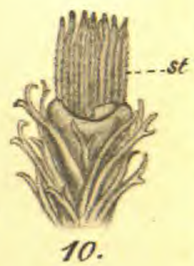

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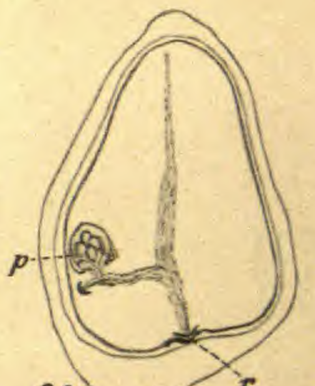

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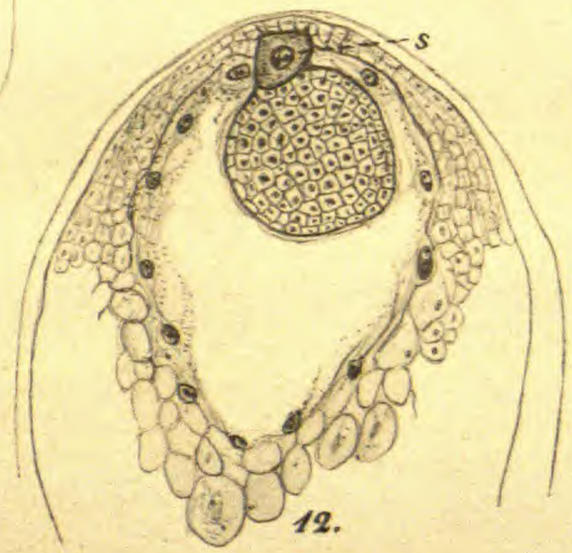

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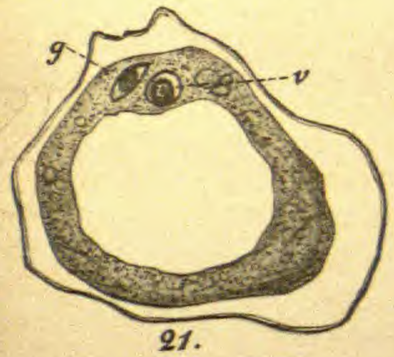

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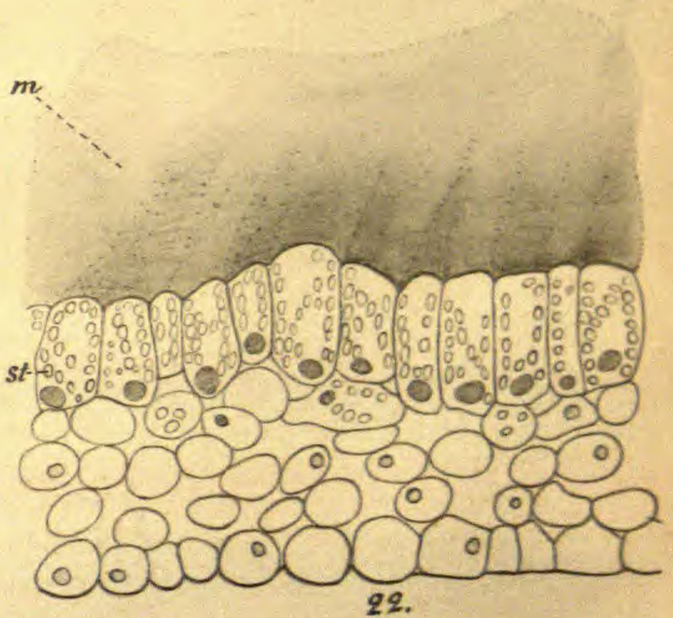

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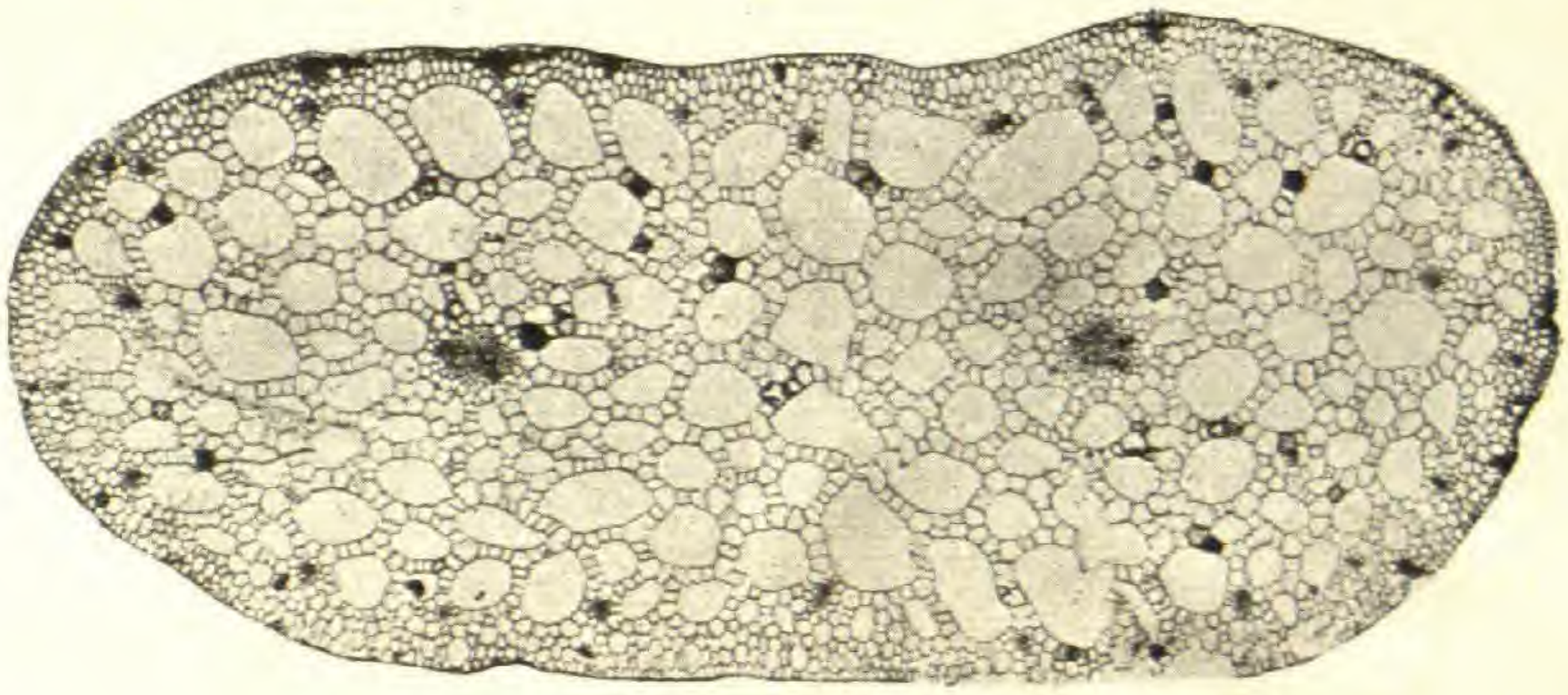

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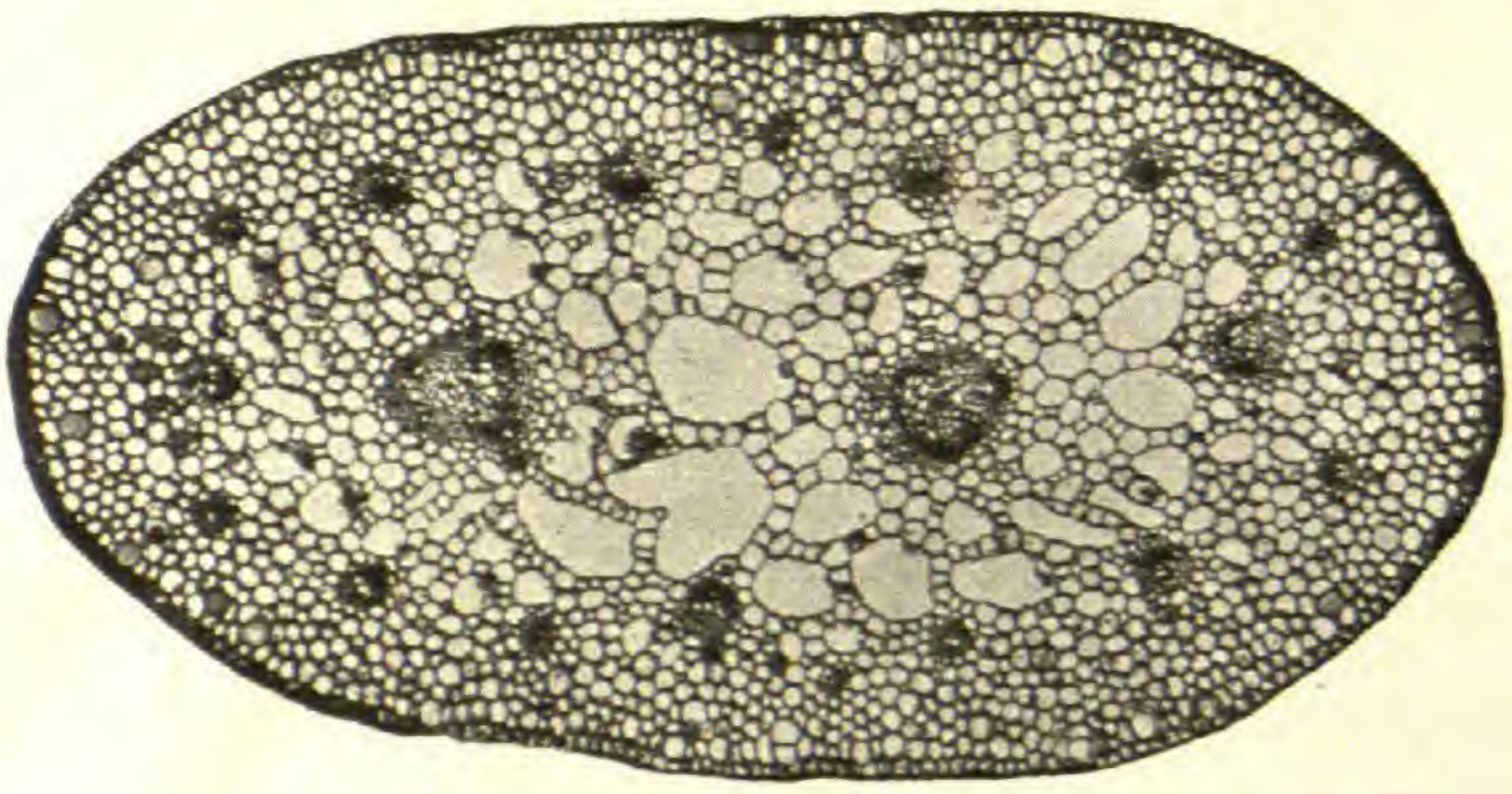

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Juel et Sved. phot. **Enalus acoroides.**

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OF THE

ROYAL BOTANIC GARDENS,

PERADENIYA.

EDITED BY

HERBERT WRIGHT, A.R.C.S., F.L.S.

LATELY ACTING DIRECTOR.

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REVIEWS.

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Studies in Plant Breeding in the Tropics.

BY

R. H. LOCK.

The publication of this number has been seriously delayed, not by lack of material, but on account of the serious accident that befel Dr. Willis last March. It should have appeared in May. The next number will appear after as short an interval as possible.

Summary.

IN a previous communication to these Annals* some account was given of those recent advances in our understanding of the physiology of inheritance which have been derived from studies in the cross-breeding of plants; and in the same paper was embodied a preliminary description of certain experiments carried out by the writer, which form a contribution to the same subject. It remains to set forth a more complete account of the observations already

* Page 299, Annals of the Royal Botanic Gardens, Peradeniya, Vol. II., Part II., August, 1904.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. II., Part III., October, 1905.]

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Studies in Plant Breeding in the Tropics.

BY

R. H. LOCK.

(Fellow and late Frank Smart Student of Gonville and Caius College, Cambridge.

II.—EXPERIMENTS WITH PEAS.

CONTENTS.

Introduction: Climate and acclimatization. Methods.
1.—Telegraph crossed with Native Pea No. 1.
2.—Telegraph crossed with Ringleader.
3.—Telephone crossed with Native Pea No. 1.
4.—Telephone crossed with Ringleader.
5.—French Sugar Pea crossed with Native Pea No. 1.
6.—Native Pea No. 2 crossed with Satisfaction.
7.—Other crosses.
Summary.

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partly announced, and to add to the number some further experiments which bear in the same direction.

The object of these experiments was two-fold. They were designed in the first place to test the conclusions of Mendel and of those other botanists who in recent years have extended and confirmed his observations; and they were also undertaken with a view to applying these theoretical principles to the practical processes of plant breeding. To this attempt was added a special interest from the fact that it was to be made in a tropical country, under circumstances in which very little work of this kind had been previously carried out.

At the outset attempts were made to effect cross-fertilization between varieties of a considerable number of different species of plants, some of them natives of the tropics and others introduced from a temperate region. Many of these attempts met with only partial success, as indeed was to have been expected, and others were quite unsuccessful. Including all the cases of plants from which fertile offspring were obtained by crossing, a considerably larger number of experiments was begun than could have been completed if all had progressed without misfortune. But the progress of the work met with a variety of difficulties; and furthermore, the surviving cross-bred plants underwent a kind of natural selection, the losses being determined by such factors as an unfavourable climate, a want of experience of the best conditions of growth, the attacks of fungi, insect pests, and the like. In the end the experiments with Indian corn and with peas were found to be the only ones which yielded results of any importance. In the present instalment I shall confine myself to an account of the evidence derived from peas.

In the case of experiments with peas, Mendel's own results, as well as a number of more recent observations, could be put to a practical test. In work of this kind, if it is desired to pass beyond the stage of merely confirmatory experiments, it is often necessary at the outset to make crosses more or less at random between such forms as may be at hand, in the hope that some of the results will

afford interesting exceptions to the ordinary routine of Mendelian experience. And the work of the practical breeder must usually have its beginning in similar speculative experiments; since from the present state of our knowledge no one can foretell with any degree of certainty the result of a particular cross which has not been previously made. Indeed, one of the chief aims of this class of experimental work is the attainment of a system of knowledge which will in some degree enable us to foretell the results of new combinations; but this stage of the inquiry is still far from being realized. The accurate prediction of phenomena is one of the most important effects of all classes of codified scientific knowledge, and there can be no doubt that in the case of the present branch of physiology a similar degree of cognition is attainable; indeed, the advance in this direction has already been one of phenomenal rapidity.

Theoretical reasons led me to select the following strains of *Pisum sativum* for particular study. The pea Telephone was chosen for examination owing to its alleged erratic and exceptional behaviour on crossing. Telegraph, a form nearly allied to Telephone, has been regarded as showing rather less irregularity. As a fresh specific test of these forms they were crossed with a smooth yellow seeded pea commonly grown by natives in Ceylon. For studying the colour characters of the testa, a large "French Sugar Pea" was made use of;* and also a form of *Pisum arvense* of very primitive appearance, and closely similar to one which is known to the natives of Northern India as Chota matar, but which is only rarely grown in Ceylon.

From a practical point of view the method adopted was to grow a series of good European varieties of peas and to cross those which flourished best under the new conditions both with each other and with varieties obtained locally. As large a number as possible of the offspring of these crosses was then grown, and the progeny which showed the best combinations of characters were picked out for further propagation.

* Identical, it appears, with the "Purple Sugar Pea" described by Bateson.

A method which deserves particular emphasis is one which has yielded valuable results in the hands of De Vries, and consists in deducing the character of a particular plant—whether originating in a cross or otherwise—from a study of its offspring by self-fertilization. For this purpose all the seeds of the plant under examination should if possible be sown; but in cases where these are too numerous, at least a considerable sample. The nature, or Mendelian constitution, of any particular cross-bred plant can in this way be deduced, sometimes from the examination of one, or as a general rule of at the most three generations. This method is particularly applicable in a climate under which as many as three generations can be grown in a single year.

In addition to this work on crossing, the writer also attempted some experiments in definite selection on lines similar to those recently described by Johannsen; one of the characters examined being the size of individual pea seeds. These attempts were given up however owing to the apparent impossibility of arriving at anything approaching to uniform conditions between plant and plant, or between generation and generation. The latter difficulty was perhaps the more serious of the two, owing to differences in the rainfall and other conditions of climate at different times of year. In order to carry out such an experiment properly, only one generation must be grown each year, and further, the sowing should take place each year at a corresponding season. But the differences apparently caused by irregularities of nutrition in a potentially uniform batch of seedlings were also sometimes astonishing; and it was found most difficult to obtain an even preparation of soil in the seed beds by native assistance, even under the closest personal supervision. This difficulty would appear to be a fundamental one in all exact experiments of this kind, and renders such work of little value unless carried out on a very large scale for many generations, in order that accidental differences of soil, &c., may become equalized. Moreover the crop obtained from uncrossed strains of peas was very small at the best of times, and when the conditions were unfavourable it became almost nothing. In such circumstances it was thought better to confine the attention to

observing the behaviour of the more definite characters on crossing.

CLIMATIC CONDITIONS—ACCLIMATIZATION.

The most important differences in climate between different parts of the year in Ceylon depend especially upon variations in the amount of precipitation. Thus a general idea of these differences, so far as they affect the growth of plants, may best be obtained from a table of the monthly rainfall. Such a table is given below, and covers the period during which the work in Ceylon was carried on.

Rainfall at Peradeniya in Inches, and Number of Rainy Days.

	1902-1903.		1903-1904.		Average 21 years.	
	Rain.	Days.	Rain.	Days.	Rain.	Days.
September ..	9·00	17	11·36	27	6·86	16
October ..	25·15	28	13·73	24	14·00	20
November ..	17·43	22	2·71	13	10·86	17
December ..	7·46	18	10·20	19	8·44	13·5
January ..	2·69	8	11·20	19	3·32	7
February ..	1·86	8	1·87	4	1·59	4
March ..	·14	2	3·55	7	4·52	8
April ..	6·88	11	3·54	9	9·59	14
May ..	12·33	17	9·90	17	6·95	12
June ..	5·74	17	18·98	30	10·43	20
July ..	7·36	27	11·71	29	7·87	19
August ..	3·13	17	3·70	12	5·75	17

The above table may be left to tell its own story. As regards temperature, the mean is very uniform all the year round, ranging from about 74° F. in January to 78° F. in May. The difference between the maximum and minimum temperature is greater in dry weather than in wet. Thus the greatest daily range of temperature occurs in January or February, at the beginning of the relatively dry season terminating the north-east monsoon, when the difference between day and night temperatures may be as much as 25° F. The smallest range is recorded during the wet weather of the south-west monsoon in June and July, when the *average* difference between maximum and minimum is about 10° F.

I shall proceed to give a short account of the changes in the weather and general conditions to which each generation grown was exposed.

(1*a*) The first batch of seeds was sown on September 19th, 1902. The earlier half of the month had been wet, but no rain fell between September 21st and 30th ; and the hot sun caused some damage to the seedlings just as they were appearing above the ground. Abundant rain set in at the beginning of October, and the weather continued to be very wet during the remainder of the life of the plants—a total period of a little more than three months. The plants, however, failed to recover and were all very weakly. This result was partly due to insufficient manuring, for the soil proved much poorer than I had been led to anticipate.

A number of pollinations was performed upon the flowers of these plants, but only a small proportion of them was successful, and the pods which developed gave rise to a very small number of seeds. The seeds ripened in somewhat drier weather at the end of December, but there was very little crop to gather.

(1*b*) A further series was sown on October 20th ; and afterwards serial sowings of a few varieties were continued up to the middle of December. Heavy rain did some damage to the earlier series during October and November ; and a strong north-east wind cut off the tops of the later plants in January and February. A batch sown towards the end of November did best, and upon these a few more crosses were made with better success, the seeds being gathered in dry weather during February and March.

(2) Seeds obtained as a result of some of the crosses between the plants of series (1*a*) were sown between December 12th and 19th, (1902). Nearly all the seeds that were sown germinated and the plants did well at first, appearing to derive some benefit from the cooler nights of January. Later on they suffered greatly from wind and drought, and many were killed in this way ; those which survived gave only a poor crop.

Trial plants from seeds sown in January and constantly watered produced quite remarkably stunted plants, which

began to flower at half the usual height* and produced almost no seed.

Plants from seeds sown in February or March rarely reached the flowering stage at all, owing to the excess of sun and lack of moisture.

(3) Offspring of crosses, both F_1 and F_2, were next sown on the 2nd and 5th of May. Twelve inches of rain fell between the 2nd and 21st of May, and this was followed by a drought until June 4th. At the beginning of June the plants were found to have been attacked by a mildew which subsequently became very serious. Practically all the seeds that were sown germinated and very few of the plants died; as a consequence the plants grew too close together (allowance having been made for a certain number of casualties) and the fungus was thus enabled to spread rapidly. The plants were also damaged by an alternation of showers and bright sunshine, which occurred frequently in June and caused a blistering of the young leaves and stipules.† The seeds were gathered at the beginning of August and the crop was a particularly poor one.

(3*a*) A series of the original strains which was sown early in April grew moderately well, and some further crosses were made upon them.

(4) The seeds from these last were sown immediately they were ripe, that is to say on the 9th of July. These fared even worse than the previous series, meeting with dry weather in August, when rain was much needed, and ripening in very wet weather at the beginning of October. They were somewhat mildewed and yielded hardly any seeds or useful result, and none of their progeny were reared.

(5) The next series—F_2 and F_3, the offspring of (3)—were sown on October 26th, 1903. A very large number failed to germinate (*i.e.*, about 80 per cent. of those sown, a state of things which is doubtless to be explained by the bad conditions to which the plants

* *I.e.*, of plants sown in November.

† Showing very clearly by contrast the protection afforded the older foliage by its thick epidermal covering of wax.

which bore these seeds were exposed); those which survived developed into the best plants which I had yet seen, the conditions of growth being good almost throughout; in spite of a dry November, during which however the rain that fell was well distributed. During the last week of January, just when the seeds of this crop were ripening, there fell more than 8 inches of rain. The early part of February however was rainless, and I was able to get many of the seeds dry.

By this time the process of selecting the strongest offspring of certain crosses appeared to have had a considerable effect in the direction of producing vigorous plants. For the third and fourth generations of the original uncrossed strains, grown at the same time as the above and from seeds taken in each generation from the strongest surviving plants showed practically no advance upon the original generation, as grown at first from English seed, and were very poor in comparison with the cross-breds, and this effect was still more clearly seen in a further generation.

(6) This arose from seeds sown on April 6th, 1904, and underwent a drought lasting from the 14th to the 27th of the month, during which time the young plants were with difficulty kept alive by constant watering and shading. Even then very little rain fell until the south-west monsoon "broke" with considerable violence on May 20th. After this constant heavy rain continued to fall during the whole of June and July and the plants ripened their seeds in very wet weather. Thus the conditions during the whole of the life of these plants appeared to be distinctly unfavourable. Practically every seed sown germinated, a fact which evidently depends upon the favourable conditions enjoyed by the previous generation; and although a good many seedlings perished—especially the offspring of certain combinations—enough were left to make a very good show at the time of flowering. The wet weather which prevailed at the time of ripening caused much damage; nevertheless the crop was by far the best obtained throughout the whole series of experiments, and would doubtless have been most valuable as a source of profitable varieties if it had been possible to dry the seeds.

It is unfortunately true that in the case of all these experiments no two generations were strictly comparable one with another as regards the external conditions under which they were grown. Moreover external conditions have unmistakably a large influence upon the growth of the plants, an influence which, as De Vries has pointed out, probably extends over more than one generation. It is nevertheless clear that a marked improvement in the vigour and prolific habit of the plants was arrived at by the process of crossing and then selecting the strongest plants from among the progeny of the cross-breds. Natural selection also played a part in determining the later generations, as may be gathered from the above account. Simple selection of uncrossed strains, in conjunction with rigorous natural selection, did not lead to any advance of a comparable kind.

The effect of the climate of Peradeniya upon pure strains of English peas next demands attention. The exact result seemed to vary in different cases. Thus, when sown in November, French Sugar Pea grew to a considerably greater height than was to be expected from the description accompanying the sample. On the other hand Earliest Blue Pea was much more dwarf. The particular effect in different cases will be described later on, but in this place I would emphasize the fact that the whole result appeared at once in the plants grown at Peradeniya from English seed, and that subsequent generations grown from the seed which these produced closely resembled this first generation. The following races retained for five generations the characters distinctive of the first generation as grown at Peradeniya :—Telegraph, Telephone, Ringleader, French Sugar, Fillbasket, Satisfaction, and Sutton's Earliest Blue Pea. The last-named, which was also the most modified, may be more particularly described by way of example.

The first generation (English seed) was sown on November 29th, 1902. 426 seeds were sown in a bed manured as evenly as possible. The seeds were planted in two rows 4 inches apart and 2 inches apart in the rows. The seeds were ripe on January 20th (seven weeks and three days after sowing), and 398 plants were then gathered

in. The height of these plants varied from 6 to 22 inches, the mean height being about 14 inches. The great majority of plants produced only one pod each, five plants bore two pods each, and sixteen plants had no pods at all. The total number of seeds was 776, or on the average a little over two per pod. The seeds were less rounded and more irregular in form than the original sample—doubtless an effect of nutrition.

400 of these seeds were sown on January 27th, for the second generation, and 388 plants were gathered in on March 17th. The mean height of the plants was about 15 inches, and the heights were rather more uniform. The plants bore 595 seeds in 397 pods.

400 of these seeds were sown on June 4th, and 327 plants were gathered in on July 26th. These plants produced 1,065 seeds in 444 pods. The average height was only very slightly greater than in the previous generation and the seeds were similar in form and size. Now Earliest Blue Pea as grown in England is described as being on the average 3 feet in height, and the crop must be of course on quite a different scale from that which is here described—consisting of only two or three seeds per plant.

The effect of climate shown in this case was exceptional in degree, but the immediate result and the preservation of the type of the first generation are points typical of all the kinds of peas examined.

METHOD.

In making the following crosses, the stamens were in all cases removed from the flower to be pollinated previous to the opening of the anthers, and no case of erroneous self-pollination was recorded. The flowers after they had been pollinated were covered with bags of parchment paper, chiefly for the purpose of protecting the buds thus prematurely opened, from the effects of rain and sunshine.

In the succeeding generations the plants were in all cases left to themselves, no attempt being made to cover the flowers. In no case, whether of a pure strain or of a cross-bred plant, was there any indication that anything but self-fertilization had taken place.

EXPERIMENTS IN CROSSING.

1.—Telegraph crossed with Native Pea No. 1.

A.—*Description of Parents.*

Sutton's Telegraph pea.—This is described as being on the average 5 feet in height, and as being "Singularly free from the frequent objectionable sports."

The sample obtained consisted of large seeds which varied a good deal in shape, and as regards surface might usually have been described as almost dimpled. The starch grains however are of the form typical for "round" peas, and the seeds therefore belong to the "round" group as distinguished from the "wrinkled"* The cotyledons were of a deep green colour with hardly any tinge of yellow in the great majority of cases. The testas were white and semi-transparent. The seeds varied in longest diameter from 7 to 10 mm., the average of 500 being 8·7 mm.

As grown in Ceylon the average height of the plants was about 5 feet; but the height was also very variable, ranging from 3 to 7 feet in different individuals. The stems were stout and the foliage large. The flowers were always pure white. The pods were large—about 20 mm. in width—and well inflated, and they tapered to a point at the apex. The seeds were not so well "filled out" as those of the original sample, but were elongated and nearly square in cross section.

447 seeds, gathered in February, 1903, from plants of the first generation, included 68 per cent. fully green seeds, 30 per cent. piebald or tinged with yellow, and 2 per cent. fully yellow.

Selection of the roundest and of the most wrinkled seeds of the original sample had practically no effect upon the form of the offspring, which was slightly more irregular than in the first generation.

Native pea No. 1.—The plants of this form are slim and the foliage small. The height varied enormously according to the time of sowing and the amount of moisture. In this way the *average* height varied from 3 feet to 5 feet 6 inches; but the variation among the individual plants was less than in the case of Telegraph. The

* Cp. p. 324.

pods were small and narrow (about 13 mm. in width) and were truncated at the apical end. They were always fully inflated. The flowers were white.

The seeds were from 4·5 to 8 mm. in greatest diameter; and 6·5 mm. was the average length of 2,000 of them. They were nearly spherical and usually quite smooth (starch grains of the round type); the cotyledons were always of a bright and uniform orange-yellow colour. The testas were white and semi-transparent, but sometimes slightly tinged with green in the case of seeds which had dried off rapidly in the upper pods of a plant.

B.—*The Cross-bred Plants.*

1.—*Native pea No.* 1 × *Telegraph.**—In all 20 crosses were attempted, of which 12 were successful and gave rise to 31 seeds. All closely resembled the seeds of No. 1 in every visible respect. Four of these crosses, which were made in January, 1903, resulted in the production of 5 seeds per pod (the normal average number for the maternal kind), but the others, which were made in November, 1902, gave relatively a very poor result.

The latter seeds were sown in December, 1902. The plants which arose from them were about 5 feet in height and in their somewhat large foliage and stout habit approached the type of Telegraph. The pods were intermediate in general form, but with a truncated apex, and were from 15 to 18 mm. in width.

2.—*Telegraph* × *Native pea No.* 1.—As the result of 30 pollinations 17 pods were obtained containing altogether 50 seeds. In shape these closely resembled the normal seeds of Telegraph, but the colour of the cotyledons was in all cases bright yellow. The plants arising from these seeds, sown at the same time as those of the reciprocal cross, closely resembled the latter. Other seeds sown on May 2nd produced much taller plants. Some of the characters of the latter are indicated in the accompanying table, together with the cotyledon characters of their seeds, which belong of course to the next generation—F_2. In size and shape, which appear to be maternal

* Here and subsequently the seed-parent is placed first and the pollen parent second. × is thus to be read "fertilized with pollen from."

characters, the seeds of the same plant were all nearly alike—the size intermediate, the shape nearly that of Telegraph.

Table I.

Date of Sowing.	Number.*	Height (Inches).	Number of Nodes.	Average Length of an Internode (Inches).	Number of Branches.	Number of Pods.	Width of an Average Pod (mm.).	Number of Seeds.	F^2.		
									Yellow.	Green.	Bad.
19-12-02	181.1	58	28	2·1	—	10	—	23	10	5	8
	180.1	58	28	2·1	—	5	—	15	14	1	—
	304.1	59	29	2·1	—	5	—	15	7	8	—
	.2	46	25	1·8	—	2	—	7	4	3	—
2-5-03	371.1	88	31	1·8	2	4	16	7	5	2	—
	.2	84	27	3·1	—	6	17	17	11	6	—
	.3	89	29	3·1	—	6	15	11	10	1	—
	.4	91	32	2·8	2	15	17	27	20	7	—
	.5	95	32	3·0	1	7	17	19	14	5	—
	372·1	88	35	2·5	2	10	16	21	15	6	—
	.2	85	34	2·5	2	1	16	3	2	1	—
	.3	99	35	2·8	—	10	18	32	24	8	—
	435.1	87	26	3·3	—	6	16	14	11	3	—
	.2	90	29	3·1	1	8	17	23	20	3	—
	.3	95	31	3·1	1	10	16	26	21	5	—
	.4	100	32	3·1	1	5	19	18	13	5	—
	.5	80	27	3·0	1	8	17	22	17	5	—
	436.1	76	24	3·2	—	6	15	14	10	4	—
	.2	86	32	2·7	—	5	17	14	10	4	—
	.3	98	33	3·0	—	5	18	9	6	3	—
	459.1	80	31	2·6	—	2	15	3	2	1	—
	.2	85	31	2·7	—	3	16	6	6	—	—

* The numbers which are prefixed to the different hybrids and their progeny require a word of explanation. The crosses of all kinds made at Peradeniya were numbered consequtively; the plants arising from each seed of a cross-bred pod then received a distinguishing number, when these were more than one; and in the next generation a further number was added to distinguish the different offspring of each of these plants. Thus 371.1, 2, 3, &c., are plants arising from different seeds of the same cross-bred pod.

The greater length of the internodes of the plants which developed from seeds sown on May 2nd is partly due to the fact that the plants

were grown much too close together, and partly to the different season with more moisture and less sunshine. The plants were all badly mildewed. Half the plants grown at this time produced one or more branches.

C.—*Further Generations.*

1.—*Native pea No.* 1 × *Telegraph*, F_2, *and* F_3.—Six plants from F_1 seeds sown on December 8, 1902, produced the following seeds :—

No.	Yellow.	Green.
157.1 ..	11 ..	5
186.1 ..	11 ..	5
.2 ..	10 ..	4
238.1 ..	10 ..	5
.2 ..	8 ..	7
303.1 ..	18 ..	13
Total ..	68	39 or 1·74 : 1.

In only two cases could any trace of yellow be detected in a "green" seed, as examined through the semi-transparent testa—a proportion of 5 per cent., which may be compared with the 30 per cent. found in the uncrossed strain of Telegraph.

Of the 107 seeds, 66 were sown on May 2nd, 1903, but only the plants arising from 21 yellow and 11 green seeds produced fruits. They ranged from 45 to 102 inches in height, the average being nearly 7 feet.

Table II.

Number.	F_2. Height (Inches).	Number of Nodes.	Width of a Pod (mm.).	Number of Pods.	Number of Seeds.	F_3. Yellow.	Green.	F_2. Colour of Seed sown.	Nature of Seed sown.
180.1.1	64	20	12	2	5	4	1	y	DR
.2	83	27	16	3	6	4	2	y	DR
.3	88	28	17	5	16	—	16	g	R
.4	90	32	15	5	13	—	13	g	R
.5	85	30	18	1	5	—	5	g	R
.6	77	27	17	1	3	—	3	g	R

D. The yellow seed was a pure dominant.
R. The green seed was pure recessive.
DR. The yellow seed was a heterozygote.

Number.	F_2.					F_3.		F_3.	
	Height (Inches).	Number of Nodes.	Width of a Pod (mm.).	Number of Pods.	Number of Seeds.	Yellow.	Green.	Colour of Seed sown.	Nature of Seed sown.
186.2.1	?	?	18	9	28	28	—	y	D
.2	75	27	15	7	27	22	5	y	DR
.3	102	40	16	3	8	7	1	y	DR
.4	87	30	18	3	6	5	1	y	DR
.5	84	26	16	7	14	14	—	y	D
.6	?	?	14	4	13	13	—	y	D
.7	87	32	19	2	7	—	7	g	R
.8	61	20	17	2	4	—	4	g	R
238.1.1	80	35	16	2	9	7	2	y	DR
.2	65	28	14	4	15	13	2	y	DR
.3	45	32	18	6	12	11	1	y	DR
.4	?	?	14	4	12	8	4	y	DR
.5	90	33	16	2	8	6	2	y	DR
.6	88	29	17	3	11	—	11	g	R
.7	80	29	15	2	3	—	3	g	R
.8	71	25	18	5	10	—	10	g	R
303.1.1	75	25	15	2	4	3	1	y	DR
.2	80	26	16	2	4	4	—	y	D ?
.3	65	25	13	4	12	7	5	y	DR
.4	80	30	16	3	7	5	2	y	DR
.5	80	29	13	3	13	11	2	y	DR
.6	73	25	16	3	8	8	—	y	D
.7	64	23	14	2	4	4	—	y	D ?
.8	61	22	14	5	7	6	1	y	DR
.9	77	26	18	4	10	—	10	g	R
.10	72	22	17	2	6	—	6	g	R

The width of an average pod from each of the different plants showed the following range :—

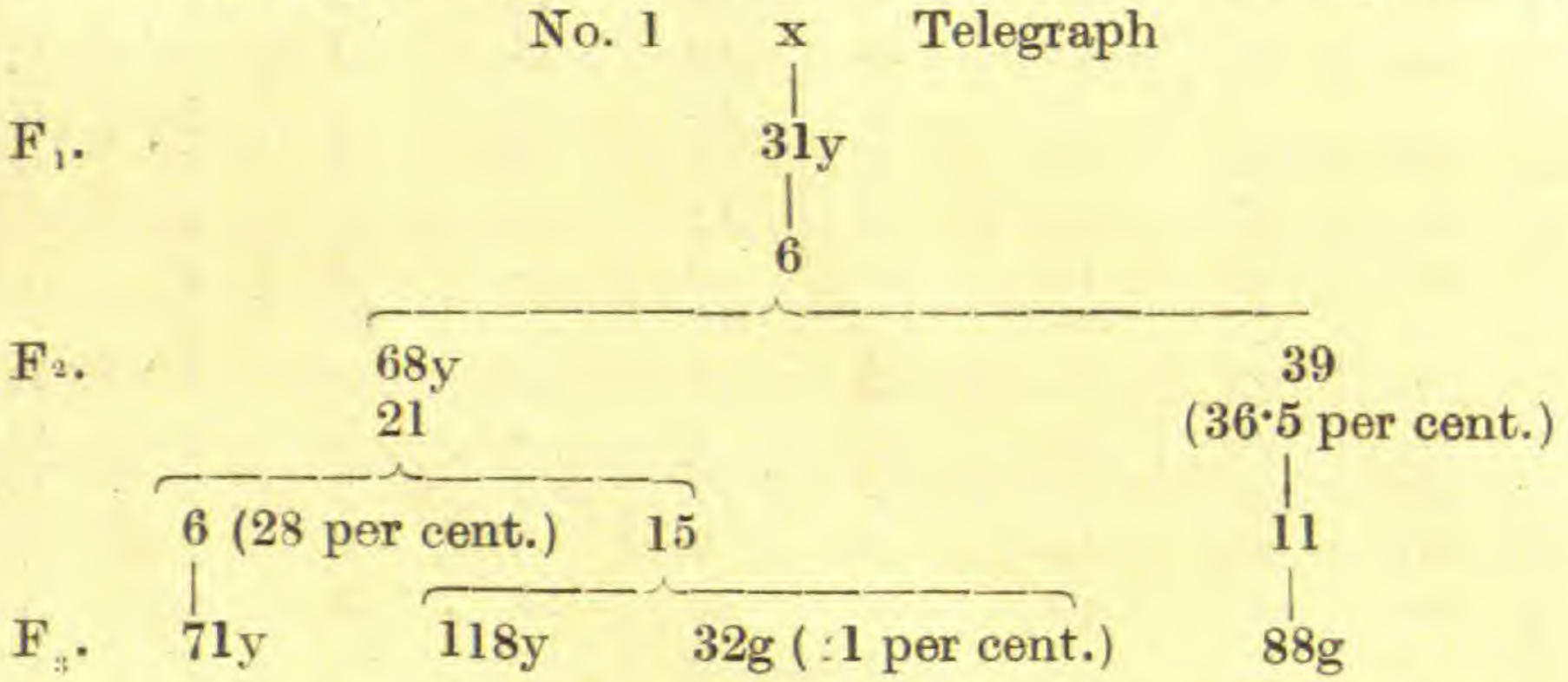
Width	.. 19mm.	.. 18	.. 17	.. 16	.. 15	.. 14	.. 13	.. 12
Number of plants	1	.. 6	.. 5	.. 8	.. 4	.. 5	.. 2	.. 1

We may regard this as indicating the proportion 7 wide : 17 medium : 8 narrow, or nearly 1 : 2 : 1. The Mendelian ratio thus makes its appearance in spite of much variability.

The 11 plants which arose from green seeds (F_2) gave rise to exclusively green seeds (F_3), namely to 88 such seeds.

Of the 21 plants arising from yellow seeds (F_2), 6 produced only yellow seeds (F_3), namely, 71 seeds all bright orange-yellow in colour. The remaining 15 plants gave rise to both yellow and green seeds—altogether 118 yellow and 32 green, or 3·7 to 1. In the most doubtful cases (perhaps half a dozen in all) in which the colour could only be seen indistinctly through the testa, on removal of the latter the cotyledons were found to be either bright yellow or bright green. It is therefore safe to assert that practically all the seeds were either fully yellow or fully green; certainly the "green" seeds did not include so high a proportion of examples mottled with yellow as in the case of Telegraph. And it thus appears as if the act of crossing had rendered the green pigment more stable in the extracted homozygotes.

The following scheme indicates the course of this experiment :—



2.—*Telegraph* × *Native pea No.* 1, F_2, F_3, *and* F_4.—The cotyledon colour of the seeds (F_2) on F_1 plants gathered in February and at the end of July, 1903, were detailed in Table I., the total being 302 yellow, 86 green. The following table embraces the same detail for a further series gathered on October 10th, 1903, in very wet weather :—

No.	Y.	G.	No.	Y.	G.	No.	Y.	G.
618.1	8	5	.3	8	6	636.1	16	10
.2	11	4	.4	6	2	.2	11	4
.3	17	4	626.1	14	3	.3	22	6
.4	9	4	.2	10	7	637.1	11	2
.5	16	1	.3	10	3	.2	4	2
.6	11	3	.4	9	4			
619.1	16	2	627.1	13	4	Total ..	263	87 or 3 : 0.99.
62 .1	8	1	627.2	10	5			
620.2	9	3	.3	14	2			

Out of a total of 87 green seeds 2 were noticed to show distinct patches of yellow and others were of a somewhat dull shade of green. All however were readily distinguishable from the "yellows" in spite of the unfavourable conditions during ripening.

The total figures for this and later generations were summed up in a previous paper on page 309. Details for F_2 are given in the following table :—

F_2.					F_3.			F_2.	
Number.	Height (Inches).	Nodes.	Branches.	Pods.	Seeds.	Yellow.	Green.	Colour of Seed Sown.	Nature of Plants.
618.1	84	31	—	7	36	25	11	y	DR
(1–6) .2	84	30	—	11	38	31	7	y	DR
.3	71	25	—	7	23	17	6	y	DR
.4	90	34	1	15	59	46	13	y	DR
.5	62	24	—	5	14	11	3	y	DR
.6	81	26	—	6	23	23	—	y	D
.7	86	29	—	9	31	24	7	y	DR
.8	80	33	2	10	50	41	9	y	DR
.9	70	28	2	12	45	45	—	y	D
.10	82	32	2	14	42	35	7	y	DR
.11	86	31	—	12	45	45	—	y	D
.12	85	29	—	9	22	12	10	y	DR
.13	75	29	—	7	33	33	—	y	D
.14	73	28	—	5	22	15	7	y	DR
.15	82	33	1	10	39	39	—	y	D
.16	98	40	1	11	56	43	13	y	DR
.17	101	35	—	13	54	54	—	y	D
.18	85	31	1	8	39	39	—	y	D
.19	94	37	—	9	40	32	8	y	DR
.20	64	29	—	6	19	18	1	y	DR
.21	72	29	—	7	34	—	34	g	R
.22	61	28	—	5	22	—	22	g	R
.23	84	34	—	17	63	—	63	g	R
.24	52	22	—	5	16	—	16	g	R
.25	43	20	—	2	6	—	6	g	R
.26	50	24	—	5	15	—	15	g	R
.27	60	—	—	9	33	—	33	g	R
.28	70	27	—	8	27	2	25	g	R

F_2.					F_3.			F_2.	
Number.	Height (Inches).	Nodes.	Branches.	Pods.	Seeds.	Yellow.	Green.	Colour of Seed Sown.	Nature of Plants.
.29	74	28	—	10	16	—	16	g	R
.30	79	32	—	8	28	2	26	g	R
.31	78	34	—	—	18	18	—	y	D
435.1.1	84	36	2	19	62	62	—	y	D
.2	84	33	2	14	50	37	13	y	DR
.3	92	35	3	21	74	53	21	y	DR
.4	94	28	—	11	32	29	3	y	DR
.5	87	33	1	14	48	39	9	y	DR
.6	90	33	—	12	39	27	12	y	DR
435.2.1	65	—	—	5	20	17	3	y	DR
.2	63	25	—	4	14	11	3	y	DR
.3	75	27	1	15	49	42	7	y	DR
.4	90	32	2	24	76	76	—	y	D
.5	71	29	—	4	15	8	7	y	DR
.6	64	27	—	5	13	10	3	y	DR
.7	70	32	—	11	38	29	9	y	DR
435.3.1	95	39	6	51	209	209	—	y	D
.2	90	31	2	18	74	55	19	y	DR
435.4.1	77	32	1	9	48	48	—	y	D
.2	92	28	—	12	41	26	15	y	DR
.3	96	39	5	46	155	118	37	y	DR
.4	90	32	3	20	82	82	—	y	D
435.5.1	80	26	1	16	64	64	—	y	D
.2	79	31	—	12	38	26	12	y	DR
.3	92	33	1	14	68	68	—	y	D
.4	—	37	4	28	108	108	—	y	D
.5	68	28	2	13	35	—	35	g	R

Thus, out of 44 yellow seeds sown, 16 plants gave rise to 1,013 yellow seeds only, whilst 28 plants yielded a mixture—altogether 877 yellow and 275 green seeds, or 3 : 0·94. Eleven plants from green seeds produced 291 green seeds and 4 yellow, the latter being probably examples of the effect of exposure upon properly green seeds, such as was described as being frequent in the case of Telegraph seeds.

Out of 55 F_2 plants 17 were reckoned to bear seeds of the spherical or No. 1 type in narrower pods, whilst 36 bore seeds of the Telegraph type in wider pods. Actual measurements were not made and the distinction was not very clear.

In F_3, 134 plants were raised, offspring of 7 plants which proved the most prolific in F_2. Of the 7, 2 included only plants with moderately narrow pods (but wider and more variable than those of No. 1); and these bore seeds which were all nearly spherical, but variable in size from plant to plant, being on the average larger than those of No. 1. These two families were the offspring of plants which had been reckoned as bearing seeds of the No. 1 type in F_2.

Of the other five families—offspring of seeds of more or less the Telegraph type—two consisted wholly of plants with pods and seeds of the Telegraph type whilst the other three included both types. In two of these cases the proportion of the two types (Telegraph : No. 1) could be distinguished as 13 : 4 and 10 : 2; in the third case there was more variability.

There thus appears to be Mendelian segregation to a certain extent in respect of the characters wide or narrow pod correlated with certain shapes of seeds. But the extracted "recessives" seem still to show signs of the influence of the more or less dominant form (wider pods). So that there is perhaps more complication than in a simple Mendelian case. One source of complication is patent in the fact that the size of seeds appears to be a character independent of their shape. Possibly there is also in some cases a mutual influence between size of seeds and width of pods.

On the other hand, colour of the cotyledons, which was the character to which attention was chiefly directed in the present experiment, was found to gain in distinctness as the result of the cross and to obey Mendel's law with the utmost precision. The green and yellow seeds obtained from heterozygotes in F_2 and F_3 showed, when looked at in bulk, a most marked uniformity among themselves and distinctness from the other type. When kept for some weeks the colour of the green seeds especially became duller, and a tinge of yellow began to appear in some of them.

A summary of the plants raised in F_3 follows, together with the total number of seeds which they produced of either colour :—

Number.	Seeds Sown.	Nature of Plants: F_3 D.	DR.	R.	Seeds F_4 Y.	G.	Bad.
435.1.2 ..	12y ..	1	.	. ..	22	—	—
,, ..	— ..	.	10	. ..	244	96	62
,, ..	6g ..	.	.	6 ..	—	171	2
435.1.3 ..	24y ..	4	.	. ..	185	—	30
,, ..	— ..	.	17	. ..	346	138	13
,, ..	12g ..	.	.	11 ..	—	307	8
435.3.2 ..	12y ..	.	10	. ..	199	75	21
,, ..	6g ..	.	.	3 ..	—	71	5
435.4.1 ..	12y ..	9	.	. ..	224	(7)†	12
435.4.2 ..	12y ..	3	.	. ..	91	—	—
,, ..	— ..	.	7	. ..	121	39	—
,, ..	6g ..	.	.	4 ..	—	126	2
435.4.3 ..	20y ..	4	.	. ..	127	—	—
,, ..	— ..	.	11	. ..	25'	79	—
,, ..	20g ..	.	.	17 ..	—	469	11
435.5.1 ..	12y ..	4	.	. ..	117	—	4
,, ..	— ..	.	7	. ..	170	51	9
,, ..	6g ..	.	.	6 ..	—	181	—

The above table repeats in rather greater detail the information given previously in Part I., page 309.

Twenty-five green and 25 yellow seeds were taken at random from a large fresh sample of F_4—offspring of heterozygotes—and were examined closely after removal of the testa. The green seeds were without exception of a deeper and more vivid green than the greenest of the 3 peas in Weldon's Fig. 1,‡ being indeed quite green. The yellow seeds were all as yellow as those in Fig. 6, but of a darker shade —almost exactly the shade of the yellow ink used for printing the figure. It is to be noticed that all these seeds were produced upon plants of much more vigorous and healthy appearance than those of F_1, a fact which suggests that the relatively "bad" results obtained in the earlier generations may have been due to the bad conditions of growth, or want of acclimatization.

* Nearly all the seeds set down in this column had been attacked by a caterpillar, causing damage which rendered the discrimination of their colour a matter of uncertainty.

† Not fully ripe.

‡ Biometrica, I., 1902, Pt. II.

2.—Telegraph crossed with Ringleader.

A.—*The Parental Types.*

1. For *Telegraph* see above. 2.—*Ringleader*.—Cotyledons perfectly yellow and smooth; seeds a little flattened from side to side. Plants on the average less than 3 feet high; pods containing very few seeds but comparatively numerous upon the plants. Flower stalks very long; pods truncated at the ends.

B.—*The Cross-bred Forms.*

1. *Telegraph* × *Ringleader*.—Twelve seeds were obtained from 3 successful crosses; all of them were fully yellow and resembled in shape the smoother examples of the normal Telegraph type. All these seeds gave rise to fruitful plants, which were of nearly the same height as Telegraph and closely resembled that parent except in the greater length of the flower stalks and the truncated ends of the pods.

2. *Ringleader* × *Telegraph*.—Eleven seeds resulted from 4 crosses, these were not to be distinguishcd from uncrossed seeds of Ringleader. The 11 plants resembled those arising from the reciprocal cross.

C.—*Further Generations.*

1. *Telegraph* × *Ringleader*, F_2.—The following seeds were readily distinguished according to colour; in shape they closely resembled those of Telegraph:—

No.	Yellow.	Green.	
427.1 ..	18 ..	5	
.2 ..	12 ..	4	
.3 ..	11 ..	3	
.4 ..	5 ..	5	
.5 ..	14 ..	5	
.6 ..	13 ..	7	
444.1 ..	15 ..	2	
.2 ..	14 ..	4	
.3 ..	20 ..	7	
.4 ..	11 ..	5	
445.1 ..	8 ..	4	
.2 ..	11 ..	5	
.3 ..	10 ..	2	
Total .. —	162	58	or 3 : 1·07

Out of 50 of these seeds which were sown (on 26th October, 1903) only 6 survived to bear fruit. These were stout plants bearing on the average 13 pods and 42 seeds each :—

Number.	Height.	Number of Nodes.	Branches.	Pods.	Seeds.	F_3.		F_2.	
						Yellow.	Green.	Colour of Seed Sown.	Nature of Seed Sown.
427.1	80	31	1	18	56	43	13	y	DR
.2	78	31	—	10	33	24	9	y	DR
.3	75	31	1	14	38	38	—	y	D
444.1	71	?	3	19	59	59	—	y	D
.2	76	26	—	10	41	41	—	y	D
.3	59	26	—	9	28	24	4	y	DR

2. *Ringleader* × *Telegraph*, F_2.—The following yellow and green seeds were readily distinguishable :—

No.	Yellow.	Green,
424.1 ..	10 ..	3
.2 ..	15 ..	3
.3 ..	9 ..	4
.4 ..	6 ..	1
425.1 ..	10 ..	5
.2 ..	12 ..	5
.3 ..	12 ..	3
446.1 ..	12 ..	4
.2 ..	8 ..	4
449.1 ..	6 ..	5
.2 ..	13 ..	7
Total ..	113	44 or 3 : 1·17

The total numbers for the two reciprocal crosses in F_2 are as follows :—Yellow 274 : green 102, or 3 : 1·1.

3.—Telephone crossed with Native Pea No. 1.

A.—*The Parental Types.*

1. *Telephone.*—(Sample obtained from Messrs. Sutton.) "Average height 5 feet." In my experience Telephone is a typically wrinkled pea. As regards colour the cotyledons show a high degree of susceptibility to the effect of light, the result of which is gradually

to change the green colour to yellow. This change does not take place uniformly, and so a piebald effect is often produced. The original sample of seeds was almost entirely green. It was kept in a stoppered glass bottle exposed to the light of an ordinary room, and by the end of six months the cotyledons on the exposed side had all become completely yellow. Other kinds of peas with green cotyledons showed a similar change, but this took place more slowly than in the case of Telephone.

A majority of the first crop seeds at Peradeniya were more or less yellow when gathered, distinctly more so even than in the case of Telegraph. They were separated into three groups—green, piebald, and yellow, respectively—the groups being as it happened nearly of equal size, and 50 seeds of each kind were sown. The crop from each group was again separated into a like threegr oups, but the offspring of yellow seeds did not include a larger proportion of yellows than the others. The exact numbers of these samples are of no value, owing to the want of definite limits to the different groups, but it was clear that the tendency to turn yellow was inherited nearly equally by the offspring of all three groups. In the above cases the seeds were left on the plants for some days after all were ripe ; cross-bred plants, on the other hand, were always taken up before the seeds in the topmost pods were quite hard, and the seeds examined at once ; under such circumstances the green colour could almost always be detected in the parental strain also.

B.—*The Cross-bred Forms.*

1. *Native pea No. 1 × Telephone.*—Twenty-one cross fertilizations were made, of which only 9 were successful. The 9 pods yielded 20 seeds, none of which differed at all from the normal seeds of No. 1.

The crosses were made in November, 1902, and the seeds were sown immediately after gathering ; all but two germinated, but only 14 plants produced seeds. The plants reached a height of 3–4 feet, nearly the same as that of the best plants of the two parental forms sown at the same time. In the character of their foliage and in stoutness of stem they resembled Telephone, but there appeared to

be a slight reduction in these features traceable to the other parent. The pods were nearly as wide as those of Telephone, but were shaped like those of No. 1 (dominance of the blunt apex). The size of the seeds was intermediate; the shape (apart from the question of smoothness or wrinkling) much nearer to that of Telephone.

2. *Telephone* × *Native pea* No. 1.—Eighteen pollinations were attempted, 12 successfully, with 27 seeds as the result. With the exception of 2 seeds contained in a single pod, all these seeds were fully yellow as regards cotyledon colour. All the seeds were nearly smooth in surface; some of them showed a very slight dimpling; but all were smoother than any which I could find among the same generation of pure bred Telephone seed. In general form and size, on the other hand, they closely resembled the smoothest seeds of Telephone, which are also closely similar to those of Telegraph, differing entirely in these respects from No. 1.

One cross out of the 12 gave rise to 2 fully green seeds, resembling in shape the other examples of the same cross. Occurring as they did on a green seeded plant the suspicion arises that these seeds may have been the result of accidental self fertilization. But I do not believe that this can have been the case; firstly because the seeds were smooth, and secondly because their offspring behaved, so far as the evidence went, like those of a cross between smooth and wrinkled. The individual plant from which the pollen was taken was not specially examined, but all the seeds were gathered from the whole row of plants used for this purpose, and none of the cotyledons showed any trace of greenness.

Of the above-mentioned crosses, 6 which were made in November, 1902, resulted in 10 seeds, from only 4 of which fertile offspring were obtained. In both cases the seeds were sown shortly after they were gathered, and the plants closely resembled those from the reciprocal cross.

C.—*The Offspring of Cross-bred Plant*—F_2.

1. *Native pea No. 1* × *Telephone*.—The seeds produced by the cross-bred plants exhibited four distinct combinations of cotyledon characters, being in almost all cases readily distinguishable as

smooth yellow, smooth green, wrinkled yellow, or wrinkled green, respectively. The green seeds appeared to show less susceptibility to the effects of exposure than those of the pure Telephone stock, and only a few, and these obviously badly developed, showed any yellow patches. Although this is partly accounted for by the fact that they were gathered sooner, this does not appear to be the whole explanation, but it seems clear that there was an actual intensification as the result of the cross. It was also noticed, on examining the seeds after the removal of their coats, that the shade of colour, whether yellow or green, was distinctly paler in the wrinkled cotyledons than in the smooth ones.*

Even without removing the coats it was hardly ever possible to confuse yellow seeds with green ones, but the discrimination between smooth and wrinkled seeds was more difficult, owing to the fact that seeds properly belonging to the smooth group were often a good deal pitted and irregular in shape. The result of the actual sampling was as follows :—

No.	sm. y.	sm. g.	wr. y.	wr. g.
159.1 ..	9 ..	2 ..	4 ..	—
202.1 ..	4 ..	4 ..	— ..	—
209.1 ..	15 ..	6 ..	2 ..	2
.2 ..	9 ..	3 ..	1 ..	2
.3 ..	— ..	2 ..	1 ..	—
210.1 ..	12 ..	5 ..	1 ..	1
212.1 ..	10 ..	3 ..	2 ..	2
.2 ..	5 ..	2 ..	— ..	2
267.1 ..	8 ..	7 ..	3 ..	2
269.1 ..	12 ..	4 ..	3 ..	2
2 ..	10 ..	— ..	2 ..	—
.3 ..	1 ..	— ..	1 ..	—
270.1 ..	10 ..	3 ..	3 ..	—
.2 ..	5 ..	3 ..	5 ..	1
		—	—	—
Total ..	110	44	28	14
Expectation ..	110	36.7	36.7	12.2

* *Cf.* Hurst, J. R. H. S., 1903.

It is perhaps noteworthy that a total so nearly approaching the expected should be derived from such small individual figures.

144 of these seeds were sown on 3rd May, 1903, only those from the weakest of the above plants being excluded. 98 plants yielded fruit, but the majority gave only a poor crop. Most were very tall, but this effect was partly due to overcrowding. In general appearance all were much alike—the pale green foliage of Telephone being still visible—and the stipules were broad. The plants were badly mildewed and damaged by alternate rain and sunshine.

The width of the pods appeared to be tolerably constant on each plant, but between different plants the variation was considerable. The width of a typical pod was measured in the case of each of 78 plants—all that had pods typically developed—with the following result :—

Width ..	19 mm.	18	17	16	15	14	13
Plants ..	2	9	22	17	9	14	5

If we draw an arbitrary line between the widths of 14 and 15 mm., as we are to some extent justified in doing, because (1) the width of the pods of No. 1 was from 13–14 mm., and (2) the figures show something of a natural demarcation at that point, we find the ratio of wide, intermediate, and narrow to be 59 : 19 or 3.1 : 1.

2. *Telephone* × *Native pea No.* 1.—The cotyledons fell into the same four groups as the above. In three cases it was necessary to remove the seed coat before the colour of the cotyledons could be ascertained with certainty: all three proved to be fully yellow, and this had been partly obscured by a greenish tinge in the testa. In these and in all other cases the two classes of colour were quite distinct, although some of the green seeds showed slight yellow patches. Smooth and wrinkled seeds were more difficult to distinguish by the eye, the former being all more or less pitted. The majority of the wrinkleds were thoroughly so.

The seeds were sorted as follows:—

No.	sm. y.	sm. g.	wr. y.	wr. g.
245.1	4	3	4	1
246.1	7	2	1	—
295.1	2	1	1	—
610.1	2	1	1	1
621.1	4	4	4	2
.2	8	3	1	1
.3	4	3	2	1
622.1	14	4	1	1
.2	3	1	3	1
.3	8	3	1	1
623.1	9	5	2	1
.2	3	1	1	—
.3	2	1	2	1
.4	10	4	4	—
.5	10	1	4	1
631.1	2	1	1	—
.2	6	1	1	1
634.1	7	5	5	1
.2	6	2	1	—
Total	111	46	40	14
Expectation	118·8	39·6	39·6	13·2

An even smoother result than in the previous case, in spite of the very small individual samples.

Exceptional case.—No. 215, which produced 2 green seeds in F_1: one of these gave rise to a plant which fruited, yielding 4 pods and 8 green seeds. Five of these were smooth and 1 was wrinkled; 2 were very small and irregular and neither of the latter germinated.

The seeds from Nos. 610–634 were gathered in October, 1903, in very wet weather. Many of them were sown on the 26th of the same month, and germinated very badly. The survivors however grew into strong plants, many of which bore a good crop of seeds. 55 plants were harvested. Of these, 13 had pods distinctly narrow and of the No. 1 form, the seeds being small and spherical, or much wrinkled, or both. The foliage of these plants was small, and they showed a general resemblance to the No. 1 type. The remaining 42 plants showed a nearer approach to the type characteristic

of Telephone, as regards the form of both the seeds and the foliage, and had wider pods. 42 : 13 = 3·2 : 1; so that it appears likely that there is Mendelian segregation of these characters, but that the form of seeds and of foliage and the width of pod are all to some extent correlated. It is possible that in the case of the reciprocal cross a similar phenomenon may have been overlooked owing to the bad conditions under which the corresponding generation was grown.

D.—*Further Generations.*

These were grown in the first place to test the accuracy of the sampling in F_2, and, this being found accurate, to test the conformity to Mendel's law in these later generations. It was also hoped to obtain improved strains by the selection of the parents yielding the largest crops and the finest seeds.

1. *Native pea No.* 1 × *Telephone.*—The following table shows how far the constitution of the F_2 seeds could be determined on examining their offspring in F_3:—

Number.	Character of F_2 Seeds.	F_3 Seeds born on F_2 Plants.				Constitution of F_2 Plant.*
		sm. y.	sm. g.	wr. y.	wr. y.	
159.1.1	sm. y.	13	—	3	—	AaB
.2	,,	—	4	—	—	?
.3	,,	9	—	8	—	AaB
.4	,,	10	4	3	—	AaBb
.5	sm. g.	—	9	—	—	AB
.6	,,	—	3	—	—	?
.7	wr. y.	—	—	9	3	aBb
.8	,,	—	—	11	7	aBb
.9	,,	—	—	20	—	aB
.10	,,	—	—	13	8	aBb
202.1.1	sm. y.	15	—	—	—	AB
.2	,,	9	1	1	—	AaBb
.3	sm. g.	—	22	—	7	Aab
209.1.1	sm. y.	2	—	3	—	?
.2	,,	7	—	1	—	?
.3	,,	3	—	1	—	?
.4	,,	3	2	3	—	AaBb

*A = Smooth (Dominant), a = wrinkled (Recessive).
B = Yellow (Dominant), b = green (Recessive).

Number.	Character of F_2 Seeds.	F_3 Seeds born on F_2 Plants.				Constitution of F_2 Plant.*
		sm. y.	sm. g.	wr. y.	wr. g.	
.5	,,	8	—	—	—	AB
.6	,,	5	—	—	—	?
.7	,,	2	2	2	—	AaBb
.8	,,	1	2	1	1	AaBb
.9	,,	5	—	2	—	?
.10	,,	8	—	—	—	AB
.11	sm. g.	—	—	—	—	Ab
.12	,,	—	9	—	3	Aab
.13	,,	—	12	—	—	Ab
.14	wr. y.	—	—	2	1	aBb
.15	,,	—	—	11	—	aB
.16	wr. g.	—	—	1?	4	ab?
209.2.1	sm. y.	8	2	2	—	AaBb
.2	,,	11	1	—	—	ABb
.3	,,	18	—	3	—	AaB
.4	sm. g.	—	20	—	5	Aab
.5	,,	—	3	—	—	?
210.1.1	sm. y.	5	2	—	—	?
.2	,,	4	—	1	—	?
.3	,,	7	5	—	—	ABb
.4	,,	1	2	—	—	?
.5	,,	—	—	12	—	aB! (*b*)
.6	,,	5	1	—	—	?
.7	,,	7	—	4	—	AaB
.8	sm. g.	—	5	—	2	Aab
.9	,,	—	3	—	1	Aab
.10	,,	—	4	—	—	Ab?
.11	,,	—	2	—	2	Aab
.12	wr. g.	—	—	—	6	ab
212.1.1	sm. y.	3	—	—	—	?
.2	,,	2	2	—	1	AaBb
.3	wr. y.	—	—	2	—	?
.4	,,	—	—	2	1	aBb
.5	sm. g.	—	3	1?	1	Aab
.6	wr. g.	—	—	—	3	ab
.7	,,	—	—	3?	—	?
215.1.1	sm. g.	—	6	—	—	Ab?
.2	,,	—	11	—	6	Aab
.3	,,	—	8	—	—	Ab
.4	,,	—	12	—	—	Ab
.5	wr. g.	—	—	—	15	ab

* A = Smooth (Dominant), a = wrinkled (Recessive).
B = Yellow (Dominant), b = green (Recessive).

Number.	Character of F_2 Seeds.	F_3 Seeds born on F_2 Plants.				Constitution of F_2 Plant.*
		sm. y.	sm. g.	wr. y.	wr. g.	
267.1.1	sm. y.	16	5	3	1	AaBb
.2	,,	7	—	—	—	AB
.3	,,	5	1	1	1	AaBb
.4	,,	3	2	—	—	?
.5	,,	10	2	—	—	ABb
.6	,,	14	—	4	—	AaB
.7	,,	5	2	—	—	ABb?
.8	sm. g.	—	6	—	2	Aab
.9	,,	—	12	—	4	Aab
.10	,,	—	10	—	2	Aab
.11	,,	—	4	—	—	Ab?
.12	wr. y.	—	—	13	1	aBb
.13	,,	—	—	5	3	aBb
.14	wr. g.	—	—	—	17	ab
.15	,,	—	27	—	—	Ab!(*c*)
269.1.1	sm. y.	7	3	—	1	AaBb
.2	,,	2	1	1	—	AaBb
.3	,,	5	1	8	—	AaBb
.4	,,	8	3	—	—	ABb
.5	,,	23	—	9	—	AaB
.6	,,	4	7	—	—	ABb
.7	,,	7	4	4	2	AaBb
.8	,,	8	—	1	—	AaB?
.9	,,	—	12	—	4	Aab!(*a*)
.10	sm. g.	—	8	—	—	Ab
.11	wr. y.	—	—	2	1	aBb
.12	,,	—	—	3	2	aBb
.13	,,	—	—	4	—	aB?
.14	wr. g.	—	—	—	8	ab
270.1.1	sm. y.	8	1	2	—	AaBb
.2	,,	7	—	2	—	AaB?
.3	wr. y.	—	—	2	—	?
.4	,,	—	—	6	1	aBb
270.2.1	sm. y.	4	1	4	—	AaBb
.2	sm. g.	—	2	—	2	Aab
.3	,,	—	3	—	4	Aab
.4	,,	—	9	—	—	Ab
.5	wr. y.	—	—	3	3	aBb
.6	,,	—	—	8	1	aBb

* A = Smooth (Dominant), a = wrinkled (Recessive).
B = Yellow (Dominant), b = green (Recessive).

Thus by the examination of their seeds in F_3 the constitution of the 72 F_2 plants for which a summary follows could be determined, as well as that of four of the offspring of the exceptional cross No. 215. Twenty other plants gave too poor a crop to allow of this being done:—

Parent Seed.	Mendelian Constitution of Parents.									Total.
	AaBb.	AaB.	AaB.	ABb.	aBb.	AB.	Ab.	Ab.	ab.	
Sm. y. ..	15	7	(1)	5	—	4	—	(1)	—	33
Sm. g. ..	—	—	12	—	—	—	5	—	—	17
Wr. y. ..	—	—	—	—	12	—	—	3	—	15
Wr. g. ..	—	—	—	—	—	—	(1)	—	6	7
Total ..	15	7	13	5	12	4	7	4	7	72

The figures are not sufficient for testing the distribution according to Mendel's law with any exactness, though so far as they go the agreement is clear enough. They do afford however a test of the accuracy of the sampling.

There are apparently three errors among the 72 cases, namely:—

(*a*) 1 seed sown as sm. y. gave rise to sm. and wr. green only.

(*b*) 1 seed sown as sm. y. gave rise to wrinkled yellow only.

(*c*) 1 seed sown as wr. g. gave rise to smooth green only.

(*b*) and (*c*) illustrate the fact already stated that smooth and wrinkled seeds are not always to be distinguished with certainty from their external appearance. (*a*) may be due to the inheritance of the property of turning yellow as the result of exposure. Taking into consideration the sources of error and the poverty of the crop, the sampling may be said to have been carried out with a fair degree of accuracy. The error is not sufficient to affect the general conformity with Mendelian expectation.

2. *Telephone* × *Native pea No.* 1.—The Mendelian constitution as regards cotyledon characters was determined in the case of the following plants of F_2 :—

Number.	Character of F_2 Seed.	F_3 Seeds born on F_2 Plant.				Constitution of Parent F_2.
		sm. y.	sm. g.	wr. y.	wr. g.	
621.1.1	**sm. y.**	9	5	3	1	AaBb
.2†	sm. g.	—	66	—	—	Ab
.3	„	—	34	—	10	Aab
.4	„	—	45	—	11	Aab
.5	„	—	19	—	6	Aab
.6	wr. y.	—	—	—	29	ab
621.2.1	**sm. y.**	45	27	10	3	AaBb
.2†	wr. y.	28	—	10	—	AaB!(*c*)
623.1.1	**sm. y.**	31	7	9	—	AaBb
.2	„	39	—	6	—	AaB
.3	„	38	—	—	—	AB
.4	„	21	4	—	—	ABb
.5	„	19	—	12	—	AaB
.6	„	7	1	—	—	ABb
.7	„	17	3	—	—	ABb
.8	„	38	11	—	—	ABb
.9†	wr. y.	—	—	97	29	aBb
.10	„	—	—	38	—	aB
.11†	„	—	—	62	—	aB
623.2.1	**sm. y.**	44	10	—	—	ABb
.2†	sm. g.	—	16	—	7	Aab
.3†	wr. y.	—	—	58	17	aBb
623.4.1†	**sm. y.**	55	20	23	5	AaBb
.2	„	48	13	17	7	AaBb
.3†	sm. g.	52	12	18	7	AaBb!(*a*)
.4	wr. y.	—	—	74	27	aBb
.5	„	53	22	17	9	AaBb!(*b*)
623 5.1	sm. y.	46	15	14	5	AaBb
.2	„	36	—	15	—	AaB
.3	„	35	12	11	3	AaBb
.4	„	100	—	—	—	AB
.5†	„	162	—	51	—	AaB
623.5.6	sm. g.	—	38	—	13	Aab
.7	„	—	29	—	13	Aab
.8	„	—	20	—	—	Ab
.9†	wr. g.	—	—	1!	49	ab
634.1.1	sm. y.	19	5	—	—	ABb
.2	„	9	4	—	—	ABb
.3	„	18	4	4	3	AaBb
.4	„	27	—	9	—	AaB

Number.	Character of F^2 Seed.	F_3 Seeds born on F_2 Plant.				Constitution of Parent F_2.
		sm. y.	sm. g.	wr. y.	wr. g.	
.5	sm. g.	—	20	2	9	Aab
.6	,,	—	30	—	—	Ab
.7	,,	—	29	—	13	Aab
.8	wr. y.	—	—	18	2	aBb
.9	,,	—	—	51	—	aB
.10	,,	—	—	79	21	aBb
.11	,,	—	—	3!	18	ab!(*d*)
634.2.1	sm. y.	41	11	10	3	AaBb
.2	,,	7	3	2	—	AaBb
.3	,,	25	6	5	6	AaBb
.4	,,	15	7	—	—	ABb
.5	,,	12	8	7	2	AaBb
.6	,,	19	6	—	—	ABb
.7	sm. g.	—	53	—	20	Aab
.8	wr. y.	—	—	29	9	aBb

Summing up as in the previous case, we have :—

Parent Seed.	Mendelian constitution of Parent.									Total.
	AaBb.	AaB.	Aab.	ABb.	aBb.	AB.	Ab.	aB.	ab.	
Sm. y. ..	12	5	—	8	—	2	—	—	—	27
Sm g. ..	(1)	—	9	—	—	—	3	—	—	13
Wr. y. ..	(1)	(1)	—	—	6	—	—	3	(1)	12
Wr. g. ..	—	—	—	—	—	—	—	—	2	2
Total ..	14	6	9	8	6	2	3		3	54

Four unconformable cases appear, namely :—

(*a*) 1 seed sown as sm. g. gave rise to all four types.

(*b*) 1 seed sown as wr. y. gave rise to all four types.

(*c*) 1 seed sown as wr. y. gave rise to sm. y. and wr. y. seeds.

(*d*) 1 seed sown as wr. y. gave rise to wr. g. seeds only.

(*b*), (*c*), and (*d*) may be accounted for as in the previous instance.

Case (*a*) remains, and in this instance I am inclined to believe that the plant may have been mistaken in gathering ; and this is the more likely because sm. g. came next to sm. y. in my system of sowing, so that if germination took place very obliquely it is possible that the seedling may have come up on the wrong side of the partition dividing these groups.

The crop obtained in this instance was so far satisfactory that it is worth while to sum up the total proportions of seeds produced by the plants of different constitutions. Thus the 14 AaBb plants bore altogether the following seeds :—

Total 846—sm. y. 477; sm. g. 165; wr. y. 150; wr. g. 54. The expectation being for 848—sm. y. 477; sm. g. 159; wr. y. 159; wr. g. 53.

The 6 AaB plants produced the following : sm. y. 311; wr. y. 103.

The 9 Aab plants produced the following : sm. g. 283; wr. g. 104.

The 8 ABb plants produced the following : sm. y. 189; sm. g. 51.

The 6 aBb plants produced the following : wr. y. 355; wr. g. 105.

All four cases together give the proportion 1,138 : 363 or 75·8 : 24·2.

A further generation was grown from the seeds (F_3) of those plants which are distinguished by a † in the preceding table; with the following results :—

621.1.1 sm. g. seeds only. 15 plants bore 440 seeds—all sm. g. (F_4).

621.2.2. (a) sm. y. seeds gave rise to 8 plants, of these, 3 bore only sm. y. seeds 43 in number ; 5 bore sm. y. and wr. y. seeds in the proportion 89 : 31.

(b) wr. y. seeds : 5 plants with 96 seeds—all wr. y.

623.1.9. (a) wr. y. seeds—22 plants, 4 with 140 wr. y. only ; and 18 with 358 wr. y.: 120 wr. g.

(b) wr. g. seeds : 15 plants with 380 seeds—all wr. g.

623.1.11. wr. y. seeds only : 16 plants with 273 wr. y. seeds.

623.2.3. (a) wr. y. seeds : 8 plants, 7 with wr. y. only—81 seeds, and 1 with 10 wr. y. : 4 wr. g.

(b) wr. g. seeds : 3 plants with 41 wr. g. seeds only.

623.4.1. (a) sm. y. seeds gave rise to 20 plants :—

(a1) 10 plants with 97 sm. y., 28 sm. g., 37 wr.y., 14 wr. g.

(a2) 6 plants with sm. y. and sm. g. seeds : 100 : 28.

(a3) 3 plants with sm. y. and wr. y. seeds : 23 : 8.

(a4) 1 plant with 9 sm. y. seeds only.

(b) sm. g. seeds—8 plants : 4 with 60 sm. g. seeds only, and 4 with 58 sm. g. : 25 wr. g.

(c) wr. y. seeds—7 plants : 2 with 57 wr. y. seeds only, and 5 with 56 wr. y. : 28 wr. g.

(d) wr. g. seeds—3 plants : 2 with 35 wr. g. only, and 1 with 19 sm. g. only. (c. p. below.)

623.4.3. (a) sm. y. seeds gave rise to 14 plants :—

(a1) 7 plants with 133 sm. y., 50 sm. g., 48 wr. y., and 22 wr. g.

(a2) 3 plants with sm. y. and sm. g. seeds : 52 : 25.

(a3) 4 plants with sm. y. and wr. y. seeds : 85 : 34.

(b) sm. g. seeds—8 plants : 3 with 105 sm. g. seeds only, and 5 with 102 sm. g. : 42 wr. g.

(c) wr. y. seeds—10 plants : 1 with 26 wr. y. only, and 9 with 178 wr. y., 53 wr. g.

(d) wr. g. seeds—3 plants with 100 wr. g. seeds only.

623.5.5. (a) sm. y. seeds gave rise to 43 plants :—16 with 323 sm. y. seeds only, and 27 with 427 sm. y. : 140 wr. y.

(b) wr. y. seeds—30 plants with 811 wr. y. seeds only.

623.5.9. wr. g. seeds only gave rise to 20 plants with 248 wr. g. seeds.

The unexpected occurred in a single case only, in which a supposed wr. g. seed of No. 623.4.1 turned out to have been really sm. g., there being thus 1 error among 249 cases of F_3 plants, all the rest of which follow exactly the Mendelian expectation.

4.—Telephone crossed with Ringleader.

A.—*The Parent Types have already been described.*

B.—*The Cross-bred Forms.*

Stated in brief the result of the present crosses was to confirm exactly Mendel's description of the effect of crossing a wrinkled green pea with a smooth yellow one.

1. *Telephone* × *Ringleader*.—15 pollinations resulted in the production of 12 pods containing 42 seeds, all smooth and yellow, though resembling in general shape the smooth seeds of Telegraph, or those of Telephone "filled out" so as to do away with the wrinkles.

2. *Ringleader* × *Telephone*.—4 pollinations : 2 pods with 2 seeds in each. These exactly resembled the normal seeds of the plants which bore them.

C.—*The Offspring of Cross-bred Plants*, F_2.

1. *Telephone* × *Ringleader*.—The seeds borne on the various plants were counted into the following groups :—

No.	sm. y.	sm. g.	wr. y.	wr. g.
428.1	15	3	6	1
.2	6	3	6	2
429.1	13	6	8	—
.2 & 3	15	8	9	2
430.1	3	4	2	2
.2	10	2	3	—
.3	10	1	2	1
431.1	11	5	3	2
.2	8	3	1	—
432.1	7	5	1	—
433.1	13	1	—	—
.2	7	2	2	—
.3	3	5	1	—
.4	5	3	2	2
.5	6	2	2	1
434.1	5	3	4	2
.2	7	2	3	—
.3	4	5	2	—
.4	3	3	2	—
.5	3	6	1	1
443.1	6	4	1	1
.2	3	3	4	1
.3	11	1	2	—
447.1	6	1	—	—
.2	3	1	2	2
452.1	3	1	2	—
.2	6	1	3	—
.3	6	1	1	1
457.1	13	5	5	1
.2	3	1	1	2
458.1	3	2	3	1
.2	7	2	1	1
Total	224	95	85	26

Sm. : wr. = 319 : 111 ; y. : g. = 309 : 121.

This generation produced fine large seeds of nearly the Telephone type throughout. Green and yellow seeds were always quite distinct, but smooth and wrinkled were rather more difficult to distinguish, and there was a slight doubt in one or two cases.

In the above cases as in others, a Mendelian total was arrived at when a sufficient number of plants were taken, in spite of the very small samples which individual plants afforded.

In a further generation the following figures were obtained :—

Number.	Character of F_2 Seed.	F_3 Seeds born on F_2 Plant.				Constitution of Parent F_2.
		sm. y.	sm. g.	wr. y.	wr. g.	
428.1.1	sm. y.	22	12	—	—	ABb
.2	,,	4	2	—	1	ABb
.3	,,	9	3	5	1	AaBb
.4	,,	38	—	—	—	AB
.5	,,	54	—	—	—	AB
.6	,,	3	—	—	—	?
.7	,,	6	3	—	—	ABb
.8	,,	31	—	—	—	AB
.9	,,	14	5	3	1	AaBb
.10	wr. y.	—	—	53	—	aB
428.2.1	sm. y.	41	—	—	—	AB
.2	,,	15	7	—	—	ABb
.3	,,	28	7	6	1	AaBb
.4	,,	49	—	—	—	AB
.5	wr. y.	—	—	21	8	aBb
.6	,,	—	—	13	3	aBb
.7	,,	—	—	50	17	aBb
.8	wr. g.	—	—	—	72	ab
429.1.1	sm. y.	42	—	—	—	AB
.2	,,	5	1	1	1	AaBb
.3	,,	17	—	6	—	AaB
.4	,,	35	—	—	—	AB
.5	,,	9	3	—	3	AaBb
.6	,,	10	—	1	—	AaB?
.7	sm. g.	—	15	—	2	Aab
.8	,,	—	17	—	4	Aab
.9	,,	—	13	—	4	Aab
.10	wr. y.	—	—	39	—	aB
.11	,,	—	—	34	14	aBb
.12	,,	—	—	14	3	aBb
433.1.1	sm. y.	13	8	10	3	AaBb
.2	,,	25	4	5	1	AaBb
.3	,,	13	4	8	3	AaBb
.4	,,	18	2	1	5	AaBb
.5	,,	14	5	6	—	AaBb
.6	,,	32	3	—	—	ABb
.7	,,	5	—	3	—	AaB?
.8	,,	13	11	—	—	ABb
.9	,,	18	—	5	—	AaB
433.2.1	,,	23	10	9	3	AaBb
.2	,,	3	—	4	—	AaBb
.3	,,	13	5	3	4	AaB
.4	wr. y.	—	—	36	17	aBb
434.1.1	sm. y.	33	—	1	—	AB
457.1.1	,,	38	8	10	5	AaBb
.2	,,	17	8	—	—	ABb
.3	wr. g.	—	—	—	34	ab

The result may be thus briefly summarized :—

Parent Seed.	Mendelian Constitution of Parent.									Total.
	AaBb.	AaB.	Aab.	ABb.	aBb.	AB.	Ab.	aB.	ab.	
Sm. y. ..	14	6	—	6	—	7	—	—	—	33
Sm. g. ..	—	—	3	—	—	—	—	—	—	3
Wr. y. ..	—	—	—	—	6	—	—	2	—	8
Wr. g. ..	—	—	—	—	—	—	—	—	2	2

5.—Native Pea No. 1 crossed with French Sugar Pea.

A.—*Description of Parents.*

Sutton's "*French Sugar Pea*" is described on the package as being on the average 5 feet high. The sample consisted of very large seeds, irregular in outline and slightly wrinkled (dimpled); they were slightly elongated and distinctly flattened from side to side. The starch grains were of the "round" type and the cotyledons were bright yellow in colour. The testa was quite opaque and of a colour varying from gray to orange-brown, and was sprinkled with purple or blackish-violet dots. On keeping, the gray testa showed a gradual change through orange to dark brown; so that in two years all the seeds preserved were of this colour and were then no longer capable of germination.

As grown at Peradeniya, the plants, under favourable conditions, reached a height of quite 7 feet; the usual number of internodes was 30, and the average length of an internode nearly three inches.

The stems were stout and branches were usually absent. The stems of young seedlings showed a red pigmentation at an early age, and a reddish purple patch appeared in the axil of each leaf. The flowers exhibited a red standard and purple wings.

The seeds resembled those of the original sample in size and form. The colour of the testa when the seeds were freshly gathered was nearly always greenish-gray; but some of the seeds in the lower pods usually showed signs of turning orange. Dark purple dots appeared

upon all of them. The pods when fresh were very large, often containing eight or nine seeds and being moreover particularly wide; when dry they were deeply constricted between the seeds and had a very shrivelled appearance, the parchment layer being quite wanting.

The first flower appeared upon the plants about 56 days after sowing and the seeds were dry some forty days later.

B.—*The Cross-bred Forms.*

1. *Native pea No.* 1 × *French sugar pea.*—From 18 pollinations there resulted 6 pods which were gathered on January 30th, 1903. They contained 26 seeds which exactly resembled those produced upon the same plants by self-fertilization. The average longest diameter of these seeds was 6·4 mm., which is almost exactly equal to the mean length of a sample of over 2,000 seeds of No. 1 which were accurately measured for another purpose.

Sixteen of these seeds were sown on May 2, and all of them germinated. The following table shows some of the characters of 14 plants which were taken up on July 30 :—

Number.	Height in Inches.	Number of Nodes.	Average Length of an Internode.	Number of Branches.	Pods.	Seeds.	Width of Pod in mm.
391·1	50	.	.	—	1	2	16
·2	55	.	.	—	3	6	15
·3	71	29	2·4	1	9	28	19
·4	74	31	2·4	2	8	29	18
·5	73	.	.	2	8	24	18
·6	82	35	2·3	2	8	26	18
393·1	94	33	2·8	2	9	34	18
·2	102	34	3·0	3	11	44	18
·3	79	34	2·3	1	9	31	18
·4	75	.	.	2	7	25	18
·5	.	.	.	1	5	16	17
394·1	80	25	3·2	1	8	21	15
·2	82	30	2·7	3	10	28	16
·3	95	33	2·9	3	10	26	17

The axils and flowers were coloured like those of Fr. sug. The pods were nearly of the shape of those of No. 1, but were much

larger. In certain areas of the pods traces of a want of the parchment layer could be detected, but these areas were small and the pods were fully inflated.

The colour of the testa was rather pale gray, with a tendency to become yellow in weathered pods. All the testas were dotted with purple—perhaps not quite so strongly as those of Fr. sug. In shape and size the seeds were intermediate and all of them were well dimpled.

The bad effects of bright sunshine alternating with showers of rain was very marked in the case of these plants, the stipules being much blistered and damaged in this way.

2. *French sugar pea × Native pea No.* 1.—The reciprocal cross was made under unfavourable conditions in October, 1902. Out of seven crosses attempted three were successful with 8 seeds as the result. These were sown on December 22, the first flowers appeared after 53 days and ripe seeds were gathered from 5 plants on March 18, 1903.

No.	Height.	Nodes.	AverageLength of Internode.	Branches.	Pods.	Seeds.
291·1	62	31	2·0	—	7	25
292·1	46	25	1·9	—	3	8
·2	68	31	2·2	3	10	37
322·1	72	32	2·2	—	5	18
·2	62	30	2.1	—	4	10

The more stunted habit of these plants is probably to be associated with the drier season in which they grew; and the absence of branches upon four out of five of them may perhaps be attributed to the same cause. In all other respects these plants resembled those derived from the reciprocal cross.

C.—*The Second and Third Generations from the Cross.*

A somewhat full account of the behaviour of seed characters in these generations has been given in a previous paper, page 328. This may be here supplemented by the following table containing a *resumé* of the characters of the plants grown in F_2 and of some of those of their offspring in F_3.

No.	F_2. Height.	Number of Nodes.	Average Length of Internode.	Number of Branches.	Pods.	Seeds.	Pod P. or S.	Pod Width.	Colour of Testa.	Surface of Seed.	Number of Seeds Sown.	Number of Plants Examined in F_3.	F_3. Plants with Pods. w	N	P	s	Plants with Seeds. p	f	w
391.3.1	72	23	3·1	1	3	17	P	N	p	d	—	—	—	—	—	—	—	—	—
2	108	37	2·9	3	12	60	P	N	p	d	25	20	—	20	20	—	15	5	—
3	94	35	2·7	2	19	60	P	N	p	d	25	24	—	24	19	5	14	4	6
4	88	33	2·7	3	16	63	P	N	p	d	30	30	—	30	25	5	19	5	6
5	80	31	2·6	—	10	30	P	N	w	s	—	—	—	—	—	—	—	—	—
6	104	41	2·5	2	13	66	P	W	p	d	30	20	?	?	13	7	11	—	—
7	95	35	2·7	—	6	30	P	W	p	d	—	—	—	—	—	—	—	—	—
8	94	35	2·7	1	15	54	P	N	f	d	25	25	—	25	21	4	—	20	5
9	99	37	2·7	—	10	28	S	W	w	s	—	—	—	—	—	—	—	—	—
10	96	33	2·9	1	14	42	P	W	p	d	—	—	—	—	—	—	—	—	—
11	100	38	2·6	3	25	104	S	W	p	d	—	—	—	—	—	—	—	—	—
12	—	—	—	1	14	42	S	W	p	d	20	14	14	—	—	14	7	3	4
13	97	36	2·7	3	13	48	P	W	f	d	25	18	?	?	16	2	—	18	—
14	106	38	2·8	3	11	45	S	W	p	d	20	16	*	*	—	16	16	—	—
15	85	27	3·1	—	3	10	P	N	f	d	—	—	—	—	—	—	—	—	—
16	100	—	—	1	8	40	P	M	p	d	20	12	*	*	5	7	7	3	—
17	—	—	—	—	5	13	S	W	w	s	—	—	—	—	—	—	—	—	—
18	102	35	2·9	—	5	21	S	W	p	d	—	—	—	—	—	—	—	—	—
19	97	36	2·7	3	15	57	S	W	p	d	25	12	?	?	—	12	7	4	1

No.	F_2.												F_3.						
	Height.	Number of Nodes.	Average Length of Internode.	Number of Branches.	Pods.	Seeds.	Pod P. or S.	Pod Width.	Colour of Testa.	Surface of Seed.	Number of Seeds Sown.	Number of Plants Examined in F_3.	Plants with Pods.				Plants with Seeds.		
													W	N	P	S	p	f	W
20	103	40	2·6	2	20	83	P	N	p	d	40	36	—	—	36	—	27	9	—
21	99	34	2·9	1	5	33	P	W	p	d	—	—	—	—	—	—	—	—	—
22	109	39	2·8	3	14	58	S	W	p	d	30	16	?	?	—	16	12	4	—
23	95	32	3·0	—	4	22	P	W	f	d	20	8	8	—	7	1	—	8	—
24	—	—	—	—	3	6	P	W	p	d	—	—	—	—	—	—	—	—	—
25	—	—	—	—	2	10	P	N	f	d	—	—	—	—	—	—	—	—	—
26	88	—	—	2	4	20	P	W	p	d	—	—	—	—	—	—	—	—	—
391, 4, 5, and 6, 1	82	27	3·0	1	16	51	S	W	w	s	25	20	*	*	—	20	—	—	20
2	80	—	—	—	5	21	P	N	f	d	—	—	—	—	—	—	—	—	—
3	96	33	2·9	2	8	32	S	W	w	s	20	15	15	—	—	15	—	—	15
4	103	34	3·0	2	10	41	P	W	p	d	20	14	10	4	12	2	11	—	3
5	104	36	2·9	1	10	33	S	W	w	s	—	—	—	—	—	—	—	—	—
6	102	33	3·1	1	13	49	P	W	p	d	25	19	19	—	19	—	10	3	6
7	90	34	2·6	—	10	33	S	W	w	s	—	—	—	—	—	—	—	—	—
8	96	32	3·0	1	7	33	P	W	p	d	—	—	—	—	—	—	—	—	—
9	86	30	2·9	1	13	40	P	W	p	d	20	19	*	*	15	4	14	2	3
10	84	31	2·7	1	12	45	P	W	p	d	20	19	*	*	16	3	9	5	5
11	97	26	3·5	—	2	11	P	W	p	d	—	—	—	—	—	—	—	—	—

12	95	35	2·7	1	11	33	P	W	w	s	20	14	*	*	10	4	—	—	14
13	—	—	—	3	13	45	P	W	w	s	20	11	*	*	9	2	—	—	11
14	96	28	3·4	—	8	29	S	W	f	d	20	18	13	5	—	18	—	18	—
15	88	33	2·7	2	18	57	P	W	p	d	30	28	23	5	23	5	16	2	10
16	92	33	2·8	1	8	40	P	W	p	d	20	9	*	*	9	—	5	2	2
17	96	35	2·7	1	7	32	P	W	p	d	—	—	—	—	—	—	—	—	—
18	106	35	3·0	—	10	33	P	W	p	d	—	—	—	—	—	—	—	—	—
19	108	39	2·9	2	18	83	P	N	p	d	40	25	?	*	25	—	18	5	2
20	99	35	2·8	3	18	75	P	W	p	d	30	21	*	*	15	6	14	—	7
21	98	38	2·6	3	18	60	P	N	p	d	30	14	—	14	14	—	7	5	2
22	98	34	2·9	2	14	60	P	M	f	d	30	25	*	*	17	5	—	15	10
23	94	33	2·8	—	5	27	P	W	f	d	—	—	—	—	—	—	—	—	—
24	113	39	2·9	3	11	47	P	M	p	d	25	24	16	8	24	—	15	2	7
25	84	23	3·6	—	3	10	P	W	p	d	—	—	—	—	—	—	—	—	—
26	109	40	2·7	2	13	71	P	W	p	d	30	23	*	*	22	4	20	—	6
27	103	33	3·1	—	6	22	P	W	w	s	—	—	—	—	—	—	—	—	—
28	87	29	3·0	—	3	10	S	W	p	d	—	—	—	—	—	—	—	—	—
29	105	36	2·9	—	8	34	S	W	f	d	—	—	—	—	—	—	—	—	—
30	101	37	2·7	2	13	60	S	W	p	d	30	19	16	3	—	19	10	4	5
31	86	34	2·5	1	13	58	P	W	f	d	25	20	*	?	15	5	—	18	2
32	71	26	2·7	—	3	11	P	W	w	s	—	—	—	—	—	—	—	—	—
33	92	34	2·7	3	30	94	P	N	p	d	40	34	—	34	34	—	26	8	—
34	97	38	2·6	2	9	40	S	W	f	d	20	12	12	—	—	12	—	12	—
35	82	30	2·7	—	6	19	P	N	w	s	10	10	—	10	10	—	—	—	10
36	85	31	2·7	—	4	12	S	W	w	s	—	—	—	—	—	—	—	—	—
37	90	30	3·0	—	6	16	P	W	p	d	—	—	—	—	—	—	—	—	—
38	88	28	3·1	3	7	22	S	W	w	s	—	—	—	—	—	—	—	—	—
39	75	—	—	—	5	13	S	W	w	s	—	—	—	—	—	—	—	—	—
40	98	31	3·2	—	11	39	P	W	w	s	10	10	*	*	10	—	—	—	10
41	110	39	2·7	2	12	65	P	N	p	d	20	20	*	*	18	2	20	—	—
42	84	32	2·6	2	19	62	P	W	w	s	30	19	*	*	19	—	—	—	19

No.	F_2.											F_3.						
	Height.	Number of Nodes.	Average Length of Internode.	Number of Branches.	Pods.	Seeds.	Pod P. or S.	Pod Width.	Colour of Testa.	Surface of Seed.	Number of Seeds Sown.	Number of Plants Examined in F_3.	Plants with Pods.				Plants with Seeds.		
43	85	25	3·4	—	3	10	P	W	p	d	—	—	—	—	—	—	—	—	—
44	96	33	2·9	—	10	41	P	N	p	d	20	18	—	18	18	—	13	—	5
45	105	37	2·8	1	12	57	P	N	p	d	—	—	—	—	—	—	—	—	—
46	108	42	2·6	1	12	40	P	W	p	d	20	18	18	—	15	3	9	4	5
47	—	—	—	2	14	54	S	W	f	d	25	19	19	—	—	19	—	16	3
48	—	—	—	2	7	43	P	W	p	d	20	18	18	—	18	—	6	5	7
49	96	31	3·1	2	11	47	S	N	p	d	20	19	*	*	—	19	18	—	1
50	94	34	2·8	2	7	27	P	W	w	s	—	—	—	—	—	—	—	—	—
51	94	25	3·8	—	3	8	P	—	f	d	—	—	—	—	—	—	—	—	—
52	67	22	3·0	—	3	8	S	W	f	d	—	—	—	—	—	—	—	—	—
53	93	30	3·1	—	2	9	P	W	p	d	—	—	—	—	—	—	—	—	—
54	—	—	—	—	—	40	P	N	p	d	—	—	—	—	—	—	—	—	—
55	114	40	2·9	5	15	58	P	W	p	d	—	—	—	—	—	—	—	—	—
56	94	37	2·5	5	25	103	S	W	p	d	—	—	—	—	—	—	—	—	—
57	120	42	2·9	2	12	42	P	W	p	d	20	3	3	—	2	1	2	1	—
58	125	49	2·6	3	14	60	S	W	p	d	—	—	—	—	—	—	—	—	—

In the above table P = inflated and S = soft or constricted pods; W = wide, M = mid, and N = narrow pods.
p denotes purple-spotted, f grey, and w white testa; d indicates dimpled, and s smooth or slightly pitted seeds.
Height and average length of internodes are given in inches.

** Plants with wide and others with narrow pods were present, but they could not be separated into two distinct groups owing to the existence of intermediates.

Considering now the various characters summarized in this table, we observe that the average length of the internodes shows a fairly continuous variation ; and we may remember that this length was not very different in the two parental strains.

Width of pod is a character which almost certainly exhibits Mendelian segregation in spite of a good deal of apparently indefinite variation. Unfortunately no actual measurements were made in F_2, but the plants with distinctly narrower pods were separated by eye from the remainder which had wider pods. There were 19 of the former and 65 of the latter. Out of 13 of the former, the seeds of which were sown, 9 plants produced only offspring with narrow pods (13-16 mm.), whilst the remaining 4 plants appeared to have been heterozygotes with exceptionally narrow pods. Out of the 31 plants with wider pods which were examined none gave rise only to offspring with narrow pods. Nine gave rise to offspring all wide podded (17 mm. and upwards), whilst the remaining 22 plants gave rise to both kinds of offspring. It seems clear therefore that Mendel's law is here followed in spite of much variability and in spite of the intermediate position of the heterozygote.

As a general rule wide pods contained flattened seeds and narrow pods contained cubical or spherical seeds ; though in this point too there was a certain amount of variability. The only exceptions were a few cases in which seeds classed as round or cubical appeared in pods which were classed as wide. In such cases, when the seeds were grown, it appeared that the plants were heterozygotes in respect of pod width.

Seeds with white testas were usually smooth or slightly pitted, whereas coloured seeds were always markedly dimpled.

In the case of some of the above characters the distinction of the allelomorphs is certainly open to criticism. In such cases it is not absolutely proved that Mendel's law is followed, although the probability may be very great that this is so. In other cases the discontinuity is complete, and in these cases the evidence that Mendel's law is followed is complete also.

Thus, in the case of the presence or absence of a parchment layer in the pods, Mendel's results were fully confirmed, with the exception

that dominance of the inflated pod was found to be not quite complete. As regards the allelomorphic characters gray and white colour of the testa the same thing is true. Purple spots appeared in addition on the testas in the case of three out of four of the plants which had a coloured testa, and the further behaviour of these characters entirely bears out the explanation given on page 331.

The presence of coloured flowers appears to be completely correlated with a coloured testa (greenish-gray) and with the presence of purple spots in the axils of the leaves. And with these characters the time of flowering is to some extent correlated. The evidence for this latter statement is given in the following table :—*

No.	In fl. May 25.		In fl. May 30.		In fl. June 4.		Total Gathered.	
	p.	w.	p.	w.	p.	w.	p.	w.
391.3.3	—	—	1	3	6	4	18	6
.4	14	4	18	6	24	6	24	6
.8	—	—	—	—	3	1	20	5
.12	—	—	3	2	8	3	10	4
.19	—	—	—	—	1	1	11	1
.22	—	—	2	3	4	5	12	5
391.4.4	—	1	—	3	4	3	11	3
.6	—	1	5	3	7	5	18	6
.9	6	3	9	3	15	3	16	3
.10	8	2	12	5	14	5	14	5
.15	3	2	12	8	15	10	18	10
.16	—	1	5	3	7	3	7	3
.19	—	—	—	—	—	—	23	2
.20	—	—	3	5	9	6	14	7
.21	1	1	5	1	9	2	12	2
.22	—	—	—	4	4	8	15	10
.24	—	2	4	4	8	4	17	7
.26	1	4	8	8	15	8	20	8
.30	—	4	4	4	9	5	14	5
.31	1	1	7	2	12	2	18	2
.44	—	—	1	3	3	5	13	5
.46	—	—	2	1	4	2	13	5
.47	—	3	5	3	10	3	16	3
.48	—	—	1	5	4	9	11	9
.49	—	—	—	—	—	1	18	1
Total ...	34	29	107	79	175	104	383	123
	1.17 : 1		1.35 : 1		1.68 : 1		313 : 1	

* p. = plants with coloured flowers; w = plants with white flowers.

6.—Native Pea No. 2 crossed with Satisfaction.

A.—*Description of Parents.*

1. *Satisfaction*, as obtained from Messrs. Sutton, is described on the package as being 3 feet in average height. "Habit robust and endures drought well. Pods straight and broad and closely filled with very large peas."

The original sample consisted of very large seeds with yellow cotyledons, much wrinkled. The testas were slightly greenish or yellowish and not very transparent.

As grown at Peradeniya the plants were always of a very uniform height, the extreme range of variation being from about 3 feet 6 inches to about 5 feet. Average 4 feet 6 inches (137 cm.). The average number of nodes was 31; the average length of an internode being therefore 1·74 in. (44 mm.). The average width of a pod was 22 mm.

The seeds were large and thoroughly wrinkled, the starch grains being of the type characteristic of wrinkled seeds. Their colour was the rather pale shade of yellow which appears to be often associated with the wrinkled character.* The testas were white, usually without any trace of pigment, and a little less opaque than those of the original sample.

Seeds gathered from my own plants and ripened in February germinated without exception when sown the following April, and scarcely any plants were lost. The variety, in fact, stood the climate of Peradeniya better at all times of year, and gave a better crop than any other English kind which was examined.

2. *Native pea No.* 2.—The average height was less than three feet, but differed a good deal at different seasons. Average number of nodes 24 and average length of an internode about $1\frac{1}{2}$ in. (3·8 cm.). Width of pod on the average 10 mm. Main stem thin; often with 3–5 branches at the base, which attain an equal height. Flowers less than half the size of those of Satisfaction; the standard pinkish-red in colour, the wings purple and changing from a reddish to a bluish purple as the flowers get older. Seeds very small, quite

* *Cf.* the account of Telephone crosses above; also Hurst, in Journ. Roy. Hort. Soc., 1904.

smooth, and nearly spherical, but being closely packed in the pod they exhibit a certain squareness of outline. Cotyledons yellow; starch grains of the round type. The testa shows fine dots of a deep purplish colour and, in addition, a marbling of brown on a pale greenish-yellow ground. The purple colouration is produced by a pigment dissolved in the sap of certain cells immediately underlying the outermost layer of the testa. The brown colour is almost or quite confined to the walls of the I-shaped cells of the outermost layer. The greenish colour seems to be a solid pigment deposited in all or nearly all the cells of the testa.

I have received a closely similar pea from the Superintendent of the Calcutta Botanic Gardens under the name of *Pisum quadratum*. The habit of the plants is slightly different, but in other respects they closely resemble one another. Certainly no one would at first sight place these plants in the same species as the ordinary forms of *Pisum sativum* grown in Europe. The former have in comparison a primitive and wild appearance, and the suggestion that they may lie somewhere near the original ancestor of European cultivated peas is supported by the fact presently to be described in greater detail, that on crossing with the white-coated form Satisfaction there were obtained in F_2 all the best known types of testas to be found in cultivated peas.

B.—*The Cross-bred Forms.*

1. *Native pea No. 2 × Satisfaction.*—Only one cross (No. 440, made in January, 1903) was successful; and various accidents prevented me from obtaining further crosses. Three seeds were produced, quite indistinguishable from the other seeds of the same plant so far as appearance was concerned. The seeds were sown on May 2, but only one plant produced seed. This plant was 70 inches in height and had 31 nodes. The average width of its 4 pods was 14 mm., and these contained altogether 8 seeds. The plant and its seeds resembled those produced upon the plants of the reciprocal cross, and they may be described together.

2. *Satisfaction × Native pea No. 2.*—Two successful crosses gave rise to 6 seeds which were gathered on February 17, 1903. These seeds closely resembled those of Satisfaction except in being filled

out so as to have a smooth surface; with the exception of a slight dimple on each side, such as was often observed in "round" seeds grown in Ceylon. The seeds were sown on May 2, and 3 plants bearing seeds were taken up on July 27. The length of life of these plants was therefore intermediate, but nearer to that of Satisfaction. The following table shows some of the characters of these plants :—

No. of Cross.	Height.	Nodes.	Pods.	Seeds.	Width of Pod in mm.	Seeds.	
						Dimpled.	Wrinkled.
440	70	31	4	8	14	8	—
439	75	30	5	15	14	12	3
441.1	79	31	2	5	15	5	—
441.2	74	31	4	8	14	6	2

None of the plants produced any branches. The average length of an internode was 2·4 in. (6·1 cm.), greatly exceeding that characteristic of either parent. The number of internodes was practically the same as in Satisfaction, but the plants were much taller. Width of pod was intermediate.

As regards the shape of the seeds we have some interesting points to consider, for all were more or less wrinkled. There were considerable differences in the degree of wrinkling, and in the case of two plants it was possible to distinguish between a group of very wrinkled seeds (5 in number) and a remaining group of 18 to which the term dimpled might better be applied. I could not satisfy myself that there were any of the truly wrinkled group upon the other two plants. The phenomenon is in agreement with a case described by Tschermak, who crossed a smooth coloured-coated pea with a smooth white-coated pea and in F_1 (of seed-coat—F_2 of cotyledons) obtained exclusively "slightly wrinkled" seeds. It appears that as a rule the dimpled character is correlated with the coloured coat, and in the present case this correlation would seem to have become restored as the result of the cross. My example is complicated by the fact that the white-coated pea used was wrinkled, so that in F_1 of seed-coat and F_2 of cotyledons there is expected a proportion of

three dimpled to one wrinkled. And the evidence goes to show that this expectation was fulfilled, although no examination of starch grains was made for the reason that the seeds were required for sowing.*

In colour the testas of these peas closely resembled those of No. 2; but the ground colour was in all cases of a distinctly yellowish shade such as appeared only exceptionally in No. 2. On the whole we may fairly say that there was full dominance of the colour characters of the testa of No. 2. The flowers also and leaf axils were coloured like those of the parent. The form of the foliage was more or less intermediate.

C.—*The Subsequent Generations.*

In F_2 no distinction was to be recognized between the separate offspring of the above four plants. The 25 plants of this generation may therefore be described together.† The majority of the characters to be considered are epitomized in the following table :—

Number.	F_2.						F_3.							
	Height (Inches).	Number of Nodes.	Average Length of Internodes.	Branches.	Character of Testa.	Seeds Sown.	Plants Gathered.	m.p.	m.	p.	f.	w.	Plants with long Internodes.	Plants with short Internodes.
440 & .1	85	42	2·0	1	mp	50	36	26	5	5	—	—	*	*
441.2	90	31	2·9	2	p	20	9	—	—	9	—	—	*	*
.3	75	42	1·8	3	m	30	24	—	18	—	—	6	*	*
.4	83	41	2·0	8	mp	150	88	48	8	7	5	20	*	*
.5	20	17	1·2	—	w	3	3	—	—	—	—	3	.	*
.6	16	14	1·1	—	p	3	1	—	—	1	—	—	.	*
.7	24	20	1·2	—	f	20	18	—	—	—	18	—	.	*

m = marbled with brown; p = spotted with purple; f = grey with faint bluish dots; w = white.

* Such an examination was however applied to the seeds of a later generation, with results which fully confirm the conclusion here arrived at.

† As a matter of fact the offspring of the reciprocal crosses 440 and 441 could not be distinguished owing to the labels having been accidentally shifted.

Number.	F_2.							F_3.							
	Height (Inches).	Number of Nodes.	Average Length of Nodes.	Branches.	Character of Testa.	Seeds Sown.	Plants Gathered	m.p.	m.	p.	f.	w.	Plants with long Internodes.	Plantswith short Internodes.
.8	29	16	1·8	—	f	2	—	—	—	—	1	1	*	.
.9	107	47	2·3	5	w	40	—	.	.	.	.	.	*	.
.10	94	44	2·1	4	p	40	21	—	—	13	3	5	*	*
.11	95	37	2·6	9	mp	60	32	16	9	1	3	3	*	.
.12	110	41	2·7	6	w	40	4	—	—	—	—	4	*	*
.13	103	40	2·6	4	w	10	3	—	—	—	—	3	*	*
.14	70	29	2·4	—	mp	8	7	3	—	1	—	3	*	*
.15	104	42	2·5	5	mp	60	20	11	1	—	—	8	*	*
.16	62	54	1·1	5	mp	20	—	.	.	.	.	.	*	*
439.1	58	23	2·5	1	p	25	17	—	—	12	—	5	*	.
.2	49	18	2·7	—	p	10	2	—	—	2	—	—	.	.
.3	25	21	1·2	—	p	6	—	.	.	.		.	*	*
.4	80	43	1·9	20	mp	80	61	30	7	—	—	24	*	.
.5	78	37	2·1	4	mp	60	44	18	3	8	1	14	*	*
.6	tall				mp	110	66	34	16	—	—	16	*	.
.7	80	44	1·8	—	mp	8	7	5	2	—	—	—	*	.
.8	85	38	2·6	1	m	26	2	—	2	—	—	—	*	.
.9	dwarf				w	.	.	.	.	.	,	.	.	.	.

As regards habit there was a great deal of variation. Some of the plants were very robust, whilst others—dwarfs, which were soon overgrown by the former—were very feeble. If we consider the character average length of internodes, we find an obviously Mendelian behaviour.

Thus, in F_3 19 plants had internodes 1·8 to 2·9 inches in length, and 6 plants had internodes 1·0 to 1·2 inches in length.

The latter produced in F_3 exclusively offspring with an average length of internodes of less than 1·3 in. Of the former 9 produced only offspring with long internodes in F_3 (1·6 in. long and upwards), but in a few cases there were only one or two plants per parent, and some of them should therefore perhaps be added to the number of the heterozygotes, namely, 10 plants, which produced both offspring with long and with short internodes in F_3.

In F_3 the plants with long and those with short internodes were readily distinguishable two or three weeks after germination. At this time the former were, as a rule, quite twice as tall as the latter and perfectly distinct in appearance. The offspring of the 10 heterozygotes was as follows in F_3, the counting being made 18 days after germination. A considerable number of these plants subsequently perished from drought, and a few had already died since germination, the mortality being greater in the case of the dwarf form :—

No.	Tall.	Dwarf.	No.	Tall.	Dwarf.
439.1	12	5	440.10	28	4
.4	48	14	.12	23	8
.6	74	16	.13	5	4
440.2	5	4	.14	6	1
.3	22	3	.15	31	13

Total—245 tall to 72 dwarf, or 3·53 : 1. The two groups are unmistakably distinct, the dwarf forms having a much stiffer appearance and foliage somewhat darker than the tall.

Length of life was found to be a character quite independent of the above, and is one which may considerably modify the final height of the plant. Thus, in the case of No. 440·16 ; flowers did not appear before the 48th internode. The offspring of this plant, which resembled the parent, all fell victims to excessively wet weather before any flowers appeared ; most of them had by that time developed about 40 internodes. It is a remarkable fact that none of the tall or dwarf forms in F_2 and F_3 were in the least like either of the original parents, in both of which the internodes seemed to be of medium length. In F_1 there appeared a form with longer internodes than either parent, and in F_2 this form persisted as a dominant type, whilst a new recessive form appeared with shorter internodes than either parent.

As regards the shape of seeds in F_2 and F_3, the phenomena observed may be briefly summed up as follows :—Seeds with a coloured testa were dimpled or wrinkled according to Mendel's law, although the difficulty of exact discrimination made it impossible to ascertain the precise ratio in more than a few cases. Small seeds were as a rule less dimpled than large ones, so that some of the smallest of the

coloured seeds were practically smooth in surface (or, on the other hand, quite wrinkled), though usually more or less square in outline. Even in the case of the largest seeds dimpled and wrinkled were usually quite distinguishable; and the point could be settled by cutting sections, when dimpled seeds were found to have starch grains of the "round" type. In other cases where the eye alone could not distinguish dimpled from wrinkled with certainty, the microscopic test was found to be conclusive.

Among the seeds with a white or nearly colourless testa, smooth and wrinkled cotyledons appeared in accordance with Mendelian expectation.* The above remarks apply without exception to F_2 and to all the seeds in F_3 which could be dried. Many of the F_3 plants were taken up in very wet weather, and in such cases it was impossible to discriminate between the shapes of the seeds.

The colour of the testa appeared to follow perfectly definite rules, some account of which has already been given in a previous paper (page 333), but the description needs elaborating in some respects. Twenty-five plants were raised in F_2, their seed-coat colours being as follows :—

Eleven plants (m. p. f.) showed testas coloured like No. 2, except that in some cases the ground colour was yellowish like that of the F_1 plants, whilst in others it was greenish like the parental strain.† The purple spots and the "maple" marking was clearly visible in all these cases.

Six plants (p. f.) resembled these in the ground colour of the testa and in the presence of purple spots, but the maple marks were quite wanting.

In two others (m. f.) the purple spots were wanting, but the maple marking was obviously present.

In two more (f.) both purple spots and maple marks were wanting, but the testas were obviously greenish and opaque.

* In F_2 all 4 plants with white testas had seeds exclusively smooth—DD—when the expectation was 1 DD : 2 DR : 1 RR. This was probably accidental, since in F_3, among the offspring of dimpled seeds, those with white coats showed the expected number of wrinkleds.

† The relative numbers of the two kinds were not counted in this or the next generation, and I do not think that they were always distinguishable.

All the above plants had coloured flowers and purple spots in the axils of the leaves. The four remaining plants had perfectly white flowers and the spots in the axils were wanting. Three of these plants had white testas like Satisfaction. In the fourth the colour was the same, but there appeared what can only be described as a kind of watermark, like the ghost of the maple pattern. It was quite distinctly visible in all the seeds of the plant.

In the remarks which follow concerning F_3, the same colours are denoted by the same letters. On white flowered plants the (invariably white-coated) seeds often showed the same maple watermark, but usually very indistinctly, and it could not always be traced in all the seeds of a plant even when some of them showed it. It seems clear that we have here a partial reappearance of the almost latent maple character, and in this case I should expect that on crossing such plants with a pure strain having pigmented testas, the full maple colour would make its appearance in some or all of the immediate offspring. It is hoped to test this conclusion by making such crosses during the present summer.*

It may tend towards clearness if I here set down at length the relative numbers of the different types of seeds which are to be expected in F_2 and F_3 on the hypothesis that the characters brown marbling (m) and purple spotting (p) can only appear in combination with the greenish or yellowish ground colour (f), but that in other respects Mendel's law is followed.

(1) Offspring of the forms showing all three colours (m. p. f.) :—

(*a*) 1 constant in F_3 (m. p. f.).
(*b*) 2 giving in F_3 (m. p. f.) and (m. f.).
(*c*) 2 giving in F_3 (m. p. f.) and (p. f.).
(*d*) 2 giving in F_3 (m. p. f.) and (w.).
(*e*) 4 giving in F_3 (m. p. f.), (m. f.), (p. f.), and (f.).
(*f*) 4 giving in F_3 (m. p. f.), (m. f.), and (w.).

* Note added July, 1905.—In a further generation (F_4), grown in England under good conditions, the distinction between plants bearing w and those bearing w (m) seeds was quite clear, and the inheritance was plainly Mendelian, w (m) being dominant to w. Crosses of the kind mentioned have been made in considerable numbers, and the result will appear next year.

(*g*) 4 giving in F_3 (m. p. f.), (p. f.), and (w.).
(*h*) 8 giving in F_3 (m. p. f.), (m. f.), (p. f.), (f.), and (w.).

(2) Offspring of the forms showing brown marbling (m. f.) :—
(*j*) 1 constant in F_3 (m. f.).
(*k*) 2 giving (m. f.) and (f.).
(*l*) 2 giving (m. f.) and (w.).
(*m*) 4 giving (m. f.), (f.), and (w.).

(3) Offspring of the forms showing purple spots (p. f.) :—
(*n*) 1 constant in F_3 (p. f.).
(*o*) 2 giving (p. f.) and (f.).
(*p*) 2 giving (p. f.) and (w.).
(*q*) 4 giving (p. f.), (f.), and (w.).

(4) Offspring of the form with simple coloured seeds (f.) :—
(*r*) 1 constant in F_3 (f.).
(*s*) 2 giving (f.) and (w.).

(5) Offspring of forms with a white testa (w.) :—
(*t*) 16 constant in F_3 (w.).

Thus 64 individuals of F_2 should include 19 forms of constitution. Out of the 25 plants obtained in F_2, 10 were found on examination of their offspring to have been of the following forms :—1 (*b*), 1 (*e*), 4 (*f*), 1 (*g*), 3 (*h*), 1 (*l*), 1 (*n*), 1 (*p*), 1 (*q*), 1 (*r*), 1 (*s*), and 3 (*t*), as may be seen on consulting the table. The remaining plants did not yield a sufficient number of offspring to allow of their character being determined. No unexpected type appeared among the whole series of 467 plants grown in F_3, and the proportions in which the visible types appeared were also in reasonable agreement with expectation.

Thus the total offspring of the 3 plants of type (*h*) was as follows :—

	Total.	(m.p.f.)	(m.f.)	(p.f.)	(f.)	(w.)
	169	82	20	21	9	37
Expectation ..	192	81	27	27	9	48

And the offspring of the 4 plants of type (*f*) were as follows :—

	Total.	(m.p.f.)	(m.f.)	(w.)
	147	75	24	48
Expectation ..	144	81	27	36

The agreement with theoretical expectation is so close that it appears reasonable to accept the hypothesis for the present. But it is hoped shortly to put it to the test by making crosses between the offspring of different types and a number of pure races.

7.—Other Crosses.

A number of further crosses were also made between the members of several different races of peas. These, so far as their decidedly feeble progeny in F_1 and F_2 allowed of estimating, afforded no exceptions to the ordinary Mendelian expectation as regards the allelomorphic characters which they exhibited, and which included representatives of cotyledon colour and shape, stature, inflation of pods, and colour of flowers and testa.

The following is a list of such crosses. None of the progeny showed much promise of developing into hardy strains and consequently none were grown after F_2.

Parents.	Number of Crosses Attempted.	Number Successful	Seeds Produced.	Characters Concerned.*
1.—No. 1 × Nonsuch ..	5	2	4	ABG x abg
2.—Earliest Blue × French Sugar ..	4	1	2	bcDg x BCdG
3.—French Sugar × Earliest Blue ..	2	2	3	BCdG x bcDg
4.—Satisfaction × French Sugar ..	4	4	11	D x d†
5.—No. 1 × Fillbasket ..	7	5	16	B x b
6.—No. 1 × Earliest Blue ..	9	3	6	B x b
7.—Earliest Blue × No. 1	4	2	4	b x B
8.—No. 1 × Satisfaction	3	3	14	A x a
9.—No. 1 × Eclipse ..	2	1	3	B x b
10.—No. 1 × British Queen	3	1	6	A x a
11.—Satisfaction × Ringleader ..	1	1	4	a x A
12.—No. 2 × No. 1. ...	3	2	5	—

* A = smooth, a = wrinkled; B = yellow, b = green; C = testa grey, c = testa white; D = pod inflated, d = pod constricted; G = tall, g = dwarf.

† Development of the parchment layer decidedly intermediate in F_1, although the pods are obviously inflated.

Summary.

A somewhat complete summary of the more important of the facts dealt with in the present notice has already been given in a previous paper, see pages 308, 312, 328, 333; the account which follows deals chiefly with a few phenomena not previously referred to.

The result of the crosses made with Telegraph and Telephone was on the whole fully to confirm Mendel's account of the behaviour of cotyledon characters on crossing. In the crosses with Ringleader the agreement with expectation was complete; in the case of those with the small smooth yellow native pea (No. 1) a single absolute exception appeared in F_1, in which green appeared instead of the expected yellow. In F_2 and F_3 a few minor irregularities were observed, also in respect of colour, which are probably to be accounted for by imperfect ripening. In later generations the behaviour of these characters was more regular than in the earlier ones, and this is perhaps to be partly associated with the better health of the plants, but also, almost certainly, to an intensification of the characters following upon the cross. Nevertheless, even in F_2, when the total number of seeds born upon individual plants was often very small, totals closely approximating to Mendelian expectation were obtained when the figures for several plants were combined.

A summarized account of the crosses between French Sugar and No. 1 will be found on page 328 (example VI.). The colour characters of the testa gave in F_2 the proportion 9 : 3 : 4, already observed by Tschermak in several instances, but not described by him in terms of gametes. Other definite characters such as presence and absence of the parchment layer in the pod, follow Mendel's law, although dominance is not perfect in this case; and certain other less definite characters very probably behave in the same way.

The cross between No. 2 and Satisfaction, briefly described on page 333 (example VII.), was only represented by a few individuals in the earlier generations, but on account of its rather peculiar interest and because many of its offspring still survive for further experiment, it is here described at considerable length. The colour characters of the testa yield in F_2, almost certainly, the proportion 27 : 9 : 9 : 3 : 16,

also observed by Tschermak in the case of certain flower colours of Matthiola, and an explanation of this proportion is attempted on the same lines as in the previous instance.

This cross seems also to afford an example of remarkable intensification of both the allelomorphic characters of the same pair, namely, tallness and dwarfness—the former in F_1, and both in F_2 and later generations. As regards shape of the seeds a complication is introduced by the appearance of the plant character, dimpled seeds, in the offspring of a cross between parents which showed the allelomorphic characters, smooth and wrinkled cotyledons respectively.

A few other crosses support Mendel's experiments and conclusions, which are indeed already sufficiently well established.

Cambridge, July, 1905.

Foliar Periodicity of Endemic and Indigenous Trees in Ceylon.

BY

HERBERT WRIGHT.

(*With plates XXV. to XXX.*)

A STUDY of the behaviour of plants in a tropical region where the conditions for growth are more favourable than in Europe has always attracted the attention of botanists, and since 1900 a considerable amount of time has been spent in studying the foliar periodicities in plant life with the object of tracing out some of the laws which govern these phenomena. There are several problems to consider, such as the relationship between the time, manner, and frequency of defoliation of trees in the tropics and in middle Europe; also how far the phenomena of leaf-fall and foliar renewal, in the tropics, are affected by external and internal forces, and to distinguish cases in which either or both of these factors are of importance.

The amount of variation to be met with in trees commonly deciduous in various parts of Ceylon, the relation of defoliation to transpiration, and the independent effects of heat, light, and moisture, are some of the problems which are here considered. The following synopsis will indicate the general arrangement of the present paper :—

1.—General.

2.—Periodicity in Growth.

Periodicity in temperate and tropical zones.

Periodicity of vegetation in Ceylon; herbaceous and shrubby.

Periodicity of trees in Ceylon.

Forest types.

Frequency of foliar activity.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. II., Part III., October, 1905.]

3.—Climate in Ceylon and Java.
4.—The Leafless Phase in the Tropics.
General characteristics.
Variation in different climates.
Parts of Ceylon.
Ceylon and Java; Peradeniya, Buitenzorg, and East Java.
Ceylon and Ursprung's species.
Variation in the same climate.
Variation in successive years.
5.—Transpiration in Ceylon.
General.
Periodicity and transpiration.
6.—The relative importance of the physical factors: temperature, rainfall, humidity, and light.
7.—External and Internal Factors.
8.—Advantages of Periodical Phenomena.
9.—Relation of Foliar, Floral, and Fruit Periodicities.
10.—Foliar Periodicity of Fossil Plants.
11.—Foliar Periodicity of Endemic Species.
12.—Foliar Periodicity of Indigenous Species.
13.—Ceylon Indigenous Species in India.

Sachs in his "Lectures on the Physiology of Plants," in 1887, stated that, from a study of plants in European climates, one is led to infer that foliar periodicity depends upon the alternation of seasons and therefore chiefly upon temperature and moisture, and, without wishing to deny the co-operation of these factors, he suggested that periodicity may depend chiefly upon changes which take place in the plant, independently of external influences or only indirectly affected by them. Haberlandt in his book "Botanische Tropenenreise" in 1893 draws attention to the fact that botanists are inclined, from their knowledge of European floras, to connect the periodicity of leaf-fall and

foliar renewal with the periodical change of seasons in such areas, but quotes many instances which indicate that in tropical districts internal factors can be recognized. Schimper* and Ursprung† also dwell upon the tendency to interpret the phenomena in the tropics in terms of our knowledge of temperate zone plants.

It is one of the objects of this paper to prove that generalizations respecting foliar periodicities and their significance should not be made until a study of plants has been carried out in tropical areas where the physical conditions are compatible with a display of the autonomy of the plants. In temperate zones the vegetation only shows outward signs of life in spring and summer, whereas in the tropics conditions may exist for a perpetual display of activity on the part of one or more functions of the plants.

It need only be pointed out that there is not a month in the year, at Peradeniya, when all the plants are in full possession of their leaves; that some plants may produce a complete set of new leaves once or twice each year, others a complete and several sets each year, and others every month in the year, to convince anyone of the necessity of formulating plant-laws only after considering the vegetation in tropical areas.

The influence of temperature alone, suggested as being of importance by Sachs, Schimper, and many others, has been shown to be of minor importance in affecting the phenomena of leaf-fall and renewal in Ceylon. It is only in parts of the tropics where there is a minimum climatic periodicity and minimum variation in humidity and rainfall that the influence of temperature alone can be thoroughly worked out. If one attempts to work out the influence of temperature on the various functions of plants in a temperate zone he is necessarily handicapped, since he is dealing with

* Pflanzen-Geographie auf physiologischer Grundlage; Dr. Schimper, 1898.

† Anatomie und Jahresringbildung Tropischer Holzarten; Alfred Ursprung, 1900.

functions in plants, the characters and periodicities of which are to a great extent controlled by the adversities of the climate in which the plants and their ancestors have lived.

In this paper an account of observed foliar activities of known endemic and indigenous arborescent species in Ceylon, and their variation in the same or different climates is given; the adaptability of introduced species will be dealt with in a subsequent paper. Exact information of the foliar periodicities of trees in the tropics has been repeatedly asked for by Ursprung, Schimper, and others who have worked at the subject of tropical vegetation. It is only by the possession of such information that the question of internal factors in plant life in equable or tropical areas can be determined.

The investigation has also been carried out to determine how far external environment in a tropical area affects the annually recurring period of leaflessness. The information on this point has been gleaned from a study of the same species in various parts of Ceylon, Java, and countries mentioned by Ursprung.

The subject has also been studied with the view of throwing some light on the time-value of rings of growth in the stems of trees which are evergreen, partially or completely deciduous, and the general relationship of foliar periodicity to xylem differentiations in tropical or equable countries. Some palæontologists have contended that the rings of growth in the stems of fossil plants indicated the existence of a temperate-zone climate; and their absence, a more equable or tropical climate. The facts on this part of the subject will probably throw some doubt on such hypotheses.

It was generally thought that there were very few trees which pass through a leafless stage in Ceylon. In Trimen's "Flora" 16 species are described as being deciduous. The number of deciduous species herein described (excluding foreign ones) is only about ninety.

The number of species now known to be deciduous will probably be greatly increased at a later date, when the

Shrubby vegetation has been more closely studied. Shrubby plants are, on account of their being so small and having so few leaves, liable to be overlooked. It is only when they attain the size of a mature plant of Pavetta indica, or Brucea sumatrana that a heavy fall of leaf is likely to be noticed.

2.—Periodicity in Growth.

Though there are great differences in the periodicities of vegetative growth in all climates, they can usually be traced to external forces such as moisture, food supplies, temperature, &c., or they are the expression of apparently independent activities of the whole or parts of the plant or plants under consideration. We are here concerned with the periodicity of defoliation and the production of new leaves.

Periodicity in Temperate Zones.

In temperate zones, where seasons are pronounced, the leaves of certain trees discolour and fall during autumn and new leaf production is delayed until the warm spring time arrives. This is characteristic of trees which have thin and tender leaves. Those trees the leaves of which are tough and leathery, reduced in area, or covered with a thick cuticle may retain their leaf throughout the year. Examples of the former class are the Birch, Beech, Hawthorn, &c., and of the latter, Holly, Gorse, Conifers, &c. It is usual to regard the leafless period of these plants as one of rest, and in so far that there is a cessation, almost entirely in species with woody twigs, of the work of assimilation and the processes associated with this function, a period of relative inactivity of these functions may be acknowledged. Complete rest, however, would involve the cessation of all functional activity, and this cannot occur until the death of the plant. Schimper stated that during the winter months of temperate climates various changes may be taking place in the plants, such as conversion of starch into oil, chlorophyll into red colouring matter, production of cyanophyll in the epidermis,

and the growth in length of roots, and concludes that there is no season which does not set certain functions of the plant in activity. There is however a foliar periodicity of temperate zone vegetation which is obviously directly associated with the seasons.

Periodicity in the Tropics.

In the tropics there may or may not be a climatic periodicity analogous to the seasons of temperate zones. In all tropical areas heat and light are intense, and these, together with the heavy rainfall of many places, result in a conspicuous growth of vegetation at most times of the year. Schimper stated that his observations in tropical districts, with an abundant rainfall at all seasons, convinced him that the life occurrences of the plant show a rhythmical change of periods of rest and activity.

The investigations of Sachs and Muller-Thurgau have proved that there is no such thing as a resting period for the whole of the life occurrences of the plant, but only resting periods for certain functions.

The tropical plants are just as subject to periodical changes of rest and activity as the plants of cooler zones.

Schimper asserted that where a marked climatic periodicity prevails the functions of the plants are influenced thereby, the dry seasons operating in many respects like cold ones. He contended that where the climate is nearly uniform the internal causes are chiefly or alone influential for the change of rest and activity. Such periodicity is founded on the existence of the organism and not on external conditions. Schimper believed that their connection with the latter is quite secondary and an adaptation. He also stated that the difference between such a vegetation and one subject to the influence of alternating favourable and unfavourable seasons is that in the first case the amount of rest and activity in every period or generation remains approximately the same, while in the second case it has a periodic increase and decrease.

The effect of climate on the type of vegetation is well known. The rainfall may not, in parts of Ceylon, greatly exceed that of certain portions of Great Britain, yet the scarcity or abundance of it in certain areas determines whether a desert or jungle flora shall obtain. The low-lying trees, the production of small bushes, abundance of succulent leaved plants like Suæda maritima, Salicornia species, Portulaca quadrifida, L., and others which prevail along the north-west coast of Ceylon suggest how xerophytic vegetation may become when the rainfall is below fifty inches in tropical areas.

Periodicity of Vegetation in Ceylon.

When one considers the arborescent forms in Ceylon a variety of phenomena is exhibited among the endemic and indigenous species. Schimper stated that in those parts of the tropics where there is a distinct climatic periodicity—and Peradeniya is one of these—the vegetation is influenced by this, and that plants are likely to show periods of rest and activity as in temperate zones. This is only obvious in certain species, and the phenomena observed for the different species are so complicated that they can be better studied in detail in a subsequent section.

In parts of the tropics where the rainfall is more or less evenly distributed throughout the year—as at Buitenzorg—periodicity in vegetation is still met with. Schimper believed that in districts continually supplied with abundant rain there are phases of rest and activity at all times of the year in the life-history of the plants.

In parts of the tropics like Peradeniya there is a definite climatic periodicity, and the trees may or may not show periodicities in association with this, but before describing these we will briefly summarize the conclusions which can be drawn from a study of the general vegetation in such a district.

One of the first things to impress a new arrival in Ceylon is the absence of any period during which the herbaceous and

shrubby plants are all in full bloom. During the dry weather many species produce flowers in profusion, but in these cases each species seems to have a periodicity unrelated to any of those of the surrounding species and usually of very limited duration. This is best seen in plants of Bignonia Ungui, Pavetta indica, Pancratium species, Bignonia venusta, Ruellia tuberosa, and others.

On the other hand, many liliaceous plants die down in the dry weather and the bulbs burst out into new leaf immediately after the arrival of the monsoon rains. Similarly with the haulms of the giant bamboo (Dendrocalamus giganteus), which begin to elongate in June.*

Though certain herbaceous plants show a definite period of leaf or flower activity, the majority seem to be more or less productive during all times of the year, *e.g.*, Mussenda frondosa, and species of Anthurium, Clerodendron, Vinca, Panax, Allamanda, &c.

A case of unusual interest is to be seen in connection with the periodicity of species of Strobilanthes, Bl., in Ceylon, and I am indebted to Mr. Thomas Farr, Bogawantalawa, for much of the information on this subject. Trimen states that many of the species are remarkable for their gregarious occurrence in vast abundance and over large areas. The principal species form unbroken sheets of undergrowth in the forest. They usually live for several years without flowering, and though a few flowers may here and there be found every year, it is not until the plants have reached a certain age, apparently from ten to thirteen years, that the whole patch or area bursts simultaneously into blossom. These patches or districts are, according to Trimen and Farr, often of great extent, and the boundaries between those of different ages are very conspicuous, often being as distinct as if artificially sown. After this general and profuse flowering the

*Lock, R. H. : On the Growth of Giant Bamboos, with special reference to the relation between Conditions of Moisture and the Rate of Growth. Annals of the Royal Botanic Gardens, Peradeniya, Vol. II., Part II. August, 1904.

whole patch begins to wither and ripen the seed, and then dies down.

Mr. Farr informs me that there is one species, rather rare, which flowers and dies down every year, but that S. sexennis, Nees; S. pulcherrimus, And.; S. viscosus, And.; and S. calycinus, Nees, flower and die down with the most perfect regularity every twelve years.

We have therefore a periodicity which cannot be correlated with an interval of twelve months, and one which adds interest to the observations of Warming, Brandis, and others on this subject.

The arborescent vegetation is similarly striking. The fact that the trees do not all become leafless during certain months, and the irregularity in the production of new leaves and of flowers, impresses one with the great difference between the growth of vegetation in the tropics and temperate zones.

The absence of a general time agreement in floral or foliar periodicity in Ceylon vegetation at a given place is one of its striking characteristics.

Periodicity of Arborescent Plants in Ceylon.

There are about 770 endemic species in Ceylon, over 280 of which are trees. About 17 of our endemic and 78 indigenous species pass through a leafless phase at more or less regular intervals, showing that only a remarkably low proportion of Ceylon trees are deciduous. The number of deciduous introduced trees is equal to the number of deciduous indigenous and endemic trees put together, a fact which superficially considered seems to suggest that the Ceylon climate favours deciduous introduced species.

Ceylon Forest Types.

The appearance of the forest vegetation in Ceylon at various times of the year has not been described, and as many opportunities have presented themselves to the writer, an

account of the forests in various parts of Ceylon— a tropical island where a definite climatic periodicity prevails—is now given.

Selecting as our first locality the forests of the Peak Wilderness, Singhe Raja, and Hinidum, where the rainfall varies from 100 to over 200 inches each year and the force of the north-east and south-west monsoons is experienced, we find that we are surrounded with some of the largest trees and most magnificent forest in the whole of the island. It is here that the species of Diospyros (ebony) reach their maximum dimensions, and where the huge trees of species of Doona, Dipterocarpus, Vatica, Garcinia, Canarium, Calophyllum, Chrysophyllum, Palaquium, and Bassia abound. I have visited these forests on many occasions and have been principally struck with the absence of any fixed period of the year when the plants undergo their change of leaf. Were it not for the occasional fall of leaf, or leafless condition of scattered trees of Dipterocarpus zeylanicus, Canarium zeylanicum, Bassia longifolia, and Trema orientalis, one might imagine that he was in the original "*Regenwälder*" so forcibly depicted by Schimper and Haberlandt. Each species seems to be acting on its own initiative, and its occupation on sloping hillsides, along river banks, or on flat areas does not appear to influence the phases of leaf-fall and production in the least. And even during the time of relative drought there is only a slight increase in the number of species which pass through their phase of defoliation, many effecting a change of leaf without ever being leafless—a phenomenon noticed by Warming in the forests of Minas-Geraes in Brazil—others remaining leafless for a few days and others for several weeks or months.

If one passes to a district where the temperature is much higher and the rainfall only 50 inches or less each year, as in the forests of the Northern Province, the same facts respecting foliar activity present themselves. In some of these forests one may meet with colossal trees of Mimusops hexandra, Chloroxylon Swietenia, Diospyros Embryopteris,

Mesua ferrea, and others which, if one can forget the more oppressive atmosphere, strongly suggest the forests of wetter and cooler zones. In such dry forests one may meet with a few more species which habitually pass through a leafless stage, than in the damp districts. During the dry season from May to September, the partially or completely leafless trees of Vitex altissima, Berrya Ammonilla, Cassia fistula, Cratæva Roxburghii, and Spondias mangifera, suggest that the local vegetation is influenced more by climate than in other districts of Ceylon. But wherever one goes in Ceylon, whether along the sea coast, to the north or south of the island, on the coral islands in the Gulf of Mannar, or into the forests in the wet or arid zones, there are signs of the independence of defoliation with respect to external factors to be observed. Under the same climatic environment trees are to be seen in all stages, from the fall of the first leaf to the leafless branches and the flush of fresh green leaves, the former suggesting winter and the latter the spring time in a temperate zone. In most of the districts the leafless condition when at its maximum is always less uniform than what one is accustomed to meet with in any zone other than a tropical one.

As Holtermann* states, there are no forests in Ceylon the trees of which lose their leaves periodically for a long time ; the majority are evergreen, and the manner in which the deciduous species drop their leaves varies considerably. If one confines his studies to the trees growing in or near the Botanic Garden, Peradeniya, he may be misled as to the probable character of the forest trees, as at Peradeniya there are more deciduous species introduced from other countries than in the whole of the Ceylon flora.

Frequency of Foliar Activity.

It is not so much in the number of species which become leafless as in the manner in which defoliation and foliar

* Dr. Carl Holtermann: Anatomisch-physiologische Untersuchungen in den Tropen ; Berlin, 1903.

renewal are effected that the chief point of interest lies. A description has been given in another part of this paper of how the evergreen species may produce new leaf every month in the year, twice per year, or annually, and the behaviour of the deciduous species will now be described. The necessity for an annual defoliation, though obvious for many species in temperate zones, is far from apparent in tropical areas where there is no cold season analogous to a winter. In parts of the tropics where the monthly humidity and rainfall are relatively high throughout the year it is difficult to understand why the cycle of leaf-fall and renewal should coincide with that of a period of twelve months, and it would be natural to expect that the trees would become partially or completely defoliated at any time when the condition of the plant required either a change in the intensity of activity of certain functions or when the old leaves had become comparatively useless. In all parts of Ceylon, however, there is a more or less constant change of the climatic factors, and the behaviour of the plants is consequently more interesting.

The Age of the Trees when they undergo their first Leafless Stage.

This question is of the utmost importance in determining the time-value of rings of growth. It is obvious that the central cylinder of wood in the stem may be uninterrupted by rings of growth so long as the young tree continues to acquire new leaves and does not pass through a leafless phase.

Generally speaking, once a tree has passed through a normal leafless phase it becomes defoliated every succeeding year. It has also been pointed out that some trees are not defoliated until they are several years old—Bassia longifolia; and there are others which though leafless every year in their early life become more or less evergreen at a later date. This has been noticed for trees of Poinciana regia at Peradeniya and for Dalbergia Sissoo,

Roxb., by Brandis. Brandis in his Forest Flora of India states (p. 149) that Dalbergia Sissoo drops its leaves from December to February, and remains leafless until April, but that though young trees are occasionally leafless for a few weeks, old trees are hardly ever without leaves.

There are some cases, in which the trees undergo defoliation and pass through a leafless stage in their first year; this has been observed with trees of Eriodendron anfractuosum, with suckers of Bombax malabaricum, and cuttings of Erythrina indica. Trees of Castilloa elastica undergo defoliation in their second year; but trees of Tectona grandis, Bassia longifolia, and Couroupita guianensis do not pass through a leafless stage in their second year. Trees of Hevea brasiliensis become defoliated in their third year, Cassia nodosa in their fourth, and Poinciana regia and Ficus religiosa in their fourth or fifth year. There are very few recorded observations available for most of our deciduous species, but in most of them it is quite possible that the leafless stage is not passed through until the trees are more than one or two years old.

The fact that defoliation during the first year of a plant's life is characteristic of quick-growing species, and that slower-growing trees do not become leafless during the first few years suggests that there may be a relative constancy between the amount of foliage and the first period of leaflessness.

The frequency of Defoliation of Trees.

I have been surprised to notice that certain trees, apparently old and vigorous, which were classed as evergreens, have during certain years (some only once during four years' observation) begun to drop their leaves and have undergone a complete renewal of foliage. Kurz* remarks that in the evergreen forests of Burma some trees lose their leaves after a certain number of years. Warming, when

* T. Kurz: Flora of British Burma, Vol. I., 1877.

describing the vegetation of the Campos of Minas-Geraes in Brazil, states that the majority of the leaves remain on the trees from twelve to fourteen months, and usually for a longer period in the forests than on the prairies. Some trees, according to Warming, retain their foliage for twenty-four months and even longer. Such cases are comparatively rare in Ceylon, but they prove that an annual defoliation is not universal with deciduous trees, and that a change of leaf at periods coinciding with our year of twelve months is not necessary for every species.

Once per year.—The majority of the observed species do not show a long or irregular interval between successive periods of defoliation. Nearly all of them pass through their leafless state once each year, and I need only mention Bombax malabaricum, Spondias mangifera, Careya arborea, Gmelina arborea, Terminalia belerica, Ficus Arnottiana, Oroxylum indicum, Bridelia retusa, Canarium zeylanicum, &c., as examples of this group.

Twice per year.—There is only one species which undergoes a change of leaf twice each year, this being Terminalia Catappa; the change of leaf in the Peradeniya district usually takes place in February to March and August to September. The tree is a native of Malaya, but is naturalized in the low-country of Ceylon, where it is known as the "kottamba" of the Sinhalese and the "country almond" of the English.

There are a few other species which are completely defoliated once a year, but which pass through the leafless stage twice during certain years. Examples may be seen in a tree of Ficus asperrima, at Peradeniya, which, though usually defoliated in March only, was defoliated in March and October in 1903. Similarly with some specimens of Couroupita guianensis.

Still another combination of foliar activity is seen in Ficus Trimeni, which appears to be subject to complete or partial defoliation in December and January, and to a partial leaf-fall in June and July of certain years. A description of the

periodicity of a prominent tree of this species from 1900 to 1905 has been given in the section dealing with deciduous species indigenous to Ceylon and India. It is by no means rare to find that a particular tree which produces a complete set of new leaves after the leafless stage produces small quantities of leaves during other months of the year; such activities may be observed in trees of Swietenia Mahogani, Chloroxylon Swietenia, Terminalia belerica, Bassia longifolia, and others.

It is also not unusual to find that every alternate year the production of new leaves on certain trees is very copious, this being particularly striking in evergreen trees of Garcinia Mangosteen, Durio zibethinus, and Mangifera indica.

Abnormal Defoliation and Foliar Renewal.

In certain cases the abnormal production or fall of leaves is due to a condition of vigour, undue exposure to wind, or the attacks of animals. Trees of Acacia Suma and Canarium zeylanicum, which have lacked the vigour of other specimens of the same species, have been observed to take a much longer period to renew their foliage. The periodicities of such specimens are usually variable and unreliable.

The effect of the strong winds during certain months of the year can be observed on exposed trees of Mangifera indica, Tecoma stans, and others, these trees becoming more nearly leafless than other specimens of the same species.

I have also had an opportunity of recording the change of periodicity due to cutting away the upper parts of trees of Mangifera indica and Terminalia Catappa. A tree of Mangifera indica which normally produced its leaves in February and March was lopped in May after the full set of foliage had been established; the tree produced a large quantity of leaves during July to September of the same year, but in the following year the leaf production due in February and March was not observed. A tree of Terminalia Catappa was similarly treated in May, with the result that there was a large output of new leaves in July and August,

unaccompanied by a heavy leaf-fall ; the periodicity of this tree was changed for a couple of years.

Another case of interest has been observed for several years, where the flying foxes regularly visit certain trees of Bombax malabaricum along the riverside of the Botanic Garden and devour the whole of the leaves, and thus lead to the production of two sets of foliage each year. A similar defoliation is effected on trees of Portlandia grandiflora by some insect pest and a second crop of leaves is produced each year, though the trees do not appear to be able to stand such waste for many years more.

3.—The Climate in Ceylon.

It is necessary when dealing with plant phenomena which are influenced by external and internal forces to fully understand the variation in rainfall, air-temperature, and humidity at the different places where observations have been made. Most of the facts recorded in this paper have been obtained at Peradeniya and Hakgala, a few in the low-country between Henaratgoda and Colombo, others in the dry Northern Province between Anuradhapura, Vavuniya, and Mannar, and the remainder in the Badulla and Passara Districts of the Province of Uva.

The rainfall in various parts of Ceylon is associated with definite monsoon periods, and the amount of rain accompanying each varies considerably at different places.

The south-west monsoon, according to the Government Meteorologist, usually lasts from February to July, and the north-east monsoon from August to January.

It is necessary to consider each district separately, though they all agree in having rain every month in the year, a high temperature, and an atmosphere which is comparatively moist, the average humidity rarely being below 70 degrees.

The Climate at Peradeniya.

At Peradeniya the south-west rains are heavy during April and June, and those of the north-east still heavier in

October and November. To be brief there is a warm dry period during February and March, a hotter but moister one during April and May, followed by seven to eight months of rainy weather when the temperature is comparatively low and humidity high. We can therefore speak of one hot dry and hot moist season of four months and a cooler moist period for the rest of the year. (See plates XXVI. to XXVIII.)

The Climate at Hakgala.

Hakgala is 5,581 feet above sea level. The climate resembles that at Peradeniya in having both monsoons, but differs from it in so far that (*a*) there is a heavier rainfall, mainly from October to December ; (*b*) the average yearly temperature is 15° F. lower than at Peradeniya ; and (*c*) the yearly humidity is 9 degrees higher. The periodicity of the climate is almost the same as at Peradeniya, but the air is cooler, the rainfall heavier, and the atmosphere always more moist. (See plates XXVI. to XXVIII.)

The Climate in Colombo.

Colombo is at sea level, and the climatic periodicity prevailing there is almost the same as at Peradeniya. Compared with Peradeniya the annual rainfall is nearly the same ; the temperature is on an average 5° F. higher and the air more moist. (See plates XXVI. to XXVIII.)

The Climate at Badulla.

The climate at this place is quite different from that at Peradeniya. The rains fall mainly in the north-east monsoon, and the annual rainfall is about 5 inches less than at Peradeniya. The temperature is more regular, but usually 2° F. lower than at Peradeniya. The curves show that the dry hot period is from June to September and that the rest of the year is relatively moist and cool. (See plates XXVI. to XXVIII.)

The Climate at Mannar.

The differences between the climate at Mannar and Peradeniya are obvious from the various curves, and may be

summed up as follows :—The rains fall mainly in the north-east monsoon, the temperature and humidity are higher than at Peradeniya, though the annual rainfall is not half so great, and there is one dry hot season from June to September. (See plates XXVI. to XXVIII.)

We have therefore the Colombo climate at sea level, and Hakgala at over 5,000 feet, with almost the same climatic periodicities as at Peradeniya. At Mannar—sea level—and at Badulla over two thousand feet altitude, the climatic periodicities resemble each other, but differ widely from that at Peradeniya. In order to make these points still clearer I now give a tabulated synopsis taken from the Surveyor-General's report for 1902 :—

	Average Annual Rainfall. Inches.	Mean Annual Temperature. Fahrenheit.	Average Mean Annual Humidity.	Altitude in feet.
Peradeniya	82·16	75·5	78	1,560
Hakgala	91·70	60·3	87	5,581
Colombo	88·15	80·7	79	40
Mannar	38·59	81·8	82	12
Anuradhapura	54·20	80·2	78	295
Jaffna	45·47	82·0	83	—
Badulla	76·93	73·2	79	2,225

Peradeniya and Buitenzorg.

The climate at Buitenzorg differs from that at Peradeniya in many ways. At Buitenzorg the rain during 1901 to 1904, inclusive, fell on an average of 263 days in each year. The humidity of the air in 1904 ranged from 75 in August to 85 in December, and the average for the years 1901 to 1904, inclusive, was 79. The average monthly temperature ranged in 1904 from 23·6° to 25·3° C. Though the climate in Buitenzorg is more equable than that at Peradeniya it must be borne in mind that a definite periodicity does exist, and a reference to the curves on plate XXX. will show that the rainfall and humidity throughout the year approximate to those at Badulla.

Reference has been made in another part of this paper to the marked climatic periodicity prevailing in East Java, and I

amindebted to Dr. Treub for the information in the following synopsis of the monthly rainfall, humidity, and temperature at Pasœrœan in East Java and Buitenzorg.

Climate during 1904 in Java.

	Rainfall in mm.		Monthly Average mean humidity.		Monthly Average Mean Shade Temperature in °C.	
	Buiten-zorg	East Java.	Buiten-zorg.	East Java.	Buiten-zorg.	East Java.
January ...	417	221	83	77	24·0	27·2
February ...	455	192	85	80	23·6	26·9
March ...	169	287	80	80	24·5	26·6
April ...	204	33	79	76	25·0	27·4
May ...	541	155	80	76	25·3	27·3
June ...	389	27	78	73	25·1	27·1
July ...	312	48	79	71	24·8	26·7
August ...	344	18	75	67	25·1	27·1
September ...	388	—	76	64	25·3	27·7
October ...	799	11	81	64	24·9	28·7
November ...	312	24	80	67	25·2	28·7
December ...	498	110	85	74	24·2	27·9
Average mean, yearly 1901—1904	4,416	1,200	79	71·9	25·0	27·6

4.—The Leafless Phase in the Tropics.

In studying this part of the subject we find that plants of the same species may show variation in different climates, and in the same neighbourhood, and in several cases even the same tree exhibits differences in foliar periodicities from year to year.

The facts recorded in this section lead to certain conclusions which form the stepping stones for subsequent deductions of some importance. They prove first and foremost that under tropical conditions with regular rainfall, heat, and light, and in the absence or presence of climatic periodicities certain plants undergo defoliation at a particular time of the year. They prove that in a tropical district supplied with rain during every month of the year—

Peradeniya—there is a rythmical change of periods of rest and activity. It can also be shown that the observed variability of certain species in different climates is repeated when individuals of these species are grown in the same climate or individually from year to year. It is by a consideration of such observations that one is led to infer that foliar periodicity is inherent and that in many tropical areas the internal factors are responsible for many phases of the vegetation.

On the other hand, these facts also teach us that the climatic periodicity in parts of Ceylon and Java is so marked as to influence the foliar activities. The inherent periodicity in foliar production can be affected by external climatic forces such as obtain in these places.

Variation of a Species in different Climates.

It is a matter of common knowledge that the same species grown in different climates or changed environments presents many differences. We have seen that in various parts of Ceylon different climates exist, and a discussion of the variation of plants of the same species in such localities can be conveniently introduced in this part of the paper.

The variation in foliar periodicity due to a difference of climate in Ceylon is usually one of time only, and in very few cases can it be shown that plants of the same species may be evergreen or markedly deciduous according to the climate in which they are growing. There are three species which though evergreen in the Peradeniya and wet districts in Ceylon, are partially deciduous in the dry Mannar Districts, these being Thespesia populnea, Sol.; Diospyros ovalifolia, R. Wight, and Diospyros montana, Roxb. This statement is only intended to apply to parts of Ceylon, and does not hold good when species common to Ceylon are introduced into other countries.

It will be necessary, in order to avoid confusion, to first consider the variation of a species in parts of Ceylon and

then deal with the variation of indigenous species when grown in other countries.

The most conspicuous differences are met with when the foliar periodicities of plants common to Peradeniya and the Uva District are considered. In the case of Careya arborea we find that at Peradeniya the leafless stage is passed through in February or March, but at Passara in the Uva District it is usually during May and June.

Trees of Ficus Arnottiana, though passing through their stages of foliar activity at Peradeniya in March and April, show in the Passara and Lunugalla districts a production of new leaves and flowers in May and June.

Again trees of Gyrocarpus Jacquinii, though they undergo defoliation at Peradeniya during February and March, do not pass through the leafless stage until May to July in the dry parts of the Northern Province. In each case we find that defoliation occurs during the dry hot weather, and the variation in the climates already described will alone account for the change in the periodicity of these species. These examples can be used in support of the contention that the time of defoliation is associated with the external factor of climate.

Many instances can also be quoted to prove that there is considerable variation in districts which have relatively similar climatic periodicities, but which show slight differences of rainfall, temperature, and humidity. The differences in plant phenomena in such districts cannot in every case be assigned to the slight differences of climate, because we know that even in the same district the same species may exhibit considerable variation in manner and time of foliar periodicities.

Trees of Terminalia belerica usually drop their old leaves in February and March at Peradeniya, but at Ambalawa near Gampola I have seen leafless trees during the first week in January.

A still better example is seen in trees of Albizzia stipulata. In the Peradeniya district the leafless phase

is during late January and early February. At Henaratgoda in 1902 the leafless period was just over with certain trees on the 12th February. At Pitakande in the Matale District, 3,000 feet above sea level, on the 20th March, one tree was leafless, one had not dropped its old leaves, but the majority were in full new leaf. In most parts of the island this species usually passes through its leafless phase during the month of February.

The most interesting case is however to be seen in Bombax malabaricum. This species is one of the most conspicuous deciduous trees in Ceylon. The frequent occurrence, huge dimensions, and long leafless period of trees of this species give the Peradeniya and low-country places quite a barren appearance from January to April each year. The period of leaf production and fall for this species shows a variation equal to a very large part of the year, and it is one instance which strongly suggests that if trees of other deciduous species were only more abundant and conspicuous the time of foliar periodicity would be proved to extend over a longer period than has been recorded for them up to the present.

Several trees have been under observation, and the following is a synopsis of records taken. The earliest dates on which leaf-fall commenced were 29th September in the Royal Botanic Garden, and on the 21st October, 1903, for a tree on the Peradeniya race-course. The majority of the trees at Peradeniya have by the 15th December each year dropped a great part of their foliage. They rapidly become leafless, and by the 15th January they are usually leafless and in flower. The flowers are produced in January and February, the fruits set in March, and disburse their seeds and cotton in April while the trees are absolutely leafless. During late April and early May the majority of the trees burst into new foliage.

Some trees were seen in flower along the Kandy road on the 12th December, 1903. On the 15th December one young

tree was observed at Gangaruwa, Peradeniya, in flower before leaf-fall had commenced, a condition also noticed in the Passara district in 1902.

At Henaratgoda on 15th February, 1902, the majority of the trees had shed all leaves and flowers.

In the Gampola district on the 5th February, 1902, many trees had finished flowering and the fruits were setting.

In the Passara district, where one gets less south-west monsoon rain and where from April to August and September it is dry and hot and from September to March the rains are heavy, the trees behave differently.

Between Passara and Lunugalla at an elevation of 2,000 to 3,000 feet, on the 25th May, 1901, some of the trees were quite leafless, and others in partial new foliage; very few had a good output of leaf on that date. In several specimens the flowers were produced long after the trees had regained complete new foliage.

Variation in Ceylon and Java.

Now we can consider the variation which occurs in climates so dissimilar as Ceylon and Java—two tropical islands near to but on opposite sides of the equator. I am indebted to Dr. Treub for much information respecting the periodicities of certain plants in Java, and the comparison obtained is interesting in many ways, particularly as details of some of the periodicities have been obtained at Buitenzorg and Peradeniya.

Peradeniya and Buitenzorg.

The best example is perhaps to be seen in trees of Bombax malabaricum. At Peradeniya the fall of old leaf is very conspicuous during December; the leafless phase extends from December to April or May, the flowers and fruits appear in January and February, and the burst of new leaf occurs in April and May. Plants of this species rarely possess any old leaf during January and very few put on new

leaf before the end of April. Yet at Buitenzorg this species commences to drop its old leaves in July, five to six months after those in Ceylon.

Almost the same dissimilarity is seen in the fall of old leaf of Erythrina indica, at Peradeniya in January and February, and at Buitenzorg in July. This variation is analogous to the great differences in time between the periodicities of trees at Peradeniya and in the Province of Uva, and is all the more interesting on account of the fact that the species concerned are common in both islands.

There are several species which have been introduced to Java from Ceylon and to both islands from other countries, and the differences in their foliar periodicities are extremely interesting.

One of the most surprising examples is seen in the behaviour of Schizolobium excelsum. At Peradeniya the leaf-fall is very regular every year, but at Buitenzorg it is as irregular as it can possibly be. Dr. Treub wrote that in trees of this species, from three to ten years old, the branches of the same tree behave in different ways, some being leafless for two or three months and others at the same time having their full fresh foliage. Dr. Treub wrote that the only way to explain such remarkable differences was to assume that the climate at Buitenzorg was so equal all the year that even branches of the same tree were able to follow their own "inspiration" and thus show their autonomy.

Other equally noteworthy instances are seen in the behaviour of Hevea brasiliensis and Manihot Glaziovii, which at Buitenzorg drop their leaves during July and August, but at Peradeniya during February and March. The differences in the periodicities of other well-known species are obvious when one realizes that at Buitenzorg, Ficus religiosa, the Bo-tree, drops its leaves in March and Lagerstrœmia flos-reginæ in September.

A study of the differences of the species at these two tropical places brings forward two important facts. The first is that those species which are very dissimilar in their foliar periodicities at the two places, undergo defoliation in Ceylon during or about the only hot dry season in the year. In cases like Bombax malabaricum the leafless period coincides, very regularly, with our hot dry and part of our hot moist months, and further examples may be cited among our introduced species such as Schizolobium excelsum, Hevea brasiliensis, Manihot Glaziovii, and many others which reserve their leafless period until during the hot dry season in Ceylon. In the second place species such as Tectona grandis and Terminalia Catappa, which are irregular in foliar periodicity at Buitenzorg, are markedly deciduous during our hot dry season.

Ceylon, Buitenzorg, and East Java.

According to Ursprung the climate at Buitenzorg is relatively equable throughout the year, but in East Java there is a dry period during part of the year which gives a marked periodicity to the climate prevailing there. At Buitenzorg, in the absence of marked climatic periodicities, the development of plant life is rarely periodic, and what does occur is mainly the result of internal rather than external forces. Though such is the case, the differences in the behaviour of certain species at these two places and in Ceylon show distinctly that defoliation is considerably influenced by climatic changes.

At Buitenzorg, trees of Tectona grandis, *L.*, are never leafless at the crown, but in East Java they become absolutely leafless. In most parts of Ceylon the tree becomes quite leafless during the hot season.

Trees of Poinciana regia, Boj., are never leafless in Buitenzorg, though they pass through a leafless phase in East Java. At Peradeniya young trees become leafless, but old trees rarely pass through a leafless phase though they undergo an annual change of leaf.

I now quote a synopsis of deciduous species which show a wide variation in foliar periodicities in Ceylon and Java :—

Species.	Periodicity. Buitenzorg (Treub).	Peradeniya.
Albizzia Lebbek	... Leaves fall in March	... Leaves fall in December and January.
Bombax malabaricum	Leaves fall in July	... Generally speaking, the leaves fall in December, flowers appear in Januaryand February, fruits set and disburse their seeds in March and April, and new leaves appear April to May.
Cassia nodosa	... Leaves fall in May and July	Leaves fall in January to March ; new leaves appear in April.
Chickrassia tabularis	Leaves fall in April	... Leaves fall in January to February and new leaves appear in March.
Derris robusta	... Leaves fall in March	.. Leaves fall December to March.
Dalbergia Melanoxylon	Leaves fall in March to May	Leaves fall from January to March and new leaves appear in April.
Plumeria acutifolia	Leaves fall in July to August	Usually the leaves drop during December and January.
Peltophorum ferrugineum	Leaves fall irregularly ; July (1898) ; March, 1899	Leaves fall irregularly during December to January and June to July.
Schizolobium excelsum	Leaves fall very irregularly	Very regular. Leaves fall from the end of January throughout February, and by the 10th March the tree is leafless ; is in flower and new leaf by 15th March.
Schleichera trijuga	Leaves fall in April	... Leaves fall during February and March on tree in open, and irregularly on a tree under partial shade.
Sapium biglandulosum	Leaves fall in April	... Leaves fall from February to April.

Species.	Periodicity. Buitenzorg (Treub).	Peradeniya.
Terminalia Catappa	Leaves fall very irregularly, often twice a year	Undergoes defoliation and foliar renewal regularly twice per year, first from January to February, and second from August to September (1900 to 1904).
Tectona grandis	... Almost evergreen	... Markedly deciduous. Leaves fall from January to March and the tree is perfectly leafless for about one week.
Erythrina indica	... Leaves fall in July	... Leaves fall in January and February and new leaves appear in March and April.
Ficus religiosa	... Leaves fall in March	... Variable, but the leaves usually fall from December to March.
Ficus infectoria	... Leaves fall in March and April	Leaves fall during February and March.
Ficus elastica	... Leaves fall in April, new leaves appear in April	Irregular; leaves fall from September to February.
Ficus altissima	... Leaves fall in March	... Irregular. Leaves fall during the dry weather from February to May.
Hevea brasiliensis	... Leaves fall in July	... The leaves usually fall in February, some a little earlier, and others later. Nearly every tree is in full new leaf in March.
Lagerstrœmia flos-reginæ	Leaves fall in September	Leaves usually fall in January to February and in March new leaves appear.
Manihot Glaziovii	... Leaves fall in August	... Leaves usually fall during February and March and new leaves appear in April and May.
Pithecolobium Saman	Leaves fall in February, March, and July	Variable. Usually old leaves fall in January and February and new leaves appear in February and March.

To further prove the effect of external forces on foliar periodicity I need only draw up a tabulated list showing the behaviour of species quoted by Ursprung for various parts of the world and the same species at Peradeniya :—

Species.	Ursprung.	Peradeniya.
Ficus infectoria	... India. Throws off large quantity of leaf	Markedly deciduous.
Ficus glomerata	... India. Evergreen	... Deciduous.
Ficus elastica	... Evergreen	... Partially deciduous.
Anona reticulata, Mart.	Leafless in dry season	... Evergreen.
Persea gratissima, Gaer.	In tropical America, evergreen with two conspicuous periods of leaf production. In Mexico, evergreen with development of young leaves in September. In Mexico there is no rain from October to April, plenty of rain May to September	Evergreen with one period of active leaf production in April.
Thespesia populnea, Corr.	East Indies. Evergreen...	Evergreen. Partially deciduous in Gulf of Mannar.
Erythrina velutina, Willd.	In Venezuela, leafless during September and October	Leafless January to March.

Variation of Individuals of a Species in the same Climate.

A glance at the tabulated periodicities will convince anyone of the great individual variation, particularly in specimens of Bridelia retusa, Careya arborea, Ficus Arnottiana, Lagerstrœmia flos-reginæ, Bombax malabaricum, Oroxylum indicum, Berrya Ammonilla, and many others.

The differences between the periodicities of several trees of Lagerstrœmia flos-reginæ are shown in the tabulated list. Generally speaking, defoliation at Peradeniya is conspicuous during January and February, and in March new leaves appear. Nevertheless on any date during the months of March and April it is possible to find trees which show

every stage from the discoloured leaves ready to fall to the trees in full new leaf and flower.

Individual trees of Eriodendron anfractuosum show at Peradeniya a production of new leaves during the months of December, January, and February.

Bridelia retusa is also very variable. In the Peradeniya and Henaratgoda districts the fall of leaf is most conspicuous during the months of February and March, but many trees of this species undergo defoliation during April and May, and in these cases the production of new foliage is correspondingly delayed. During February to April, trees in the Peradeniya district may be seen dropping their old leaves, absolutely leafless or in full new leaf.

Again Terminalia belerica, though it usually behaves as quoted in the list, is subject to some variation. The majority of the trees at Peradeniya have shed all their leaves by the end of February, and are in full new leaf before the end of March. One tree under observation does not drop its leaves until a much later part of the year, becoming leafless from the 1st to 7th April each year. Others have been recorded which do not produce new leaf until the middle of May, and some have been observed to shed their leaves, in part, during November, December, and January.

It is only logical to expect much variation between individuals of the same species in the same climate, seeing that even the same tree may show a variation from year to year.

Variation of the same Tree, in successive Years, in time of Foliar Activity.

The same tree may undergo depletion and renewal of foliage at approximately the same time during each year. But there are others which are variable. The periodicities described for each individual tree of the species common to India and Ceylon show that several may exhibit a slight inconstancy from year to year, a phenomenon also to be observed for species belonging to other countries. The

species of particular note are Anogeissus latifolia, Bridelia retusa, Careya arborea, and Ficus Tsjakela.

One tree of Anogeissus latifolia was leafless during 1902 from the 10th to 12th March ; in 1903 from 24th March to 6th April, and in 1904 the tree was never absolutely leafless.

A tree of Bridelia retusa was leafless during 1902 from the 12th to 24th March, and in 1903 from 24th March to 7th April.

Similarly a specimen of Careya arborea was leafless during 1902 from 15th Februáry to 15th March ; from 12th to 24th March, 1903 ; and in 1904 from 7th February to 8th March.

Again, a tree of Ficus Tsjakela was leafless from 12th to 20th February in 1902 ; from 6th February to 1st March, 1903 : and from 18th February to 16th March in 1904.

In three out of four cases the leafless period was delayed in 1903, compared with 1902 ; in one case for 1904 the periodicity was delayed, and in another defoliation was earlier in 1904 than in 1902 and 1903.

Similar differences have been noticed for individual trees of other species, as for instance Gmelina arborea and Berrya Ammonilla, common to Ceylon, India, and the Malay Archipelago.

The date at which leaf-fall commences is very variable and is not of much importance. The actual length of time during which the tree is leafless is of much more importance.

The variation in time, of the foliar periodicities of species like Spondias mangifera, Bombax malabaricum, Eriodendron anfractuosum, Bridelia retusa, or Lagerstrœmia flos-reginæ, is usually greater than the variation exhibited by an individual tree during successive years. For instance, the foliar periodicity of different trees of Bombax malabaricum may in the same district vary by one or two months in the same year, but an individual tree during 1900 to 1905 does not vary in its periods of leaf activity by more than a few days or a few weeks at the most. In many of the cases under observation the trees were

nearly all of the same size and age, and the difference in their periodicities during a given year points to the importance of the individual requirements of each tree and the relative insignificance of external or climatic forces in connection with foliar periodicity.

5.—Transpiration in Ceylon and the Tropics generally.

The production of new leaves is closely associated with root activity and the transpiration of water from the leaves. The phenomenon of defoliation at regular intervals is similarly related, and for a proper understanding of foliar periodicity in Ceylon and the tropics generally it is necessary to consider the subject of transpiration in such regions. In temperate zones the deciduous trees lose most water by transpiration from the young spring leaves, or during the summer months when the full complement of foliage is exposed to a relatively hot and dry atmosphere; in autumn the loss by transpiration is reduced, and during winter the trees are leafless.

From the foregoing remarks it is obvious that in tropical areas there is no period exactly analogous to a temperate zone winter. In many parts of the tropics the conditions allow of transpiration throughout the greater part of the year, and in other areas short periods of dry weather may intervene. The available literature dealing with this aspect of the subject is somewhat scanty, and the following remarks are mainly in reference to observations made in Ceylon.

The transpiration of plants is influenced by the temperature and humidity of the air. In the tropics the temperature is usually high and the humidity high or low. Where the temperature and humidity are uniformly high, the vegetation is rarely xerophytic, as is evidenced in parts of Ceylon and Buitenzorg in Java. If however the temperature is high and the rainfall meagre, the plants become spiny or succulent and the xerophytic type of vegetation may predominate;

this is seen in the flora of the Iranativu islands in the Gulf of Mannar. When the temperature is high and the air saturated with moisture, as in the hilly districts in the south of Ceylon, the vegetation is abundant and succulent types frequently occur. Roughly speaking, as one passes from an area where the humidity is medium to one where the air is very dry, or where it is very moist, the plant adaptations against excessive transpiration are on the increase. The adaptations are such that the trees transpire partially or wholly by means of their stems, and the leaves become more or less negligible in the function of transpiration; in other cases the leaves may reduce their stomata in number and size and increase the water capacity of the internal tissues. In the other class of plants about to be considered the adaptations to transpiration are seen in the partial or complete defoliation of the trees and the output of new leaves at various periods, and in order to understand this it is necessary to first discuss the question as to the relative amount of water lost by transpiration in temperate and tropical zones, a point which has been the subject of much experiment.

Giltay states, according to Schimper, that the daily transpiration in plants of Helianthus tuberosus grown at Buitenzorg and Holland is approximately the same, viz., 0·6 gram per hour, though transpiration at midday, at the former place, is considerably greater than that in the latter. Haberlandt made determinations of the relative amounts of moisture lost from the leaves of trees like Albizzia moluccana and Theobroma Cacao, at Buitenzorg, and Pyrus communis, &c., at Graz. His experiments proved that the transpiration in shade, in moist tropical climates, is much weaker than in middle Europe.

Haberlandt's results have been criticised by Burgerstein* and others, who point out that the conclusions can only be applied to a few plants under the conditions described by

* Burgerstein, A.; Die Transpiration der Pflanzen; Jena, 1904, p. 161.

Haberlandt, and that it would not be fair to assume that the loss by transpiration would be so small from forest and other trees exposed to tropical conditions.

Wiesner* worked with herbaceous plants such as Coleus, Adiantum, Jatropa, and Mimosa pudica and proved that these plants, at Buitenzorg, lost very large quantities of water during hot cloudless days.

Wiesner also proved that in the temperate zones the early deciduous species may lose a greater quantity of water than those which drop their leaves later in the year, and in some cases even more than those which are evergreen.

Transpiration in Ceylon.

Holtermann, who worked in various parts of Ceylon, has published some interesting results bearing on this subject. Describing the humidity of the air at Peradeniya, he points out that on ordinary days with a clear sky, in the dry season, evaporation commences after sunrise and remains feeble up to 10 A.M., but from this time it increases until between twelve and three it reaches its maximum, and then decreases until sunset, and subsequently dew is formed. Transpiration stops nearly or completely after sunset, when saturation point is being approached. The stomata are usually closed during the night.

At Peradeniya, from January to March there is a dry wind, and during this period transpiration is greater, and may even continue all through the night. The evaporation on moist days, when the air is saturated, is very slight or scarcely perceptible. In order to emphasize the great difference between the transpiration during hot dry and wet days he states that Asplenium Nidus during misty days lost from 0·00 to 0·21 gram of water per day, but on a sunny day it transpired as much as 3·50 grams.

Holtermann worked with various plants. Cymbidium bicolor—a common epiphytic orchid—was selected among

* Wiesner, Julius: Über Laubfall infolge Sinkens des absoluten Lichtgenusses (Sommerlaubfall); Botan. Gesel., Berlin, 1904.

others. This plant possesses thick stiff leaves (which are protected by a strong thick cuticle and a layer of cells running under the epidermis on the upper surface of the leaf) and narrow stomata. He proved that the transpiration from one plant of this species was, from the 23rd to the 27th January, both days inclusive, only 0·457 gram, or at the rate of about one gram in ten days. This means approximately one pound of water in 13 years, a very small quantity indeed.

Alstonia scholaris was also experimented with. The leaves of this commonly occurring tree are not xerophytic; they possess normal stomata and internal tissues, and a cuticle of average thickness. One shrub of this plant possessing 100 leaves lost during the 13th and 14th February, when the sky was cloudless and the temperature high, 1·24 gram; but during the 15th and 16th when rain was falling only 0·06 gram of moisture was lost by transpiration. Discussing the value of these and other observations Holtermann proceeds to state that there is between 12 and 2 o'clock on clear days in the tropics a much greater loss of water by transpiration than in Europe, though the total transpiration of a tropical plant in 24 hours may be less than in Europe.

There are in the tropics a large number of plants which though exposed to the full rays of the sun only lose a small quantity of moisture by transpiration; *e.g.*, Euphorbia antiquorum, Cereus triquetra, and others. The leaves of these plants are small, and the green stems often carry on the greater part of the work of transpiration and assimilation. The stems of such plants are provided with a thick epidermis and deeply sunk stomata. On a very hot day in a very exposed place Cereus triquetra lost, according to Holtermann, from 8 A.M. to 6 P.M., only 0·01 gram per square decimeter.

Holtermann also carried out experiments which proved that the tobacco plant lost twice as much moisture at Jaffna as at Peradeniya, and that *the transpiration in the drier districts of north Ceylon is considerably greater than in the moist climate in the south-west of the island.* He also states that though a change of external conditions did not

lead to any great difference in the transpiration from Cyanotis zeylanica, yet other plants which had been transplanted into pots transpired more than those cultivated under natural conditions, and showed striking changes in the anatomy of their roots. He also states that the transpiration in moist tropical climates is less significant than that from quick-growing plants in the warm and sunny part of an European climate. On the other hand at certain hours of a clear sunny day in the tropics the transpiration is undoubtedly much greater than in Europe. He also points out that transpiration in the dry districts of the Northern Province is much greater than in the moist warm climate of Peradeniya.

The actual weight of water lost by large tropical trees cannot be determined with ease, and it would not be safe to estimate the probable amount from the results of experiments with branches and seedlings of particular species. Certainly the amount of water lost from branches of trees can be determined, and more or less approximate calculations made of the amount likely to be lost by the whole of the tree, but the absence of a proper system of roots on such cuttings prevents one from using the results with an assurance of their general applicability. The experiments do, however, suggest that in many of the ordinary arborescent forms growing in the tropics, the transpiration is not necessarily greater than in Europe. In all probability the transpiration from certain trees at Peradeniya in the moist dull months of June and July is less vigorous than in Europe during summer—certainly the assimilation processes in the leaves are almost at a standstill at Peradeniya during that time. The transpiration throughout the year at Buitenzorg, and at Peradeniya from May to December, is apparently not much more vigorous than in middle Europe in summer. There is therefore no reason to expect that special structures should be formed in tropical plants to meet the exigencies of transpiration during the months mentioned, and the possession of abundance of foliage in both areas during such periods is what one may logically expect to find. But the

climate is not always so moist and dull, and during the remaining part of the year certain changes may occur. At Buitenzorg, with a relatively equable climate and transpiration throughout the year, the trees are more or less evergreen, and foliar periodicity is mainly determined by internal forces.

In a tropical district like Peradeniya, where a marked dry season sets in, a large number of trees drop their leaves during the hot dry season between January and March, probably because they find it impossible to obtain the amount of water in the soil equal to that which would be lost by transpiration if they retained the full complement of foliage. Certain forms retain their full amount of foliage, and others are provided with adaptations which allow them to pass through a period of drought unimpaired.

In a temperate zone the roots cannot absorb the required amount of water during the cold months, and the trees therefore drop their leaves for the winter and remain in that state until the warm spring weather arrives.

We are therefore led to conclude that foliar periodicity is associated with transpiration, and that the latter varies according to the temperature and moisture of the air and soil. It remains to be shown how far the results of the observations made in Ceylon agree with these conclusions, and the questions connected therewith can now be considered.

Periodicity and Transpiration.

From the foregoing considerations several interesting questions arise. The first is a question as to the extent of the reduction in transpiration which is effected by species passing through their leafless phase during the hot period in Ceylon.

That defoliation in deciduous trees is associated with the hottest and driest period, and therefore probably with reduction of transpiration, seems obvious from the facts: (1) that

a large percentage of our endemic and indigenous species are deciduous during this dry hot period ; and (2) that the greater number of our introduced species obtained from such widely different climates as Brazil, Java, Australia, America, Africa, West Indies, &c., undergo defoliation from January to March. These facts suggest that reduction of transpiration is perhaps one of the objects in view. During these months when the air is usually dry and the temperature high, the leaves of many evergreen plants begin to flag during midday and only expand in the late evening and early morning. Throughout this period the leaves transpire copiously and probably thus allow the greater part of the water supplied by the roots to escape. The temperature, two feet below the ground, rises to 83° F., and during this period the water supply to the superficial root system is somewhat limited. Under these conditions one can see the advantage of, and in certain cases almost the necessity for, a reduction in transpiration such as may be achieved by passing through a leafless phase. The actual variation in temperature—one to two feet below ground—is not very great, but the maximum during certain months is high, and the water supply to the feeding rootlets at two feet below ground must be appreciably affected.

The following are the temperatures in Fahrenheit from January to May, 1903, recorded at the Experiment Station, Peradeniya :—

	Jan.	Feb.	March.	April.	May.
One foot below ground ...	73 to 78	73 to 78	76 to 81	79 to 83	76 to 83
Two feet below ground ...	74 to 79	75 to 78	77 to 80	80 to 82	78 to 82

Having shown that the leafless phase is associated with our dry hot period and that the conditions of air and soil are such as to necessitate a reduction in transpiration during the drought, the question of the unanimity between the foliar activities of the different species during this period can be studied.

If the reduction in transpiration is really of vital importance or even an appreciable advantage to the plant, one would expect to find some semblance to order and regularity, particularly in the period during which the plants are leafless and the time of production of young tender foliage.

Holtermann proved that transpiration was greater from young leaves than from old ones, and greater during the hot dry period at Peradeniya than during other parts of the year. Yet there are many trees, *e.g.*, Albizzia procera, with tender thin foliage which retain all their leaves during the period when transpiration is at the maximum; and, on the other hand, trees such as species of Ficus, with tough leathery leaves coated with a thick cuticle and therefore probably losing less by transpiration, become leafless. If, however, species such as Bombax malabaricum or Cratæva Roxburghii be considered, the reduction in transpiration will be found to be very great. The Bombax trees remain leafless for 32 to 96 days during our hottest and driest period, and usually produce new leaf at the end of the drought. One tree of Cratæva Roxburghii has been observed to be leafless for 31 to 76 days each year, and this specimen never regains full foliage until March or April. But when species such as Phyllanthus indicus, Careya arborea, Ficus Tsjakela, Sterculia Balanghas, Terminalia belerica, Chickrassia tabularis, and many others are studied it is seen that though they become leafless during the hot months for one or two days or weeks, they always produce their complete outfit of new tender foliage while the hot dry season is prevailing.

For these reasons one must assume that checking transpiration is only a consideration to certain species, and that others may, by passing through their foliar stages like those last mentioned, actually lead to *an increase in transpiration at a time when the minimum quantity of water is available in the soil.*

6.—The relative importance of the physical factors: temperature, humidity, rainfall, and light.

It has been shown that the climatic changes at Peradeniya are coincident with periodical foliar phenomena, and that when the atmospheric humidity is low and the rainfall scanty, there is a large increase in the number of trees which drop their leaves and remain leafless for varying periods of time.

It is now necessary to deal analytically with the separate factors, and if possible to determine the relative significance of a variation of temperature, humidity, rainfall, and light on the foliar periodicities of plants in Ceylon. The factors, when acting together in different intensities, have been shown to produce an effect on the *time* of defoliation, in the section dealing with the influence of climate. The power of each factor can be considered in regard to the effect on the manner and time of defoliation and also on the *number* of deciduous species.

Temperature.

The high temperature in the tropics so forcibly impresses the ordinary visitor that he naturally expects that its influence on plant growth and therefore foliar periodicity will be considerable. Sachs, when speaking of vegetative activity and rest, suggested that the periodicity may chiefly depend upon *temperature* and moisture. He stated that in any one species, each vegetative phenomenon possessed its cardinal points of temperature, and when dealing with deciduous trees in temperate zones he asserted that it was mainly the lower temperature of winter which led to defoliation, and the rise in temperature in spring which made it possible for the shoots to burst into new leaf.

Vines states that for any given degree of temperature there is a corresponding rate of growth.

Pfeffer points out that in certain cases the growth of leaves is unaffected by variations of temperature.

Schimper, after describing the high temperature and luxuriant vegetation in the tropics, stated that the importance

of temperature as a factor influencing the development of tropical forests is less significant than that of the hygrometric conditions of the air.

In this part of the paper we are concerned with the possible effect of a high temperature or variation of temperature on the fall of old leaves and the production of new ones.

To determine the effect of a difference in temperature alone it would be necessary to select districts where the rainfall, humidity, and climatic periodicities were the same—an agreement which it is impossible to find in any part of Ceylon.

Colombo and Hakgala are approximately similar to Peradeniya as regards annual rainfall and climatic periodicity, but the humidity at Hakgala is much higher than at either place, and our comparison is therefore confined to Colombo and Peradeniya. At Colombo the humidity is one degree higher and the rainfall about six inches greater than at Peradeniya. The temperature is 5° F. higher at Colombo than at Peradeniya. The higher temperature in the Colombo district is not accompanied by a notable increase in the number of deciduous species. The differences in temperature alone in parts of Ceylon appear to have very little, if any, effect on the phenomenon of defoliation. It is true that at Hakgala and other places at high altitudes the temperature is 15° F. lower than at Peradeniya, and the vegetation is almost evergreen; but it is equally true that at Mannar with a temperature more than 6° F. higher than at Peradeniya there is not a proportionate increase in the number of deciduous species. A slight increase in the deciduous species may be met with in the inland hot northern parts of Ceylon, but it can usually be ascribed more to the poor rainfall and low humidity rather than to the high temperature. Disregarding differences of climate, there occurs in Ceylon a decrease in the number of deciduous species with a fall in temperature, and equality or slight increase with a rise of temperature. In passing from the tropics to the temperate zones there is an increase in the percentage number of deciduous trees with a decrease in temperature.

The general facts may be summarized as follows :—

(1) A high temperature in the tropics compared to Europe is not necessarily accompanied by an increase in the percentage number of deciduous arborescent species (*cf.* Colombo and England).

(2) A decrease in temperature accompanied by a marked climatic periodicity is associated with an increase in the percentage number of deciduous species, if the tree flora of Great Britain is compared with that of Ceylon.

(3) A decrease in temperature in parts of Ceylon where the climatic periodicity is nearly the same does not lead to an increase in the number of deciduous species (*cf.* Hakgala and Peradeniya).

(4) An increase in temperature in other parts of the same tropical island is not necessarily accompanied by a proportionate increase in the number of deciduous species (*cf.* Colombo, Mannar, and Peradeniya). This appears to contradict (3).

(5) An increase or decrease in temperature in the same district (Peradeniya) is not concomitant with an increase or decrease in the number of deciduous species. At Peradeniya the temperature gradually rises from February to May, and the number of deciduous species first increases and then steadily declines. In May the temperature is at the maximum and is on an average 3·6° F. higher than in February, but the number of species which are either leafless or undergoing defoliation in May is five times *less* than in February. If the temperature and number of deciduous species throughout each month of the year be considered, it will be seen that from January to March there is a rise in temperature and an increase in deciduous species, a further rise in temperature from March to May with a decrease in the deciduous species, a fall in temperature and a decrease in the number of deciduous species from June to January. (See plate XXVI.)

These facts seem to suggest that in parts of Ceylon, and probably in the tropics generally, the effect of a high

temperature alone, or the variation in temperature on defoliation, is of minimum importance, and in comparison to the power of other factors may be almost neglected. It would be much more difficult and perhaps impossible to determine the effect of temperature on defoliation in Europe, where the great differences in seasonal climate are so powerful and all important.

Of the three factors, temperature, humidity of the air, and rainfall, the variation in temperature is probably of least importance in determining whether a tree shall or shall not be deciduous.

Moisture.

The effect of changes of moisture on vegetative growth has been worked out for many plants in the temperate zones and for a few species in the tropics.

Reinke worked with species of Helianthus, Datura, and others; Baranetzky and Godlewski with Brassica, Phaseolus, &c.; Darwin with Cucurbita and Kraus, and Lock with tropical bamboos.

In most cases a relationship between the rate of growth of various parts of plants and the hygrometric state of the atmosphere was established, and in the results of Lock one is struck with the remarkable dependence of the rate of growth on the changes in the humidity of the air. The relationship between the production of new leaf on the tropical trees here considered and the change in hygrometric conditions is equally striking, and furnishes another proof of the great importance of this factor in the growth of leaves in the tropics.

(*a*) *Rainfall.*

In a district like Peradeniya there is a coincidence between the period of drought and the number of deciduous species, the minimum monthly rainfall and the maximum number of species undergoing defoliation being in February and March. During August and September there is a marked decline in the monthly rainfall, but only one or two species are conspicuous in their leaf-fall during that

period, the rains preceding and following this miniature drought apparently being such as to obviate the necessity for a more general leafless condition.

At Hakgala, though there is a drought during February and March very similar in intensity to that at Peradeniya, yet the vegetation is by no means strikingly deciduous, and if it were not for the few leafless trees of Meliosma Arnottiana, the introduced fruit trees, and species of Cedrela, Michelia, &c., it might be described as typically evergreen. Nevertheless there is a response to the period of drought in so far that a large number of the deciduous trees pass through their leafless phase at that time.

Similarly it can be shown that in parts of the Uva and Northern Provinces the periods of drought, though occurring at widely different times of the year compared with Peradeniya and Hakgala, are coincident with the fall of leaf from a large number of trees. But in all these cases it should not be forgotten that the minimum monthly rainfall is coincident with the minimum monthly humidity of the air—a point which suggests that either factor may be equally potent in leading to the production of a temporary deciduous character in the vegetation.

In comparing various districts in Ceylon which are widely different from Peradeniya in their annual rainfall, say Hakgala with 91·7 inches, Badulla with 76·93, and Mannar with 38·59 inches, it will be noticed that the annual quantity of rainfall is not arithmetically related to the number of deciduous species in each district. For instance, Hakgala with a heavier rainfall shows less deciduous species than Peradeniya, but Badulla and Mannar, though they have less rainfall than Peradeniya, do not necessarily show a larger number of deciduous species, and it is therefore necessary to consider the united influence of humidity of the air and rainfall.

(*b*) *Atmospheric Humidity.*

The humidity of the air is probably one of the most important factors in the defoliation of trees in the tropics.

It can be shown by comparing Peradeniya, Hakgala, Colombo, Badulla, and Mannar, that the maximum yearly humidity obtains at Hakgala where the vegetation is more nearly evergreen than at any of the other places, and that the minimum humidity is at Peradeniya where the vegetation is perhaps more deciduous than in any of the places mentioned. The high humidity at Mannar—four degrees higher than at Peradeniya—is probably responsible for the stunted and often succulent nature of the vegetation and for the non-increase in the number of deciduous species compared with Peradeniya.

It is important to notice that the Peradeniya, Hakgala, Colombo, and Badulla districts, which represent different climates, ranging from sea level, to over five thousand feet above sea level show a definite relationship between a particular stage of humidity and defoliation. In all these districts it is only when the humidity falls *near to or below 70 degrees* that the majority of the deciduous species drop their leaves.

The best agreement is, however, between the varying humidity and number of deciduous trees at a given place, throughout the year. In each of the districts mentioned the number of deciduous species increases with increased dryness of the air and decreases with an increase in the dampness of the air. If the curves showing the relationship between humidity and number of deciduous species at Peradeniya are examined it will be seen that the minimum humidity is experienced in February and March, and these are the months when the maximum percentage number of deciduous species drop their leaves or become leafless. In April and May, when the temperature is higher, the number of leafless trees does not increase, but actually decreases on account of an increase in the dampness or

humidity of the air. During the rest of the year when the air is very damp the number of deciduous species which become leafless is very small, and when the maximum humidity obtains from June to October the number of leafless species is at the minimum.

The main points may therefore be briefly summarized in order to see which factor or factors are most instrumental in the phenomena under consideration.

In the following table the monthly humidity, temperature, and rainfall at Peradeniya are given, and also a column showing the number of species which are either leafless or passing through some stage of defoliation during each month in the same district (*cf.* plate XXIX.).

Month.	Rainfall in Inches.	Mean Monthly Humidity.	Mean Monthly Temperature, Fahrenheit.	Number of Species, Leafless or undergoing Defoliation.
January ...	4·75	77	73·2	37
February ...	2·37	71	75·0	47
March ...	3·48	71	77·3	45
April ...	7·59	77	77·5	24
May ...	5·95	78	78·6	10
June ...	9·11	81	75·5	5
July ...	6·85	81	74·9	3
August ...	5·74	81	74·9	3
September	5·69	80	74·9	2
October ...	10·99	82	75·2	5
November	10·69	79	75·3	9
December...	8·95	81	73·4	24

It is in the combined effect of rainfall and atmospheric humidity that one can discern the principal agent in connection with foliar phenomena, in various parts of the tropics. The relative humidity of the air can be correlated with the amount of moisture lost by transpiration, and on the rainfall depends the supply of water to make good that lost by the leaves. Both factors are therefore of great importance in connection with leaf-fall and foliar renewal. At a given place the increase in atmospheric humidity usually follows or accompanies that of the rainfall, and during a period of drought the humidity is correspondingly reduced.

A glance at the curve indicating the number of species which are leafless or undergoing defoliation during each month shows that in February when the rainfall and humidity are at the minimum the defoliation of the species is most active, and the same conclusion holds good for the dry month of March. But in April the rainfall and humidity of the air increase considerably, and though the temperature is higher than in February or March, the number of trees undergoing their leaf change is considerably reduced. Equally striking is the fact that from June to October the humidity is near the maximum, the rainfall is abundant, and the defoliation of the deciduous trees is at the minimum. A better or more complete comparison could not be desired to prove that in a climate like that at Peradeniya there is an increase in the defoliation or leafless stage of deciduous species during the dry period and a decrease during the hot moist or relatively cool and moist periods.

In other parts of the island such as Nuwara Eliya and Hakgala there is a coincidence between high humidity and heavy rainfall and the prevalence of a more or less evergreen vegetation. At Mannar a low rainfall and high atmospheric humidity prevail, and there is an approximate similarity in the number of deciduous species to that at Peradeniya. Such facts indicate the importance of humidity in connection with defoliation in the tropics.

From considerations of the humidity, rainfall, temperature, and foliar periodicity in Buitenzorg, East Java, and parts of Ceylon, it may be concluded that (1) a high temperature is of the minimum importance, and (2) low humidity and scanty rainfall are clearly associated with leaf-fall. Where the humidity and rainfall are more or less constant throughout the year there is less agreement between the time of foliar activities; where there is a wide variation in these factors throughout the year there is a more marked leaf-fall at the driest time of the year.

The effect of Light.

Wiesner worked with several plants in Europe and showed that transpiration decreased with a diminution in the intensity of light, and that the reduction of the latter as autumn advanced exercised an indirect influence on the leaf-fall.

It has often been observed that the completeness of defoliation of individual trees belonging to the same species at Peradeniya is variable, and in most cases this variability can be associated with the conditions of canopy under which the trees are growing. When dealing with the deciduous species indigenous to Ceylon, India, and Java, the periodicities of two trees (A) and (B) of Schleichera trijuga will be given. The two trees of this species growing at Peradeniya are differently situated and behave differently in their foliar periodicity.

Tree A is on open ground and receives light from all directions. The trees around it do not rob it of much light.

Tree B only receives the midday sun and is well protected from excessive light in the morning and afternoon. In behaviour it differs from tree A in that the defoliation is less simultaneous over all parts of the tree and the active foliar period is of much longer duration. These differences may be due to the conditions of canopy under which the trees live.

Many trees of Lagerstrœmia flos-reginæ, grown in the open, drop their old leaves more or less simultaneously over all parts of the tree and remain absolutely leafless for one or more weeks; other trees drop their leaves gradually and put on a few new leaves before the old ones have fallen. Trees belonging to the latter class take a longer period of time to effect complete renewal of foliage, and are usually growing under conditions of partial shade.

The same remarks apply to trees of Bridelia retusa, Ficus religiosa, and a few introduced species. In all cases the existence of dense shade seems to prolong the period of defoliation, and in some cases may prevent simultaneous leaf-fall from taking place.

This is an important point to notice, as it suggests that the difference between a conspicuously deciduous tree and one which undergoes partial defoliation at intervals may be due to the difference in the extent of exposure to light and wind. It certainly shows that by a slight change in the external environment the completeness and duration of defoliation is considerably altered.

Another point of some importance is the direction of defoliation, which in most cases is probably influenced by exposure to light. Trees of Berrya Ammonilla, Spondias mangifera, and Bertholletia excelsa, growing on open ground at Peradeniya are invariably defoliated from above downwards.

Trees of Ficus altissima, F. bengalensis, and Lecythis Pohlii, growing under unequal shade are, on the other hand, defoliated first on one side only. The order of appearance of new leaf usually follows the same sequence as the fall of the old, the twigs which are first leafless receiving the first set of new leaves independent of their age.

7.—External and internal Factors.

Haberlandt, when discussing the question of internal forces, stated that in those tropical districts where there is abundant moisture throughout the year and where the evergreen "rain forests" are seen at their best, periodicity in leaf production is not to be observed, the trees throwing off their old leaves and developing new ones the whole year round. In such cases foliar phenomena can only have their origin in forces other that those of climate. He also points out, however, that in those districts of the tropical zone where there is a rainy season and a dry one the winter of the temperate zones is represented by the latter.

Sachs, when dealing with the periodic alternation of vegetative activity and rest, stated that this matter must depend chiefly upon changes which take place in the resting plant, independently of external influences, or only indirectly affected by them.

It remains to be shown how different species in Ceylon give evidence of their independence or dependence on external conditions.

Internal Factors.

The fact that very few species pass through a leafless period each year, and that many evergreens produce new leaf at all times of the year suggests that foliar periodicity is largely a question of the individual convenience of the plants and is influenced only slightly by the climatic environment. The differences in climatic conditions throughout the year at Peradeniya are apparently not such as to afford any great advantage to change of leaf during a specified period, and the majority of the plants therefore produce new leaf at the initiative of internal requirements.

Out of a total number of 650 endemic and indigenous arborescent species, no less than 560 are evergreen, and the foliar periodicity of the evergreens is as irregular as it can be. There is not a month in the year when some of the species are not producing new leaf or shedding the old. The foliar renewal of the evergreens may take place annually, as in Mesua ferrea, bi-annually as with species of Diospyros, or monthly as with species of Cinnamomum. Even species which produce very large quantities of new leaves at a particular time of the year are subject to periods of minor foliar activity during the rest of the year. The individual branches produce leaves at irregular intervals, apparently without any concord with the rest of the tree of which they form a part.

The second fact of significance is that the deciduous endemic and indigenous trees do not select the same time of the year for shedding their old leaves or for foliar repletion, and there is not a month in the year when the deciduous species are all in full leaf. This irregularity obtains though all the plants may be growing under the same climatic condi-

tions. The curves on plate XXIX. show that one or more species may be defoliated during every month in the year.

In the third place it is of interest to note that plants of the same species, *e.g.*, Cassia Fistula, may undergo defoliation and foliar renewal at approximately the same time of the year, though growing in the dissimilar climates of Peradeniya, Colombo, Vavuniya, and Mannar; this suggests that the foliar periodicity is inherent and will make itself evident even under a variety of exacting climatic conditions.

Another point which indicates the power of internal forces is that outwardly similar plants of the same species, within a score or two of yards from each other, are deciduous at periods varying by many weeks and months. Haberlandt quotes Palaquium macrophyllum as a species which at Buitenzorg shows an independence of external meteorological conditions in so far that individual trees growing in the same neighbourhood throw off their old leaves and produce new ones during different months.

If one selects trees of Lagerstrœmia Flos-reginæ, Retz., Bridelia retusa, Spreng., or species of Canarium or Palaquium, he will find that though they exist alongside each other under conditions which are physically identical, yet the time of fall of old leaf, production of new leaf, and of flowers differs considerably in specimens of the same species. In the case of Bridelia retusa the variation is one of months, and to see individuals of this species on the same plot, some dropping their leaves, others quite bare, many in full old leaf, and others in full new leaf and flower impresses one with the significance of the internal forces.

Another consideration which may be put forward to indicate independence of external forces is the behaviour of the trees in respect to the dry period of the year. If there is one part of the year when the climatic conditions are likely to exercise their power it is the relatively dry period during February and March. It cannot be questioned that conditions favour excessive transpiration during that period,

and one would expect that a species would, by preference. pass through its leafless phase at that time. But what do we find? In the first place some deciduous species are in full possession of their new foliage during the hot dry season, as Bassia longifolia; in the second place some produce all their new leaf when the temperature and dryness of the air is at the maximum, as with Swietenia Mahogani, Careya arborea, Ficus asperrima, Gmelina arborea, Sterculia Balanghas, Phyllanthus indicus, Spondias mangifera, Terminalia belerica, Sterculia Thwaitesii, Lagerstrœmia Flos-reginæ, and others, and finally trees of Albizzia procera and often of Pterocarpus echinatus defer their leafless phase until the wet cold months of June and July, when transpiration and assimilation are usually near the minimum. Such species show that they are either able to carry on their inherent foliar periodicities in the face of a periodic and exacting climate or that they are less plastic than others. It may be that they have, in the migration of species, found themselves at a place where the climate is not in harmony with their original periodicity, and time will be required for an adaptation to be accomplished. From these and other considerations, it may be concluded that the seeming irregularity is an expression of the autonomy of the species, and is not likely to be changed by the climate under consideration.

There are several other observations which seem to suggest that the internal factors are of great importance.

If one tree be selected and the length of its leafless phase be observed from year to year it may transpire that there is a variation considerably greater than what one expects to find. One species may vary from 32 to 96 days for its leafless phase, another may vary from 2 to 14 days during different years, or a particular tree may not always pass through a perfectly leafless stage each year. In dealing with the frequency of defoliation several cases have been cited which thus indicate an independence of environment. The differences in such behaviour cannot always

be correlated with climatic differences, and may in a great measure be due to internal requirements only.

An interesting point was also observed in connection with cuttings of Erythrina indica. Several cuttings in October, 1903, about 4 feet long, were stripped of all leaves and put into ordinary soil for cultivation as a green manure. They soon burst into leaf, many of them continued without a break in full vigour, but a very large number dropped all their leaves and passed through the leafless period during February and March. Many regained their foliage. This may indicate that the fall of leaf from the trees is an inherent character and must be of a curious nature, since it is not much changed by propagation from a cutting, the cutting behaving like a tree though it is not a year old.

External Forces.

Our knowledge of the different behaviour of the same species at Buitenzorg and East Java, of the many well-known instances of acclimatization in various parts of the world, and the behaviour of introduced species in Ceylon, convince us that climate exerts a recognizable influence on the foliar and floral periodicities of tropical plants.

Previous observations have shown that certain species are not affected by the climatic periodicity, and those cases which indicate that the time of foliar activity is influenced by the climate can now be dealt with. The most striking fact which impresses one with the power of the dry period is that more than half of the deciduous endemic and indigenous species pass through their leafless phase from January to March. These species show a response to climate, in so far that in districts similar to Peradeniya they drop all their old leaves and remain leafless during a part of the hottest and driest season. During this period the leafless twigs of Bombax malabaricum, Eriodendron anfractuosum, Spondias mangifera, Careya arboreya, Gmelina arborea, Ficus Arnottiana, Berrya Ammonilla, Terminalia

belerica, Cassia nodosa, Bridelia retusa, Lagerstrœmia Flos-reginæ, and numerous others give a barren appearance to the arborescent vegetation. With certain exceptions the deciduous trees seem only to recognize one dry period as against the alternating dry and wet months of the remainder of the year. Terminalia Catappa undergoes a complete change of leaf during the dry part of each monsoon, and other species are probably subject to foliar depletion twice during certain years.

Another fact which points to the effect of the Ceylon climate on foliar periodicity is seen in the behaviour of trees in the north of the Island. The majority of the Ceylon species of Diospyros are evergreen and grow in the wet and intermediate zones. There are two species, viz., D. montana, Roxb., and D. ovalifolia, Wight, which in the dry hot district between Madawachchi and Mannar are partially deciduous and pass through a semi-leafless phase prior to the beginning of the rainy season ; yet they are evergreen at Peradeniya.

That the climate of Ceylon has a decided influence on the periodicity of the deciduous species is obvious if one leaves the Peradeniya district in May and proceeds to the north of the Island, where there is very little rain in the south-west monsoon, and where the weather from January to October is relatively dry and hot. The defoliation and foliar repletion have been considerably delayed in the Vavuniya and Mannar Districts compared with Peradeniya, the species common to all districts dropping their leaves at times which differ by many weeks and months. In the northern districts so long as the plant drops its leaves during any of the eight or nine months the same climatic advantages, if any, will accrue.

The maximum number of species undergoing defoliation is always found to be coincident with the dry period in all parts of Ceylon, and it is not necessary to do more than refer to the various observations recorded in the section

dealing with the leafless phase and the importance of the climatic factors.

In a tropical district like Peradeniya the foliar periodicity may be determined by internal and external factors, and each species must be considered separately. The more equable the climate in different parts of Ceylon the more conspicuously will the internal forces operate, and the more independent they will be of climatic influences. My statement at the British Association Meeting of 1902 that botanists desirous of studying the internal forces in plant life should select a tropical country other than Ceylon is still supported by the further results of this investigation.

In a general way it may be said that the nearer to the tropics the more the personal equation influences the phenomena of plant life, and as we pass from the equator—north or south—the less the power of the internal forces and greater the power of climate in determining the periodicity of plant life.

Even in those parts of the tropics where there are definite seasons, the phenomena appear to be the outcome of climatic and individual forces. In more equable tropical zones, with the minimum climatic variation, the plant phenomena are almost entirely determined by the individual requirements.

Respecting the effect of internal and external factors the main points may be summarized as follows :—

(1) The foliar periodicity of deciduous trees is inherent in tropical and temperate zones since it is observable in all these areas.

(2) The more equable and tropical the climatic conditions the larger is the number of arborescent species and the larger is the proportion of the evergreen trees in the flora. (*Cf.* British and Ceylon tree flora.)

(3) The more marked the climatic periodicity the less the internal forces are obvious and the more evident are the external forces. At Buitenzorg, where the climate is relatively equable throughout the year, the power of the

internal forces is obvious on every hand. In East Java and in Ceylon the climate is not equable throughout the year, and the power of internal and external forces is to be seen in various degrees. In the temperate zone, the climatic periodicity is more strongly pronounced and the internal factors almost obliterated.

(4) There is evidence to show that a marked climatic periodicity in which a drought is involved tends to induce a partial deciduous phenomenon in trees which, under a less exacting climatic periodicity are evergreen, *e.g.*, Thespesia populnea, Sol., Diospyros ovalifolia, and D. montana. The same may be said of Tectona grandis in East Java and Buitenzorg.

(5) There is also evidence to prove that a species which is deciduous in its natural home where a climatic periodicity is pronounced, may, when introduced to other countries, retain its periodicity if a climatic periodicity prevails, or it may tend to become evergreen if the climate is equable throughout the year, *e.g.*, Poinciana regia at Buitenzorg, East Java, and Ceylon, and Schizolobium excelsum in Buitenzorg and Ceylon.

(6) The arborescent flora in a temperate zone is mainly deciduous, and it seems possible that those plants the periodicities of which were or have been made to coincide with the winter months are among the most likely to survive.

In the temperate zones the flora is mainly comprised of plants which have survived the exigencies of extremes of climate such as the carboniferous rocks and glacial epochs indicate, and which are even now annually subjected to the frosts of winter and dry heat of summer. On the other hand it can be asserted that the plants in the equatorial zones are the phylogenetic outcome of forms long existing there, since there has been an unbroken condition for the development of plants, undisturbed by glacial periods or by temperate zone winters.

8.—Advantages of Periodical Phenomena.

It is impossible to assign one reason only to explain why the various species undergo a leafless phase once or twice each year. In parts of Ceylon the conditions are favourable to growth throughout the whole year. The flora is mainly of an evergreen type, but many of the deciduous species select the driest period for their leafless phase. In the temperate zones only those trees the leaves of which are tough and leathery, or are surrounded with a thick cuticle, or are so constructed that transpiration can never be rapid, retain their leaves throughout the winter months. The advantages which accrue from a leafless period in Europe are obvious, and on the defoliation may depend the life of the species in such districts. The trees throw off their relatively thin leaves before the winter sets in; if they did not they would probably soon be destroyed by the melting of the ice crystals formed within their tissues; furthermore they could not obtain the water required to make good that lost by slow transpiration during cold months, owing probably to the temperature of the soil being against root activity and the absorption of the necessary quantities of water. But it is obvious that such forces can be left out of consideration when dealing with trees in Ceylon.

A period of rest is characteristic of most temperate zone herbaceous plants, such as annuals which rest in the seed stage, perennials resting by corms, bulbs, &c. This resting feature is met with in many Ceylon herbaceous plants, such as Oxalis corniculata, *L.*, species of Caladium and Amaryllis, Drosera peltata, Sm., &c., though there is perhaps not the same necessity for such a phase since the temperature and humidity are always more or less favourable to plant growth, and the soil of medium quality.

It has been pointed out that the deciduous species in Ceylon do not pass through their leafless period at the same time, but during any month in the year even in the same district. The tropical species may choose a limited period of a few days or weeks or longer for dropping their old leaves and

for complete renewal of foliage. Trees classed as evergreens may undergo the same change within the year and the question often resolves itself, in the tropics, into one of the possible advantages which accrue from throwing off the old worn-out leaf tissues quickly.

There is, in this phenomenon, a withdrawal of materials from the leaves before they are allowed to fall; this is followed by a leafless period during which the assimilation of carbon compounds, circulation of materials and constructive metabolism generally, are at the minimum. This semi-stagnant period of relative rest is followed by one of great activity, first in the using up of store materials for production of new leaves, then in transpiration and root activity, due to the exposure of the numerous thin leaves and the absorption of water and plant food. The alternation of rest and activity is the principal feature in these phenomena, and species which exhibit it may thereby obtain certain advantages, though what the latter may be is by no means always clear.

There appear to be in Ceylon three possible sources of advantage, which may be of importance in this phenomenon, viz.—(1) checking the loss by transpiration during the drought; (2) throwing off worn-out tissues and useless ingredients; (3) functional changes during the different periods. With respect to the first question it has been pointed out, when discussing transpiration and foliar periodicity, that a reduction in the amount of water lost by transpiration is effected by species which behave similarly to Bombax malabaricum, Spondias mangifera, &c., but that in other cases the loss by transpiration may not be reduced but actually increased.

In the second case it is suggested that the defoliation of tropical species in a climate which is comparatively regular throughout the year is probably more a question of casting off useless ingredients and worn-out cells and tissues than anything else. It is well known that the leaves of nearly all our tropical trees do not possess a cambium, and they can

therefore only obtain new tissues by casting off the old members and producing entirely new leaves. It is obvious however that the same change can be obtained by a monthly fall and production of leaf. With respect to the possible necessity of throwing off the useless chemical ingredients when they have accumulated beyond the desirable degree of concentration, it may be stated that the yellow leaves of Erythrina indica as they fall from the tree contain 7 per cent. of lime. Nevertheless, it is erroneous to suppose that trees when throwing off their old yellow leaves are casting off members containing hardly any valuable food ingredients. Mr. Bruce analyzed several of the yellow fallen leaves of the common dadap (Erythrina indica) and found that they contained no less than 1·4 per cent. of nitrogen, 0·56 per cent. of potash, and 0·11 per cent. of phosphoric acid. These ingredients are not available in large quantities in Ceylon soils and the loss to the plant, temporary though in some cases it may be, is one which is not always seriously considered.

The main advantages are, however, probably to be associated with the change in functional activity of parts of the plants. It is not necessary that the leaves be continually exposed to light in order to successfully carry on the various functions of the plant. Experiments with various plants have proved that when light is supplied intermittently to the assimilatory organs the various functions are carried on as effectively as when light is continuously supplied. And the same may be said of our deciduous species, the leaves of which may be exposed to light for a varying number of months each year. By passing through the various stages of leaf-fall, leaflessness, and foliar renewal the assimilatory organs of the plant become subject intermittently to the stimulus of light, and on this depends the varying activity of many functions.

The variation in the activity of certain functions due to annual defoliation may be attended with many advantages. The plants obtain a period of rest as far as assimilation of carbon compounds is concerned, and the check to the

transpiration current will most probably have an appreciable effect on the metabolism within the parenchymatous elements. The question of division of labour is also one which may be considered. During the resting period many changes already mentioned by Schimper are taking place. These changes are necessary and may be required to be effected before foliage is renewed in order to avoid stagnation or general interruption. During the beginning and early period of the leafless phase the cambium is comparatively inactive, and the growth which takes place will therefore consist more in the thickening of the walls and general strengthening of the existing elements than in the production of new cells. During the end of the period of defoliation there is usually formed a series of closely set thick-walled elements which contrast sharply with those formed when the new leaves are produced.

The above are a few of the possible advantages which may be associated with the foliar phenomena in the tropics, but it must be remembered that no matter how significant the advantages may be, they have not, in Ceylon, resulted in a wide distribution or persistence of a large number of deciduous species. The evergreen trees, which do not show periodic foliar phenomena in the sense that the deciduous trees do, but maintain a more or less regular rate of leaf, flower, and root activity throughout the year, comprise the greater part of the tree flora of this Island.

9.—Relation of Foliar, Floral, and Fruit Periodicities.

With most Ceylon evergreens the production of flowers is usually subsequent to that of new leaves. It is not possible, owing to insufficient information, to describe the relationship between flower and leaf production in all our deciduous species, but if one tabulates the observed results certain definite cycles are found to be characteristic of known species.

Out of twenty-one recorded species it is interesting to find that in eight of them, viz., Careya arborea, Sterculia

colorata, Bombax malabaricum, Erythrina indica, Gmelina arborea, Gyrocarpus Jacquini, Chickrassia tabularis, and Spondias mangifera the flowers are produced when the tree is perfectly leafless and the production of flowers does not usually occur after the tree is in full leaf.

In other four species the flowers always appear with the young leaves as in Dalbergia frondosa, Stereospermum chelonioides, Vitex Leucoxylon, and Sterculia fœtida.

In other three species the production of flowers is delayed until all the leaves have been produced. In Melia dubia the flowers appear soon after the new leaves, but in the case of the other two species, Bridelia retusa and Lagerstrœmia Flos-reginæ, a considerable time may elapse between the full leaf and flowering periods. Most of the deciduous species in which the relationship of these periodicities has not been observed probably belong to this group.

Other species show a mingling of the two periodicities in various ways. For instance, some trees of Albizzia stipulata and Schleichera trijuga produce their flowers with the new leaves and continue to do so when the tree is in full leaf. Others such as Pongamia glabra, Phyllanthus Emblica, and Chloroxylon Swietenia commence to produce flowers when the trees are leafless and continue to do so until the new leaves are developed. In the case of Eriodendron anfractuosum, there is a copious production of flowers when the tree is leafless and flower production continues through the young leaf stage until the tree is in full leaf.

At Peradeniya the majority of plants whether arborescent, shrubby, or herbaceous seem to produce large numbers of flowers during the dry hot periods, though this is by no means the case with every species in the district.

The foliar, floral, and fruit periodicities of Bombax malabaricum are of more than usual interest. They show a division of labour or succession of periodicities which is only rarely observable in tropical plants. In the Peradeniya district old trees first allow their leaves to become discoloured and fall in December, and, after the

trees have been leafless for a few weeks every twig bursts into red flowers, and these remain throughout the months of January and February. Fruits begin to mature in March, and by the end of April the seeds with their covering of white cotton are disbursed. When the flowering and fruiting periods are over the tree bursts into new leaf in April and May when rain can usually be relied upon. The various functions seem to each have an allotted period, and the periodicity is such that foliar and floral activities do not clash. The ripe fruits on the leafless twigs are exposed to the full force of the wind, the seeds better distributed, and leaf production occurs only when rain is plentiful.

These periodicities are of equal interest in Eriodendron anfractuosum, and it is as well to point out a common source of confusion in connection with the periodicities of this species and Bombax malabaricum. In both cases there is a copious production of flowers during the leafless period and an abundance of ripe fruits which burst and distribute their seeds before the tree regains its foliage. In the case of Bombax the fruits are from the flowers produced in the same year, but the fruits on the leafless twigs of Eriodendron are from the flowers of the previous year.

It should be pointed out that in most deciduous trees in which the flowers are produced when the tree is leafless, there is usually a time relationship between the floral and foliar activities on parts of the same tree. This can be seen in trees of Spondias mangifera, Chloroxylon Swietenia, and Chickrassia tabularis, growing in the open. These trees become defoliated from above downwards, the leaves on the lower twigs dropping a fortnight later than those on the upper twigs, and in all such cases the flowers are produced first on the twigs which shed their leaves first, and last on the lower twigs which become leafless the last.

The time relation between the production of flowers and leaves is characteristic of the species in dissimilar climates. This is seen if the periodicities of the species herein described are compared with those given by Brandis

in his Forest Flora of India, particularly Gmelina arborea, Erythrina indica, Chloroxylon Swietenia, Careya arborea, Bombax malabaricum, Cassia fistula, &c.

10.—Foliar Periodicity of Fossil Plants.

Information concerning the foliar periodicity of trees when grown in dissimilar climates is of great value. It may help one to interpret the significance of structures in plants which have existed in palæozoic and mesozoic times. We have accurate knowledge of the periodicities of trees of the same species in different climates and the behaviour of the same species when introduced to different countries. The foliar periodicity, due in many cases to climatic forces, is to some extent responsible for the differentiation of rings of growth in the stem. The xylem differentiations met with in various fossil plants have been variously interpreted as indicating the equable or variable nature of the climates in which the plants have grown. Generally speaking, palæontologists have concluded that the complete and distinct differentiation of rings of growth in the stems of fossil plants indicated periodic foliar activity, and therefore a climatic periodicity, analogous to that in temperate zones ; and also that the absence of the rings of growth was more or less associated with an evergreen type of vegetation such as one may expect to obtain in an equable or tropical climate. Many statements have been made apparently under the impression that foliar periodicity was inseparable from climatic periodicity, and the degree of distinctness of rings of growth in recent fossil woods has been frequently associated with a change from a relatively equable and tropical climate to one having a periodicity similar to that in middle Europe at the present day.

It is hardly necessary to draw attention to the erroneous idea that a period of foliar rest and activity is undiscernible in arborescent tropical plants in various parts of the world, or that the tropical vegetation is characterized by uninterrupted

growth, and therefore the production of homogeneous secondary xylem. For in addition to the existence of about two hundred deciduous trees now growing in Ceylon one must acknowledge that there are regular periodicities in a large number of evergreen plants, in many of which the phenomenon is inherent and may lead to the production of a heterogeneous wood. The observations tabulated in this paper prove that foliar and other activities may be periodic in equable or tropical regions, that many plants pass through a leafless phase at any time of the year in a district like Peradeniya, and that the foliar periodicity exhibited may or may not lead to differentiations in the secondary xylem.

It will be shown in a later paper that in the tropics many deciduous trees do not show rings of growth, and further that quick-growing evergreens may show them. The results prove (1) that the differentiation of rings of growth in the stem is not confined to deciduous species; (2) that the foliar periodicity of trees is not necessarily due to the existence of a climatic periodicity; and (3) that rings of growth are not, in all cases, determined by foliar periodicities, neither are they a guarantee of the existence of a climatic periodicity. Such phenomena may be an expression of the autonomy of the plants dealt with, and one cannot be too cautious when considering the value of rings of growth as indicators of past climatic conditions. The subject of xylem differentiations is excluded from the present paper, but it is so closely associated with the foliar activity of trees in the tropics during our hot dry, hot moist, and dull wet months that the paper would have been incomplete without some reference to this subject.

11.—The Foliar Periodicity of Ceylon Endemics.

The endemic trees of Ceylon comprise no less than 274 species, or a little less than half the total number of arborescent species native to the Island. The foliar periodicity of the endemic plants is of great importance, as it shows the behaviour of plants which are known in Ceylon only, and

from a study of these some light may be thrown on the general trend of periodicity in plants which for ages past have been accustomed to the climate prevailing here. It is more than probable that investigations of the Indo-Malayan flora will prove that many of our species, now considered endemic, are distributed in areas outside Ceylon, but such discoveries will not seriously affect the considerations dealt with in this paper. Throughout this paper the names and distribution of the plants as given in Trimen's Flora and the Peradeniya herbarium have been accepted as correct.

The endemic species are remarkable for the scarcity of deciduous forms, about ninety-four per cent. of the arborescent species being typical evergreens. The natural orders Sapotaceæ, Dipterocarpaceæ, Ebenaceæ, and the genera Semecarpus, Eugenia, Memecylon, and Symplocos, contain a remarkable high percentage of endemic species which grow into huge trees, very few of which are deciduous. The evergreen trees may produce a large quantity of new leaf once each year, some of them twice per year, but most of them are characterized by irregular leaf production during each month of the year.

Deciduous endemics.—Trimen mentions that Phyllanthus cyanospermus, Muell. Arg. (vol. IV., p. 27), a rare species found in the wet districts of Ratnapura and Ambegamuwa, and Allæanthus zeylanicus, Thw. (vol. IV., p. 102), found in the Peradeniya and Maturata districts, are deciduous. The deciduous character of these species has been confirmed, and the following species can now be added to the list of Ceylon deciduous endemics :—

Artocarpus nobilis, Thw.
Canarium zeylanicum, Bl.
Canthium macrocarpum, Thw.
Holarrhena mitis, Br.
Julostylis angustifolius, Thw.
Pericopsis Mooniana, Thw.
Sapindus erectus, Hiern.

Sterculia Thwaitesii, Mast.
Terminalia parviflora, Thw.
Dipterocarpus zeylanicus, Thw.
Hydnocarpus venenata, Gaertn.
Doona cordifolia, Thw.
Semecarpus Gardneri, Thw.
Debregeasia Wallichiana, Wedd. (=D. zeylanica, Hk.).
Ficus infectoria, Roxb. (endemic ?).

The total number of observed deciduous endemic species is therefore only 17, or less than 3 per cent. of the arborescent flora, or 6 per cent. of the endemic trees in Ceylon. Though the percentage number of deciduous indigenous species is higher than this, it is nevertheless small, and the vegetation therefore be regarded as mainly evergreen throughout the island.

Distribution of deciduous endemics.—The distribution of the deciduous endemic species is of considerable interest. From the facts related when discussing the question of transpiration and the curves showing an agreement between the defoliation of the deciduous species and the dry hot months of February and March, one may be inclined to anticipate that the endemic deciduous species would be wholly or mainly confined to the dry hot parts of the Island, and that very few would be common in the cooler moist districts. The distribution of the deciduous endemic species is, however, practically confined to the moist or very wet districts, only one species having been recorded for the dry and intermediate zones, viz., Sterculia Thwaitesii, Mast. These facts strongly suggest that the defoliation of species confined to Ceylon is not vitally associated with a high temperature or low humidity. They also compel one to realize that the foliar periodicity in the dry zones is one characterizing species which are not limited to this Island, but distributed throughout various climates in the tropical world.

It is advisable to give a detailed statement of the periodicity of this group, and the smallness in number of the species concerned allows one to do this.

Nature of defoliation and foliar renewal.—The species may be classified into three groups.

The first group comprises those species which become absolutely leafless, typical examples being Allæanthus zeylanicus, Thw., Canarium zeylanicum, Bl., Canthium macrocarpum, Thw., Holarrhena mitis, Br., Pericopsis Mooniana, Thw., Terminalia parviflora, Thw.

These species may undergo complete defoliation before any new leaf-buds appear, though this behaviour is rarely as conspicuous as in indigenous forms. The actual length of time during which they are leafless is very limited, and may be, for particular species, from 31st January to 17th February, 7th to 20th March, and 29th August to 4th September. The actual period required for a complete renewal of foliage is of course much longer. With trees of Canarium zeylanicum the leaves may commence to fall on the 3rd February and continue to do so until the 7th or 12th March, when the tree is quite leafless; new leaf-buds appear from the 20th to the 28th March and the trees regain a complete outfit of mature leaves by the 11th April. Similarly for trees of Allæanthus zeylanicus, the period extends from 6th January to the 17th March, and with Terminalia parviflora from 10th February to 29th March. One tree of Holarrhena mitis effected complete defoliation and renewal within the month of March in 1902.

The phenomenon of foliar renewal is often so quick that the change of leaf on a tree of a particular species may be unnoticed.

The second class comprises those plants which though they may undergo a complete change of foliage within one or two weeks, are never absolutely leafless, on account of the production of new leaves on one part of the tree before all the old leaves have fallen.

Under certain circumstances trees of Terminalia parviflora and Canarium zeylanicum may behave in this way, but since they often become leafless they have been included in the

former division. Endemic species belonging to the second division are such as Sterculia Thwaitesii, Mast., and Sapindus erectus, Hiern. One tree of Sterculia Thwaitesii, along the Museum road, Peradeniya, commenced to drop its discoloured leaves on the 16th January and continued to do so until the beginning of the following month ; during that time a few new leaves appeared and the dropping of old and production of new leaves continued, until by the 7th February the tree had put on a complete outfit of new leaves.

This entire repletion of leaf is effected within two to three weeks without the tree ever becoming leafless.

The third class includes trees which like Artocarpus nobilis, Thw., are never leafless, but produce large quantities of new leaf and become partially leafless at certain times of the year. This group borders on the evergreens.

This classification only holds good in a general way, and it must be recognized that the periodicity may vary during certain years and so make it possible to include the same species in more than one group.

Range in time of Foliar Periodicity.

The total range or period of time during which the deciduous endemics undergo foliar depletion and renewal is fairly wide, and extends from January to October. The endemic deciduous forms mainly recognize one dry hot period—January to March. Nine of the species undergo their change from January to March, one during March and April, one from February to April, one from April to June, one from August to September, and one from September to October. It is to be noticed that nearly all those species which are the most conspicuous and which become absolutely leafless at some time or other do so from January to April ; whereas those which are less conspicuous, such as Sapindus erectus, drop their leaves at a later date, and the species which is least conspicuous from a deciduous point of view and which has previously been referred to as bordering on

the evergreens—Artocarpus nobilis—drops its leaves the last of all, in the cool moist month of October.

Variation of the same Tree in Successive Years.

In the table quoted hereafter it is obvious that there is often a fair constancy in the period at which a particular tree begins to show discoloured leaves and commences defoliation. There is, on the other hand, a considerable difference in the length of time during which a particular tree may be leafless in successive years. Julostylis angustifolius is an example of one which may not become absolutely leafless in a particular year though a leafless phase of several days' duration is what normally occurs. The differences to be noted in the synoptical table of dates quoted are not, perhaps, entirely due to corresponding differences in climate during the years in which the plants in question were under observation.

The relation of Foliar to Floral Periodicities in Deciduous Endemic Species.

Certain species have their foliar renewal closely followed or preceded by that of the flowers. Among these may be included Allæanthus zeylanicus. In this species the flower buds appear when the tree has shed only half its leaves, and during the time the tree is quite leafless the flowers are in full bloom; only after the new leaves have appeared do the flowers begin to wither and drop: a few flowers still exist when the tree has regained full new foliage. Canthium macrocarpum though bare in February puts on full new foliage and also flowers in March, and the full new leaf in April on Holarrhena mitis is followed by flowers in May.

Others produce the flowers long before the old leaves drop or after the new leaves have been produced: Julostylis angustifolius, Sterculia Thwaitesii, Sapindus erectus, &c.

These relationships may be better studied in the more numerous indigenous deciduous forms.

Endemics.

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Flowers appeared.
	Commenced.	Finished.			
Holarrhena mitis, Peradeniya.					
1902 ...	Feb. 27	Mar. 18	Mar. 24	17 days	May 4
1903 ...	Feb. 20	Mar. 16	April 7	21 days	May 7
1904 ...	Feb. 14	Mar. 2	Mar. 17	15 days	April
1905 ...	Feb. 3	Mar. 1	Mar. 12	11 days	
Allæanthus zeylanicus, Peradeniya.					
1902 ...	Jan. 6	Jan. 31	Feb. 17	17 days	Feb. 28
1904 ...	Jan. 10	Jan. 30	Feb. 16	17 days	March 2
1905 ...	Jan. 30	Feb. 24	Mar. 17	20 days	
Canarium zeylanicum, Peradeniya.					
1902 ...	Feb. 3	Mar. 7	Mar. 20	12 days	
1904 ..	Feb. 4	Mar. 12	Mar. 28	16 days	
1905 ...	Mar. 4	Mar.	Mar.	—	
Pericopsis Mooniana, Peradeniya.					
1902 ...	Aug.	Aug.	Aug.	—	
1903 ...	Aug. 22	Aug. 29	Sept. 4	6 days	
1904 ..	Aug. 3	Aug. 20	Aug. 22	1 day	
Sapindus erectus, Peradeniya.					
1902 ...	May 9	May 30	June 6	6 days	
1904 ...	April 24	May 20	May 22	2 days	
Sterculia Thwaitesii, Peradeniya.					
1902 ...	Jan. 16	Feb. 7	Jan. 18	None	
1903 ...	Jan. 18	Feb. 6	Jan. 19	None	
1904 ...	Jan.	Feb.	Jan.	—	
1905 ...	Jan. 3	Feb. 1	Jan. 10	None	
Julostylis angustifolius, Peradeniya.					
1902 ...	Feb. 19	April 22	Mar. 12	None	
1903 ...	Feb. 1	Mar. 16	Mar. 28	12 days	
1904 ...	Feb. 7	Mar. 27	April 3	7 days	
1905 ...	Jan. 2	Mar. 20	Mar. 28	7 days	

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Flowers appeared.
	Commenced.	Finished.			
Artocarpus nobilis, Peradeniya.					
1903 ...	Oct. 10	Nov. 13	Oct. 28	—	
1904 ...	Mar. Sept.	—	Mar. Oct.	None	
Debregeasia Wallichiana, Peradeniya.					
1904–05 ...	Dec. 30	Jan. 16	Jan. 25	8 days	
Dipterocarpus zeylanicus, Peradeniya.					
1901–02 ...	Dec. 2	Jan. 3	Dec. 30	—	
1902–03 ...	Nov.	Jan.	Nov.	—	
1903–04 ...	Dec.	Feb.	Jan.	—	
Hydnocarpus venenata, Peradeniya.					
1905 ...	Jan. 25	Mar.	Feb. 4	—	
Semecarpus Gardneri, Peradeniya.					
1905 ...	Feb. 3	Mar. 18	Mar. 3	—	
Doona cordifolia, Peradeniya.					
1905 ...	Jan. 14	Feb. 26	Feb. 3	—	
Phyllanthus cyanospermus, Peradeniya.					
1903 ...	March	Mar. 24	April 3	9 days	
Terminalia parviflora, Peradeniya.					
1902 ...	Feb. 10	Mar. 10	Mar. 12	2 days	
1903 ...	Feb. 12	Mar. 11	Mar. 16	5 days	
1904 ...	Feb. 2	Mar. 3	Mar. 8	4 days	
1905 ...	Feb. 15	Mar. 25	Mar. 29	3 days	

Other trees of Terminalia parviglora appear to be leafless for a longer time in the Peradeniya district.

At Henaratgoda, in 1902, several trees were in half new foliage on 11th February.

Canthium macrocarpum, *Peradeniya*.—During 1901 and 1902 the trees became leafless in February and produced new foliage and flowers in March.

Ficus infectoria. Deciduous. Trimen, Vol. IV., p. 92. Endemic?

12.—Foliar Periodicity of the Indigenous Species

There are in Ceylon nearly 380 arborescent indigenous species. In Trimen's Flora thirteen of these, the periodicities of which have since been confirmed, are described as deciduous. To these must be added the foliar periodicities of other sixty-five species. The total seventy-eight species are distributed among twenty-four natural orders. Nearly twenty per cent. of the indigenous species are deciduous, and in order to bring forward any possible relationship between the length of the leafless phase and the distribution of the species their periodicities have been described under the headings of the countries in which they are known to occur. The following is a plan of the arrangement adopted :—

1. Ceylon and India.
2. Ceylon, India, and Malaya.
3. Ceylon, India, Malaya, China, &c.
4. Ceylon, India, Java, China, and Japan.
5. Ceylon, India, and Java.
6. Ceylon, India, and Africa.
7. Ceylon, India, Malaya, Tropical Africa, &c.
8. Ceylon, India, and East Africa.
9. Ceylon, Malaya, and Australia.
10. Ceylon, Tropical Asia, &c.

There are several natural orders containing large numbers of indigenous species which grow into large trees. such as the Guttiferæ with 9, Apocynaceæ with 7, Borragineæ and Rhizophoraceæ each with 6, and Dipterocarpaceæ and Oleaceæ each with five species, but not one of these seven orders contains an indigenous deciduous species.

The following list shows the relative deciduous character of natural orders containing a varying number of arborescent indigenous species :—

No. of Indigenous Arborescent Species.	Natural Order.	No. of Indigenous Deciduous Species.
42	Euphorbiaceæ	5
33	Leguminosæ	14
28	Urticaceæ	14
18	Myrtaceæ	4
18	Rubiaceæ	3
13	Rutaceæ	1
11	Verbenaceæ	3
9	Lauraceæ	2
9	Meliaceæ	4
8	Tiliaceæ	1
8	Sterculiaceæ	3
8	Sapindaceæ	2
6	Combretaceæ	4
6	Sapotaceæ	2

It is a noteworthy fact that the natural order—Euphorbiaceæ—which possesses by far the largest number of arborescent indigenous species of any order in Ceylon should be characterized by so few trees which become leafless. The contention that the latex of these plants is of service during periods of drought or in districts which periodically suffer from want of rain would perhaps appear to be supported by this fact, as the species concerned are able to pass through the hot dry season without becoming leafless. Parkin* states that the latex from introduced species flows more freely and is thinner in the wet than in the dry season, and that in his opinion the laticiferous tubes act as water-stores; when there is plenty of moisture in the soil, more water is drawn up by the roots than is needed at once, and finds its way into the laticiferous ducts, to be drawn upon when required. The indigenous species which are deciduous contain very little, if any latex, a condition quite unlike that which obtains for the species of Hevea, Manihot, &c.,

* Parkin, J.; Caoutchouc or Indiarubber, Circular of the Royal Botanic Gardens, Ceylon, Series 1, Nos. 12, 13, 14, 1899.

introduced from other countries. The genus Ficus, however, contains a large number of deciduous species which possess well-developed latex tubes.

The natural orders which possess the largest proportion of deciduous species are the Urticaceæ and Leguminosæ respectively. The genus Ficus is remarkable for the high percentage of deciduous trees, the laticiferous system, and the leathery leaves of its species.

The annual periodicity of most of the indigenous plants here described is fairly constant from year to year. Observations upon plants which were hitherto regarded as being of the same species have shown a great variation in the manner and time of defoliation, and have led me to doubt whether the trees concerned are really of the same species. With the object of giving a systematic importance to the phenomenon of defoliation in the tropics, the following list has been compiled. It shows the distribution of the deciduous indigenous species in the Ceylon flora.

Anonaceæ.

Polyalthia coffeoides, Benth. and Hk.

Capparideæ.

Cratæva Roxburghii, Br.

Bixaceæ.

Flacourtia Ramontchi, L'Herit.

Malvaceæ.

Thespesia populnea, Sol.
Bombax malabaricum, D. C.
Eriodendron anfractuosum, D. C.

Sterculiaceæ.

Sterculia fœtida, L.
Sterculia Balanghas, L.
Sterculia colorata, Roxb.

Tiliaceæ.

Berrya Ammonilla, Roxb.

Rutaceæ.

Zanthoxylum Rhetsa, D. C.

Meliaceæ.

Melia dubia, Cav.
Dysoxylum binectariferum, Hk. f.
Chickrassia tabularis, A. Juss.
Chloroxylon Swietenia, D. C.

Sapindaceæ.

Schleichera trijuga, Willd.
Sapindus laurifolius, Vahl.

Sabiaceæ.

Meliosma Arnottiana, Walp.

Anacardiaceæ.

Odina Wodier, Roxb.
Spondias mangifera, Willd.

Leguminosæ.

Erythrina indica, Lam.
Erythrina ovalifolia, Roxb.
Dalbergia frondosa, Roxb.
(= D. lanceolaria, L. f.)
Pongamia glabra, Vent.
Peltophorum ferrugineum, Benth.
Cassia Fistula, L.
Bauhinia tomentosa, L.
Adenanthera pavonina, L.
Adenanthera bicolor, Moon.
Acacia Suma, Kurz.
Albizzia Lebbek, Benth.
Albizzia odoratissima, Benth.
Albizzia stipulata, Boiv.
Albizzia amara, Boiv.

Combretaceæ.

Terminalia belerica, Roxb.
Terminalia glabra, Thw.
Anogeissus latifolia, Wall.
Gyrocarpus Jacquini, Roxb.

Myrtaceæ.

Eugenia Gardneri, Duth.
Eugenia operculata, Roxb.
Eugenia Jambolana, Lam.
Careya arborea, Roxb.

Lythraceæ.

Lagerstrœmia Flos-reginæ, Retz.

Rubiaceæ.

Sarcocephalus cordatus, Miq.
Stephegyne tubulosa, Hk.
Gardenia latifolia, Ait.

Ebenaceæ.

Diospyros Melanoxylon, Roxb.
Diospyros montana, Roxb.
Diospyros ovalifolia, R. Wight.

Sapotaceæ.

Bassia longifolia, L. Mant.
Mimusops Elengi, L.

Loganiaceæ.

Strychnos Nux-vomica, L.

Bignoniaceæ.

Oroxylum indicum, Vent.
Stereospermum chelonioides, D. C.

Verbenaceæ.

Gmelina arborea, Roxb.
Vitex altissima, L.
Vitex Leucoxylon, L.

Lauraceæ.

Litsea tomentosa, Heyne.
Litsea sebifera, Roxb. (= L. chinensis, Lam.)

Euphorbiaceæ.

Bridelia retusa, Spreng.
Phyllanthus Emblica, L.
Phyllanthus indicus, Muell. Arg.
Breynia rhamnoides, Muell. Arg.
Sapium indicum, Willd.

Urticaceæ.

Ficus hispida, L.
Ficus benghalensis, L.
Ficus altissima, Bl.
Ficus Trimeni, King.
Ficus retusa, L. Mant.
Ficus nervosa, Heyne.
Ficus Arnottiana, Miq.
Ficus Tsjakela, Burm.
Ficus infectoria, Roxb.
Ficus callosa, Willd.
Ficus asperima, Roxb.
Antiaris toxicaria, Leschen.
Antiaris innoxia, Bl. (see Trimen, Vol. IV., p. 97)
Artocarpus Lakoocha, Roxb.

1.—Ceylon and India.

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Remarks.
	Commenced.	Finished.			
Bridelia retusa, Spreng.; Peradeniya.					
1901 ...	January	Feb.	March	—	Flowers appeared in June and July.
1902 ...	Jan. 4	Mar. 12	Mar. 24	11 days	
1903 ...	Jan. 6	Mar. 24	April 7	13 days	
1904 ...	January	Mar. 6	Mar. 20	13 days	
1905 ...	Jan. 2	Mar. 8	Mar. 16	7 days	
Careya arborea, Roxb.; Peradeniya.					
1900–01 ...	Dec. 14	Feb. 18	Mar. 18	28 days	
1901–02 ...	Dec. 18	Feb. 15	Mar. 15	28 days	
1902–03 ...	Dec. 20	Mar. 12	Mar. 24	12 days	
1903–04 ...	Dec. 16	Feb. 7	Mar. 8	29 days	
1904–05 ...	Jan. 3	Jan. 26	Feb. 4	8 days	
Dalbergia frondosa, Roxb.; Peradeniya.					
1902 ...	May 9	June 3	June 24	20 days	Flowers appear in June, before or with leaves.
1903 ...	May 13	June 6	June 25	18 days	
1904 ...	May 2	June 1	June 8	6 days	
Tree at Warriapola, Matale.	—	—	July 4	—	
Dysoxylum binectariferum, Hk. f.; Peradeniya.					
1902 ...	Mar. 3	Mar. 24	Mar. 20	—	
1903 ...	Feb. 28	Mar. 18	Mar. 6	—	
1904 ...	Feb.	Mar. 4	Mar. 1	—	
1905 ...	Feb.	March	March	—	

1.—Ceylon and India—*contd.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Remarks.
	Commenced.	Finished.			
Diospyros ovalifolia, R. Wight.	August	Sept.	August	None	Partially deciduous in Northern Province.
Diospyros montana, Roxb.; Ceylon.	August	Sept.	August	None	do.
India ...	Feb.	March	March	—	According to Brandis.
Diospyros melanoxylon, Roxb.					
India ...	March	April	April	—	do.
Eugenia Gardneri, Duth; Peradeniya.					
1902 ...	Feb. 3	Mar. 10	Feb. 26	—	
1903	Mar. 18	April 11	April 7	—	
1905 ...	January	March	Jan. 19	—	
Ficus Arnottiana, Miq.; Peradeniya. Tree A.					
1901–02 ...	Dec. 13	April 24	Feb. 3	—	
1902–03 ...	Dec. 17	Mar. 14	April 10	24 days	
1903–04 ...	Nov. 30	Mar. 22	April 7	16 days	
Peradeniya. Tree B.					
1901–02 ...	Dec. 23	Mar. 5	April 11	—	
1902–03 ...	Dec. 20	Mar. 3	April 7	35 days	
1903–04 ...	Dec. 21	Mar. 20	May 30	41 days	
Ficus asperrima, Roxb.; Peradeniya. Tree A.					
1901–02 ...	Dec. 4	Dec. 28	Dec. 31	2 days	Very irregular at Peradeniya, and may be defoliated once or twice in twelve months.
1902–03 ...	Nov. 28	Dec. 24	Jan. 12	7 days	
1903–04 ...	Dec. 1	Dec. 26	Jan. 2	6 days	
Peradeniya. Tree B.					
1902	Mar. 4	Mar. 10	Mar. 18	7 days	
1903	Mar. 2	Mar. 9	Mar. 17	7 days	
	Oct. 1	Oct. 8	Oct. 11	2 days	
1904 ...	May 30	June 18	June 26	7 days	
1905 ...	Jan. 3	Mar. 20	Mar. 26	5 days	

1.—Ceylon and India—*contd.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Remarks.
	Commenced.	Finished.			
Ficus altissima, Bl.; Peradeniya.					
Tree A.					
1902 ..	Mar. 1	June 6	Mar. 12	None	
1903 ...	Mar. 24	June 13	April 24	—	
	Sept.	October	Sept.	—	
1904 ...	Feb. 26	June 2	Mar. 16	—	
1905 ...	Feb. 24	—	Mar. 18	—	
Tree B.					
1901-02 ...	Nov. 28	Jan. 17	Dec. 28	—	
1902-03 ...	Dec. 5	Jan. 24	Dec. 28	—	
Ficus infectoria, Roxb.; Peradeniya.					
1902 ..	Feb. 12	Mar. 7	Feb. 25	—	
1903 ...	Mar. 5	Mar. 24	Mar. 16	None	
1905 ...	Mar. 12	April 14	Mar. 24	—	
Ficus Tsjakela, Durm.; Peradeniya.					
1902 ...	Jan. 14	Feb. 12	Feb. 22	7 days	
1903 ...	Jan. 21	Feb. 6	Mar. 1	22 days	
1904 ...	Jan. 16	Feb. 18	Mar. 16	25 days	
Meliosma Arnottiana, W. & R.					
Hakgala ...	January	January	Feb.	Several weeks	Flowers in June.
Phyllanthus indicus, Muell. Arg.; Peradeniya.					
1902 ...	Feb. 4	Mar. 10	Mar. 12	1 day	
1903 ...	Feb. 9	Mar. 13	Mar. 16	2 days	
1904 ...	Feb. 20	Mar. 16	Mar. 24	7 days	
1905 ...	Feb. 18	Mar. 6	Mar. 9	2 days	

1.—Ceylon and India—*contd.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Remarks.
	Commenced.	Finished.			
Stereospermum chelonioides, D.C.; Peradeniya.					
Tree A.					
1901–02 ...	Dec. 13	Feb.	Dec.	None	
1902–03 {	Oct. 28	March	do.	do.	There are three trees known by this name. Their periodicities are described under headings A, B, and C. Tree A showed partial defoliation on more than one occasion within the same year.
1902–03 {	April 1	May	May	do.	
1903–04 ...	Dec.	March	Dec.	do.	
Peradeniya.					
Tree B.	Jan. 15	April 28	May 7	8 days	
1902 ...	Jan. 20	May 4	May 12	8 days	
1903 ...	Jan. 24	May 2	May 10	7 days	
Peradeniya.					
Tree C.					
1902 ...	January	May 4	May 10	5 days	Flowers appeared on May 13, 1902.
1903 ...	Dec.	May 1	May 7	5 days	
1904 ...	January	April 30	May 8	7 days	
1905 ...	do.	April	May		
Strychnos Nux Vomica, L.; Peradeniya.					
1903 ...	Jan. 23	Feb. 28	Feb. 3	None	
Terminalia glabra, W. and A.; Peradeniya.	—	—	—	—	Leaf-fall conspicuous during February and March, 1903.
Vitex altissima, L., f.	—	—	—	—	At Vavuniya in March, 1902, a tree shed a large part of its leaves.

1.—Ceylon and India.

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Remarks.
	Commenced.	Finished.			
Vitex Leucoxylon, L. f.; Peradeniya.					
1901 ...	Feb. 1	Feb. 18	Mar. 6	15 days	New leaves and flowers appear together in March.
1902 ...	Jan. 30	Feb. 24	Mar. 10	13 days	
1903 ...	Jan. 28	Feb. 28	Mar. 7	6 days	
1904 ...	Feb. 24	Mar. 30	April 5	5 days	
1905 ...	Feb. 15	Mar. 23	Mar. 30	6 days	
Zanthoxylum Rhetsa, D.C.; Peradeniya.					
1902 ...	Mar. 2	Mar. 24	April 15	21 days	
1903 ...	Mar. 12	Mar. 22	April 8	16 days	
1904 ...	Mar. 16	April 10	April 26	15 days	
1905 ...	Mar. 2	April 4	April 21	16 days	

Acacia Suma, Kurz ; Peradeniya.

This tree is not very vigorous, and the recorded periodicity may be slightly different from that of a tree in a healthy state.

From 1901 to 1904 the leaves have become discoloured and commenced to fall during November in each year, and the tree is nearly leafless during February to April and regains its full foliage in May.

1.—*Ceylon and India.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	
	Commenced.	Finished.			
Anogeissus latifolia, Wall.; Peradeniya.					
1902 ...	Feb. 3	Mar. 10	Mar. 12	2 days	
1903 ...	January	Mar. 24	April 6	13 days	
1904 ..	March	March	March	None	
1905 ...	February	March	March	—	

In 1901 the leaves fell during February and March, and the tree was in full new leaf in April.

In 1904 new leaves were produced before all the old ones had dropped. It appears to be very variable at Peradeniya and may or may not become leafless.

In the Bintenne district in 1902, the foliar change took place in June, many of the trees being in new leaf and others leafless during that month.

1.—*Ceylon and India.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	
	Commenced.	Finished.			
Bassia longifolia, L.; Peradeniya.					
Tree A.					
1901 ...	Dec. 4	Dec. 31	—	—	
1902 ...	Dec. 8	Jan. 12	Jan. 14	1 day	
1903 ...	Dec. 10	Jan. 12	Jan. 12	—	
1904 ...	Dec. 12	Jan. 2	Jan. 3	—	
Tree B.					
1901-02 ...	Dec. 9	Jan. 2	Jan. 8	5 days	
1902-03 ...	Dec. 16	Jan. 6	Jan. 14	7 days	
1903-04 ...	Dec. 28	Jan. 30	Feb. 5	5 days	
1904-05 ...	Dec. 3	Jan. 1	Jan. 5	3 days	

New leaves may appear before all the old ones have dropped.

Flowers appear soon after the new leaves.

During June several twigs drop their old leaves and produce new ones.

The defoliation in 1903-1904 was delayed, probably because of dry weather in November-December, 1903, and heavy rains in January, 1904.

At Bibile and Passara some trees were leafless, others dropping, and others in new leaf in May and June, 1904.

1.—Ceylon and India.

	Leaf-fall.		New Leaves produced.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Chloroxylon Swietenia, D.C.; Peradeniya.					
1902 ...	Feb. 27	Mar. 7	Mar. 11	3 days	Flower buds appear just before the new leaves.
1903 ...	Feb. 6	Mar. 19	Mar. 24	4 days	
1904 ...	February	Mar. 9	Mar. 27	15 days	
1905 ...	Jan. 8	Mar. 4	Mar. 17	12 days	

Another tree showed in 1901 and 1902 a heavy fall of old leaf in February and production of flowers and leaves in March. This tree also showed a minor activity in leaf production during the north-east monsoon in November and December.

1.—*Ceylon and India.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	
	Commenced.	Finished.			
1903 ...	Jan. 30	June 5	Mar. 1	—	
1904 ...	Feb. 3	June 9	Mar. 2	—	
1905 ...	Feb. 12	July	Mar. 4	—	
Ficus bengalensis, L.; Peradeniya.					
1902 ...	Feb. 5	June 3	Mar. 5	—	

During each of the years 1902–05 this tree commenced to drop its leaves first on the eastern side only, and the leafless twigs on that side put on a full complement of new leaves before leaf-fall commenced on the western side.

1.—Ceylon and India.

	Leaf-fall.		New Leaves appeared.	Leafless Period.	
	Commenced.	Finished.			
Flacourtia Ramontchi, L'-Herit.; Peradeniya.					
1901–02 ...	Dec. 18	January	Dec. 21	—	
1903 ...	April	—	May	—	
1904 ...	January	February	January	—	
	Sept.	Oct. 1	Oct. 14	13 days	
1905 ...	January	February	January	—	

This tree along the new Oreodoxa drive is most erratic.

1.—*Ceylon and India.*

	Leaf-fall.		New Leaves appeared.	Leafless Period.	
	Commenced.	Finished.			
Ficus Trimeni, King; Peradeniya.					
1900–01 ...	Dec.	March	Jan.	—	
1901–02 A. ...	Nov.	Feb.	Jan.	—	
1901–02 B. ...	June	October	August	—	
1902–03 A. ...	Nov.	March	Jan.	—	
1902–03 B. ...	July	October	Sept.	—	
1903–04 ...	Nov.	March	Jan.	—	
1904–05 ...	Dec.	March	Jan.	—	

The behaviour of this tree is rather peculiar. It appears to be subject to partial or complete defoliation during the windy weather in December and January and again in June and July. In neither case does the tree become absolutely leafless, new leaves appearing before all the old ones have dropped. An account of the behaviour of this tree for 1901 and 1902 is here given.

The leaves began to fall on 18th November, 1901, and on 6th December the tree was one-quarter bare. From

the 14th to 20th December, during very windy weather, there was a very heavy fall of old leaf. The tree had dropped nearly all its old leaves on January 24, but new leaves had already appeared on many twigs, and by the 15th February the tree was in full foliage. On the 20th June there was again a conspicuous fall of old leaf, many twigs becoming quite leafless; the tree remained in this condition until the end of October; after that month the leaf-fall again commenced, and a conspicuous defoliation was effected in November.

1.—*Ceylon and India.*

	Leaf-fall.		New Leaves	Leafless
	Commenced.	Finished.	appeared.	Period.
Gardenia latifolia, Ait.; Peradeniya.				
1903	... Mar. 22	... May 18	... Mar. 28	... None
1904	... Mar. 26	... May 19	... Mar. 30	... None
1905	... Mar. 2	... May	... Mar. 16	... None

The leaves fell from individual twigs, and new leaf buds appeared almost immediately afterwards.

Litsea tomentosa, Heyne; Peradeniya, 1901–1904.—This tree is usually regarded as an evergreen. It undergoes complete defoliation annually during the months of April and May. Leaf production commences in the early or latter part of April, and the tree is in possession of full new foliage before the end of May.

Polyalthia coffeoides, Bent.; Peradeniya, 1902.—This tree commenced to shed its leaves on the 14th January, but up to the 7th April only one-quarter of the old leaves had dropped. On this date the leafless twigs showed a development of new leaf. The dropping of old and production of new leaf continued throughout the month of April, and this species is therefore on the border land of the deciduous and evergreen classes. It is the only member of the Anonaceæ in which this phenomenon has been observed, and is comparable to the partially deciduous character of Diospyros montana, Roxb., a dry zone member of the Ebenaceæ.

1.—Ceylon and India.

	Leaf-fall.		New Leaves appeared.	Leafless Period.	Remarks.
	Commenced.	Finished.			
Odina Wodier, Roxb.; Peradeniya.					
1903 ...	October	Nov. 21	Nov. 30	8 days	A tree at Vavuniya shed its leaves, March, 1905.
Sapindus laurifolius, Vahl.; Peradeniya.					
1901 ...	Feb.	April	April	—	
1902 ...	Feb. 20	April 7	April 20	12 days	
1903 ...	Feb. 25	Mar. 20	Mar. 22	2 days	Flowers appeared on March 16.
Sterculia colorata, Roxb.; Peradeniya.					
1903 ...	Mar 10	Mar. 16	April 7	21 days	
Stephegyne tubulosa, Hk.; Peradeniya.	—	—	—	—	Shed a large number of leaves in March, 1902.

2.—Ceylon, India, and Malaya.

In this group there are eighteen species which exhibit a definite foliar periodicity, fourteen of them becoming absolutely leafless for a varying length of time.

It is noteworthy that here we are dealing with species which have a very wide distribution throughout the tropical world, and for this reason the following considerations are of much importance.

The range of time for their foliar activities is for most of the species limited to our hot dry season, January–March; true, a few commence to drop their leaves in

November and December, but as previously stated this is of no serious consequence. The months of February and March are coincident with the leafless phase of most of the species of this group.

The average length of time during which the trees of this group remain leafless is longer than for the members of the Ceylon and India group. For instance, we have Bombax malabaricum, the most remarkable for its leafless period, which extends with some trees from 79 to 96 days in each year; Erythrina indica (21 to 36 days), Gyrocarpus Jacquini (29 to 31 days), and species such as Berrya Ammonilla and Terminalia Belerica. The fact that these species are widely distributed may yet be correlated with the length of their leafless period and the adaptability of this to a hot dry season.

2.—*Ceylon, India, and Malaya.*

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Adenanthera bicolor, Moon; Peradeniya.					
1901–02 ...	Dec. 15	May 7	Jan. 21	None	
1903 ...	Jan. 12	May 8	Jan. 28	None	
1904 ...	Feb. 14	—	—	—	
Albizzia odoratissima, Benth.	—	—	—	—	At Vavuniya trees shed a large quantity of leaves in March.
Albizzia stipulata, Boiv.; Peradeniya.					
1901–02 ...	Dec. 30	Feb. 1	Feb. 11	9 days	The tree flowers in March and April after new leaves.
1902–03 ...	Dec. 28	Feb. 6	Feb. 28	21 days	
Antiaris toxicaria, Lesch.; Peradeniya.					
1902 ...	October	Nov.	Dec.		
	Jan. 3	Jan. 14	Jan. 24	9 days	Leafless in
1903 ...	Nov.	Nov.	Nov.	—	May to June
1904 ...	August	Nov.	Nov.	—	at Passara.

2.—Ceylon, India, and Malaya—*contd.*

	Leaf-fall.		New Leaves appeaerd.	Leafless Phase.	Remarks.
	Com-menced.	Finished.			
Antidesma Bunius, Spreng.; Peradeniya.					
1904-05 ...	March	March	March	—	
Antiaris innoxia, Bl.; Peradeniya.					
1901 ...	Feb.	March	March	—	
1902 ...	Feb. 3	Mar. 3	Mar. 4	—	
1903 ...	Feb. 6	Mar. 5	Mar. 6	—	
1904 ...	Feb. 10	Mar. 4	Mar. 7	2 days	
1905 ...	Feb. 4	Mar. 2	Mar. 10	7 days	
Berrya Ammonilla, Roxb.; Peradeniya.					
Tree A.					
1902 ...	Feb. 10	Mar. 3	Mar. 17	13 days	The defoliation is always from above downward.
1903 ...	Feb. 8	April 24	May 4	9 days	
1904 ...	Feb. 28	April 8	April 26	13 days	
Tree B.					
1901–02 ...	Dec.	Dec.	Dec. 28	—	Various trees show a foliar activity from December to February.
1902–03 ...	Dec.	Dec. 13	Dec. 28	14 days	
1930–04 ...	Nov. 27	Feb. 1	Feb. 4	2 days	
1904–05 ...	Dec. 18	—	—	—	
Bombax malabaricum, D.C.; Peradeniya.					
Tree A.					
1901–02 ...	Dec.	Dec. 14	Feb. 17	32 days	The time taken from the appearance of the leaf bud to expansion and development of full leaf may be a question of weeks and even months.
1902–03 ...	Dec.	Dec. 12	Feb. 28	45 days	
Tree B.					
1901–02 ..	Dec.	Jan. 24	May 1	95 days	
1902–03 ...	Dec.	Jan. 26	April 24	96 days	
1903–04 ...	Dec.	Jan. 30	April 21	79 days	
Tree C.					
1902–03 ...	Nov. 13	Jan. 28	Mar. 19	48 days	

2.—Ceylon, India, and Malaya.

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	
	Commenced.	Finished.			
Chickrassia tabularis, Juss.; Peradeniya. Tree A.					
1902 ...	Feb. 3	Mar. 3	Mar. 7	3 days	
1903 ...	Jan. 22	Feb. 26	Mar. 3	4 days	
1904 ...	Feb.	Mar. 5	Mar. 10	4 days	

Other trees in the Peradeniya and Henaratgoda districts are leafless during part of February and usually for a longer period than the above. In the Bibile district the leafless period was noticed in May and June, 1901. The flowers appear before the new leaves when the tree is bare.

2.—Ceylon, India, and Malaya.

	Leaf-fall.		New Leaves produced.	Leafless Phase.	
	Commenced.	Finished.			
Erythrina indica, Lam.; Peradeniya.					
1901-02 ...	Nov.	Feb.	March	—	
1902-03 ...	Dec.	Feb. 18	Mar. 23	21 days	
1903-04 ...	Dec.	Feb. 7	Mar. 27	36 days	
1904-05 ...	Dec.	—	—	—	

Most trees drop their leaves in December, January, and February, and red flowers appear during the last month and through March, while the trees are more or less leafless. The leaves appear from the middle of March to the end of April.

2.—Ceylon, India, and Malaya.

	Leaf-fall.		New Leaves produced.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Ficus nervosa, Heyne; Peradeniya.					
1901–02 ...	Dec. 23	Jan. 11	Jan. 15	3 days	Some of the old leaves may remain on the old twigs until new leaf has appeared.
1902–03 ...	Dec. 20	Jan. 10	Jan. 13	2 days	
Gmelina arborea, Roxb.; Peradeniya.					
1902 ...	Feb. 5	Feb. 21	Feb. 28	6 days	Flowers are produced when the tree is leafless. Leafless trees have been seen at Vavuniya in May and at Peradeniya in April.
1903 ...	Feb. 14	Mar. 4	Mar. 16	10 days	
Gyrocarpus Jacquini, Roxb.; Peradeniya.					
1903 ...	Feb.	Mar. 24	April 24	29 days	In flower on March 24, 1903, when tree leafless. Often leafless in Northern Province in May.
1904 ...	Feb.	Mar. 27	April 30	31 days	
1905 ...	Feb.	Mar. 28	April 20	22 days	

2.—Ceylon, India, and Malaya.

	Leaf-fall.		New Leaves produced.	Leafless Phase.	
	Commenced.	Finished.			
Mimusops Elengi, L.; Peradeniya.					
1902 ...	Feb.	Feb.	March	None	

The discoloured leaves fall rapidly in the last week of February; new leaves appear by the 3rd of March, and from that date the production of new foliage keeps pace with the fall of the old leaf, and by the first week in April a new outfit of foliage has been obtained. It undergoes annual defoliation, but on account of the absence of a leafless phase is often regarded as an evergreen.

2.—*Ceylon, India, and Malaya.*

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Pongamia glabra, Vent.; Peradeniya.					
Tree A.					
1901–02 ...	Dec. 23	Jan. 21	Feb. 19	27 days	The flowers appear either with or prior to the new leaves.
1902–03 ...	Nov. 30	Jan. 4	Feb. 4	29 days	
1903–04 ...	Dec.	Feb. 10	Feb. 27	15 days	
Tree B.					
1903–04 ...	Dec.	Feb. 20	Mar. 5	11 days	
Terminalia Belerica, Roxb.; Peradeniya.					
1901–02 ...	Dec. 8	Feb. 12	Feb. 21	8 days	
1902–03 ...	Dec.	Feb. 6	March 5	26 days	
1903–04 ...	Dec.	Feb. 2	Feb. 14	11 days	
Sterculia Balanghas, L.; Peradeniya.					
1901 ...	Feb.	Feb.	March	—	
1902 ...	Jan. 31	Feb. 28	Mar. 13	12 days	
1903 ...	January	Jan. 24	Feb. 6	12 days	
1904 ...	Feb.	Mar. 11	April 10	29 days	
1905 ...	January	Feb. 2	Mar. 1	26 days	
Trema orientalis, Bl.; Peradeniya.					
1904 ...	Jan. 1	Jan. 26	Feb. 18	22 days	
1905 ...	January	Feb.	Feb.	—	

3.—Ceylon, India, Malaya, and China, &c.

	Leaf-fall.		New leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Adenanthera pavonina, L.; Peradeniya.					
1901–02 ...	October	Nov. 6	Dec. 8	31 days	The tree regains new foliage very slowly and is rarely in full new leaf before the end of February.
1902-03 ...	Oct. 12	Nov. 1	Dec. 10	38 days	
1903–04 ...	August	Oct. 28	Nov. 20	22 days	
1904–05 ...	October	Dec.	January	—	
Cassia Fistula, L.; Peradeniya.					
1902 ...	Jan. 4	Feb. 24	Mar. 10	13 days	Trees were in full flower at Anuradhapura and Dambulla on September 1, 1902.
1903 ...	Jan. 10	Feb. 27	Mar. 18	18 days	
1904 ...	Jan. 5	Mar. 3	Mar. 28	24 days	
1905 ...	Jan. 2	Feb. 27	March	—	
Ficus hispida, L.; Ficus retusa, L.; Vavuniya.					
1902 ...	Feb. March	March	March	—	
Lagerstrœmia Flos-reginæ, Retz.; Peradeniya.					
Tree A.					
1901–02 ...	Dec. 5	Jan. 24	Feb. 20	26 days	In the open; not shaded.
1902–03 ...	Dec.	Jan. 3	Feb. 5	32 days	
1903–04	Dec. 10	Jan. 8	Feb. 1	23 days	
1904–05 ...	Dec. 15	Jan.	Feb.	—	
Tree B.					
1901–02 ...	Nov. 16	Feb.	Dec. 18	—	The tree becomes nearly leafless in December. It is not in full leaf until the end of February.
1902–03 ...	Nov. 1	do.	Dec. 2	—	
1903–04 ...	Oct. 11	January	Oct. 28	—	
1904–05 ...	Nov. 20	—	—	—	

3.—Ceylon, India, Malaya, and China, &c.—*contd.*

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Tree C.					
1903 ...	January	Feb. 28	Mar. 5	4 days	
1904 ...	do.	Mar. 1	Mar. 17	15 days	
Tree D.					
1903 ...	Feb.	Mar. 5	April 7	32 days	
1904 ...	do.	Mar. 24	April 17	23 days	
Tree E.					
1903 ...	Feb.	Mar. 24	April 7	13 days	In flower, June
1904 ...	do.	Mar. 27	April 4	7 days	3, 1903.
Oroxylum indicum, Vent.; Peradeniya.					
1901 ...	January	Feb. 8	Mar. 22	40 days	
1902 ...	do.	Feb. 14	Mar. 30	42 days	
1903 ...	do.	Feb. 6	Mar. 24	44 days	
1904 ...	do.	Feb. 12	Mar. 30	44 days	

Other trees in the Peradeniya district show a heavy fall of leaf during January and February and a leafless period during February and March. One tree, probably not in full vigour, was leafless during November, 1901, and continued to produce new leaves during December, 1901, and right on until May, 1902, and is probably nearing its last day.

3.—*Ceylon, India, Malaya, and China, &c.*

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	
	Commenced.	Finished.			
Breynia rhamnoides, Muell.: Peradeniya.					
1901–02 ...	Dec. 12	Feb.	Jan. 25	—	
1902–03 ...	Dec. 3	Feb.	Jan. 28	—	

3.—Ceylon, India, Malaya, and China, &c.—*contd.*

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	
	Commenced.	Finished.			
Erythrina ovalifolia, Roxb.; Peradeniya.					
1902 ...	Feb. 4	Mar. 28	Feb. 24	—	
1903 ...	Feb.	April 1	Feb.	—	
Eugenia operculata, Roxb.; Peradeniya.					
1905 ...	Jan. 9	Feb.	Feb.	—	
Litsea sebifera, Roxb.; Peradeniya.					
1902 ...	Feb. 26	April 3	Mar. 24	—	
1902–03 ...	Nov. 9	April 1	Feb.	—	
1904–05 ...	Dec.	April	Feb.	—	
Sarcocephalus cordatus, Miq.; Peradeniya					
1904 ...	Feb. 1	March	March	—	

4.—Ceylon, India, Java, China, and Japan.

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	
	Commenced.	Finished.			
Phyllanthus Emblica, L.; Peradeniya.					
1902 ...	Feb. 3	Mar. 3	Mar. 10	6 days	
1903 ...	Feb. 2	Mar. 5	Mar. 20	4 days	
1904 ...	Feb.	Mar. 10	Mar. 16	5 days	

The flowers appear forming a compact inflorescence when the tree is leafless; the leaves soon appear at the top of each inflorescence.

5.—Ceylon, India, and Java.

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Artocarpus Lakoocha, Roxb.; Peradeniya.					
1901–02 ...	Dec. 3	Jan. 20	Jan. 14	—	
1902–03 ...	Nov. 26	Jan. 24	Jan. 3	—	
Ficus callosa, Willd.; Peradeniya.					
1902 ...	Feb.	Mar. 6	Mar. 4	—	Another tree of this species showed foliar activity in August, 1903.
1903 ...	March	April 28	April 2	—	
Schleichera trijuga, Willd.; Peradeniya.					
Tree A.					
1902 ...	Feb. 7	Mar. 3	Feb. 24	–	The flowers appear with the new leaves or immediately after them.
1903 ...	Feb.	Mar. 12	Feb. 21	—	
1904 ...	Feb. 19	Mar. 10	Feb. 26	—	
Tree B.					
1902 ...	Jan. 28	April 30	Jan. 31	—	
1902-03 ...	Nov. 8	May 16	Jan. 1	–	
1903–04 ..	Dec. 10	April	Jan. 12	—	
1904–05 ...	Dec.	—	—	–	

6.—Ceylon, India, and Africa.

There is one species belonging to this group of particular interest.

Cratæva Roxburghii, Br., Peradeniya.—This is a very slow-growing tree and is very conspicuous on account of the slow rate at which the old leaves fall and the new leaves appear.

1900–91. The tree commenced to shed its leaves in August and was almost leafless throughout November and December, 1900, and January, 1901. On the 3rd January only five new leaf buds appeared, and the tree remained with a single shoot in partial new leaf until the middle of March. Towards the end of April the tree was in full new leaf.

1901–02. On the 26th August, 1901, the discoloured leaves began to fall and continued to do so very gradually until by the 1st October the tree was bare. The tree remained leafless through the greater part of October and the whole of November; on the 2nd December two small leaf buds appeared on one twig, and on the 21st December five leaf buds were present. New leaves were not produced rapidly until the 14th February, the appearance of new leaf being quite as slow as the fall of the old leaf. On the 4th March the tree was in half new leaf, but it was not until the 31st March, 1902, that the tree was in full new leaf.

1902–03. On the 10th August, 1902, the leaves began to fall; the tree became leafless on the 25th October and remained in that condition until the 10th January, 1903. On the last date a few new leaves appeared on one twig only: on the 7th February new leaves appeared on a second twig, and full new foliage was regained by the 6th April.

1903–04. On the 30th August, 1903, the few yellow leaves commenced to fall, but the tree was not absolutely leafless until 28th November. On the 7th February, 1904, one twig put out a few new leaves and remained in this condition until the 9th March; on the 14th April the tree was in three-quarter new leaf, and by the end of April new foliage had been regained. The variability in length of leafless period is not of much consequence to a tree characterized by such a slow rate of activity.

From 1900 up to date I have not seen any flowers on this tree, though its age must be somewhat advanced. At Vavuniya, in March, 1902, I observed one tree shedding old leaves.

The following synopsis for the tree at Peradeniya is here given :—

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	
	Commenced.	Finished.			
1900–01 ...	August	October	January	—	
1902 ...	Aug. 26	Oct. 1	Dec. 2	31 days	
1902–03 ...	Aug. 10	Oct. 25	Jan. 10	76 days	
1903–04 ...	Aug. 30	Nov. 28	Feb. 7	70 days	
1904–05 ...	Aug. 15	Nov. 12	Jan. 3	51 days	

7.—Ceylon, India, Malaya, and Tropical Africa, &c.

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Albizzia Lebbek, Benth.; Peradeniya.					
1902 ...	Jan. 6	Mar. 3	Jan. 14	—	At Vavuniya trees shed their leaves in March, 1902.
1902–03 ...	Dec.	—	—	—	
Bauhinia tomentosa, L.					
1902 ...	Feb. 24	April	April ...	—	Flowered in April, 1902.
1903 ...	March	April	April ...	—	

Sterculia fœtida, L.—Observed trees at Peradeniya begin to shed their leaves on the 5th February, becoming leafless on the 14th, and remaining so for several days or even over one week. Other trees in the same district pass through their leafless phase during March.

At Elkaduwa in the Matale District trees may be seen just bursting into new leaf and flower in the first week in April. The flowers appear just before the leaves at a time when the tree is leafless.

8.—Ceylon, India, and East Africa.

Sapium indicum, Willd.; *Peradeniya.*—The leaves become discoloured in the latter part of December, and the

fall of leaf takes place at such a rate that the tree is half bare by the 3rd January, but has not thrown off the whole of last year's leaf until the end of April. New leaves appear, however, early in January when only half of the old leaf has dropped, and the tree has usually put on a complete new outfit by the end of April.

Albizzia amara, Boiv.—A tree of this species was in 1896, according to Mr. Broun, then Conservator of Forests in Ceylon, leafless for a short time.

9.—Ceylon, Malaya, and Australia.

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	
	Commenced.	Finished.			
Peltophorum ferrugineum, Benth.; Peradeniya.					
1901–02 ...	Dec. 2	January	Jan. 14	—	
	June	July	June & July	—	
1902–03 ...	Dec. 3	January	Jan. 21	—	
1904–05 ...	June	June	June	—	
	Dec.	Feb.	January	—	

10.—Ceylon and Tropical Asia, &c.

	Leaf-fall.		New Leaves produced.	Leafless Phase.	
	Commenced.	Finished.			
Eugenia Jambolana, Lam.; Peradeniya.					
1902					
1903 ...	Feb. 20	April	Mar. 10		
1904 ...	Feb.	March	Mar. 10	—	
...	Feb. 2	March	Mar. 14	—	
Melia dubia, Cav.; Peradeniya.					
1902					
1903 ...	Jan. 21	Feb. 1	Feb. 10	8 days	
1905 ...	Jan. 20	Feb. 16	Feb. 24	7 days	
...	Jan. 14	Feb. 23	Mar. 2	8 days	

Melia dubia is well distributed throughout the planting districts, and is conspicuous for the complete defoliation which it undergoes.

Observed species have commenced to drop their leaves on 21st January and have become leafless by the 3rd February. The new leaf buds can be seen within one or two days after complete defoliation, and the flowers immediately follow the new leaves.

Most trees in the Peradeniya district undergo their change of foliage from January to February each year, but occasionally they may be observed to pass through this phase in February to March.

Thespesia populnea, Soland ex Corr.—This is a species cultivated in the planting districts, where it does not usually pass through a conspicuous foliar phase, new leaves appearing irregularly throughout the year.

On the coral islands in the Gulf of Mannar this tree becomes half leafless during the dry period July to August, and puts on new leaf as soon as the rains arrive.

	Leaf-fall.		New Leaves appeared.	Leafless Phase.	Remarks.
	Commenced.	Finished.			
Spondias mangifera, Willd.; Peradeniya. Tree A.					
1901-02 ...	Nov. 18	Dec. 30	Mar. 24	83 days	Flowers were produced from the 6th to 24th February, 1903, and from 17th to 28th February, 1904.
1902-03 ...	Oct 28	Dec. 26	April 1	94 days	
1903-04 ...	Nov. 7	Dec. 28	April 10	102 days	
1904-05 ...	Dec. 6	—	—	—	
Tree B.					
1902-03 ...	Oct. 29	Dec. 28	Mar. 30	91 days	Flowers appeared on January 18th, 1903, and from 9th February to 7th March, 1904.
1903-04 ...	Nov. 13	Dec. 24	Apl. 3	99 days	
1904-05 ...	Dec. 8	Dec. 25	April	—	

Several other trees of Spondias mangifera have been under observation, and in only one case were there any conspicuous differences in foliar periodicity from those detailed above. This tree does not commence to shed its leaves until the end of December a (time when most other trees are leafless) and is in full flower and fruit on the 28th March.

This is a widely distributed species and is noticeable on account of its pronounced deciduous character. The trees of this species usually shed their leaves during December and remain leafless during January and February. The flowers always appear when the tree is leafless, and it is not until all the floral activity is long over that leaves are produced; it is therefore comparable with species of Stereospermum and several Malvaceous plants in this character.

Eriodendron anfractuosum, D.C.—This is a species distributed throughout Ceylon. During its first years and even up to ten years the tree grows relatively quickly. Trees only one year old show a partial defoliation in February at Peradeniya; the same trees showed defoliation in their second and third years from February to March. The defoliation on very old trees is often irregular, new leaves sometimes appearing before all the old ones have dropped.

In the Peradeniya district the old leaves fall during December, January, and February, and in the last month the trees usually possess nothing beyond mature fruits. The last year's fruits usually disperse their seeds embedded in white cotton while the tree is leafless (*Cf.* Bombax malabaricum); often, however, new leaves appear before the last year's fruits have disappeared. The new leaves appear with the flowers usually during April and May, after a leafless period of from two to six weeks.

At Henaratgoda and Colombo the periodicities agree with those observed at Peradeniya; in the Province of Sabaragamuwa many trees are leafless towards the end of May;

at Passara, in May and June, 1901, at an elevation of 2,800 feet, several trees were entirely leafless, and others in new leaf and flower; at Nawalapitiya and Dikoya several trees were leafless during March, 1902.

13.—Ceylon Indigenous Species in India.

In the foregoing lists a record of the periodicities of the deciduous species has been given. These usually refer to the behaviour of the plants in Ceylon, and it is now necessary to observe the behaviour of the same species in other countries.

Brandis, in his "Account of the Forest Flora of North-West and Central India," has given the periodicities of many species indigenous to Ceylon and India, and from references in his book and that of Kurz on "The Forest Flora of British Burma" the following details have been obtained.

In the dry parts and deciduous forests of India, Burma, Bengal, and South India, trees of Diospyros Melanoxylon, Diospyros montana, Gardenia latifolia, Odina Wodier, Phyllanthus Emblica, Schleichera trijuga, and Spondias mangifera usually shed their old leaves every year.

(1) *Diospyros Melanoxylon.*—The leaves are shed in March and April, and foliar renewal, accompanied by the production of flowers, is effected in April.

(2) *Diospyros montana.*—The leaves are renewed in February and March, and the flowers appear from March to May.

(3) *Gardenia latifolia.*—New leaves are produced in May; the wood has distinct rings of growth.

(4) *Odina Wodier.*—Trees of this species are leafless from January or February to June, and flowers appear while the tree is leafless. Kurz remarks that this species is frequent in all kinds of leaf-shedding forests all over Burma from Ava to Martaban down to Tenasserim and the Andamans (Vol. I., p. 321).

(5) *Phyllanthus Emblica.*—The tree is more or less leafless from February to April, and Kurz quotes it (Vol. II., p. 352) as being common in deciduous forests, especially the dry and open ones.

(6) *Schleichera trijuga* is a species which, according to Brandis (For. Fl., p. 105), sheds its leaves in February, but produces new leaves in March when most of the other trees of the dry forest are leafless.

(7) *Spondias mangifera* is common in the dry forests of many parts of India and Burma, and according to Brandis (p. 128) is one of the first trees to shed its leaves and the last to renew them, often remaining leafless until the rains have set in. The leaves are shed in November, and the flowers are produced in April.

It is interesting to note that most of the above seven species undergo defoliation and foliar renewal at approximately the same time of the year as at Peradeniya, the last three species showing almost exact agreement in time of periodicity.

Trees of Bombax malabaricum, Careya arborea, and Cassia Fistula, common to South India, Burma, and Bengal, also closely agree with trees at Peradeniya in the time of their leaf periodicities, as the following notes show.

Bombax malabaricum is leafless from November or December until April, and is covered with flowers from February to March, according to Brandis, p. 31.

Careya arborea.—According to Kurz, (Vol. I., p. 499) this is common in all the leaf-shedding forests, especially in the open, dry, lower mixed, and savannal forests of Burma; it is leafless during a part of the dry season, the new foliage appearing in March and April together with the flowers.

Cassia Fistula, which is common all over Burma and the adjacent leaf-shedding forests, is leafless for a short time in the dry season, the new leaves being produced in April and May.

Several other species have been observed to pass through a leafless state by Brandis in South India, Burma, and Bengal, and among them the following are noted.

Albizzia stipulata.—The young leaves appear in February and March.

Albizzia Lebbek.—The trees are partially leafless for some time in the hot season; leaves produced in March and April, and sometimes a second flush in autumn.

Albizzia odoratissima.—The trees are never quite leafless, but partially so; abundance of new foliage is produced in spring.

Albizzia procera is never quite leafless; the new foliage appears in April and May.

Cratæva Roxburghii.—The old leaves may remain until the flowers appear; the tree is usually bare for some time, and the young leaves appear with or without flowers in April and May.

Erythrina indica.—The old leaves are shed in autumn, young leaves produced in March and April, and flowers issue while the tree is leafless.

Gmelina arborea.—The leaves fall from February to April, new leaves issue in April and May, and the flowers appear generally while the tree is leafless.

Stereospermum cheloniodes.—Leaves fall in February and March, and new ones are produced in April.

Terminalia Belerica.—Leaves fall in February and March, and new foliage issues in April.

The periodicities of the following species found in various parts of India and described in the section dealing with indigenous species in Ceylon are also of interest.

Sterculia colorata.—In the forests along the outer valleys of the Himalaya, Burma, and in the dry deciduous forests it is leafless during the winter, flowers appear in March and April, and young leaves appear with or soon after the flowers.

Flacourtia Ramontchi.—On rocky hills and in open warm localities throughout India; sheds its leaves in January and February, and the tree remains bare until spring, the new leaves appearing in March and sometimes in May.

Chloroxylon Swietenia.—This is common in the Satpura range, Dekkan, and the Konkan; it produces its new leaves in May, at about the time the old leaves fall.

Anogeissus latifolia.—A common tree in South and Central India; is leafless during the greater part of the dry season; from November the old leaves acquire a copper tint, fall in February, and new leaves appear in May.

Pongamia glabra.—Common in South and Central India, Burma, and Bengal; drops its leaves in April, but new leaves appear quickly.

Eugenia Jambolana.—This species is common in India; the new leaves are produced in March; in the Punjab the tree is not evergreen, the old leaves being shed in January and the new leaves appearing in March to May.

Eugenia operculata.—Common in parts of India; puts on its new foliage in April.

Shorea robusta, Gaertn., common in parts of India; is never quite leafless, but produces abundance of foliage in March.

Ficus bengalensis, F. infectoria, Ficus glomerata, and F. hispida; common in various parts of India; undergo their leaf change from January to April.

In concluding this paper I take the opportunity of expressing my gratitude to Dr. J. C. Willis, Peradeniya, for first suggesting the subject on my arrival in Ceylon and for help repeatedly given; to Dr. Treub, Buitenzorg, for much information concerning the climate and foliar periodicities in Java; to W. Nock, Esq., and H. F. Macmillan, Esq., for several notes; to the Surveyor-General, Colombo, for records of climate; and to M. Wright for various translations and reading proofs.

MAP of CEYLON showing Average Annual Rainfall

ISOTHERMS IN RED LINES

- Under 50 ins
- 50 ins and more
- 75 ins and more
- 100 ins and more
- 150 ins and more
- 200 ins and more
- Observatories
- Rain Gauge Stations

81°
80·5°
80°
79°
78°
77°

Udupiddi 51
Jaffna 53
Mullaittivu 50
Mannar 38
Mantota Hospital 39
Medway 61
Trincomalee 63
Anuradhapura 54
Kantalai 67
Allai 72
Puttalam 47
Wilhelmina 54
Dambulla 62
Batticaloa 58
Chilaw 93
Kurunegala
Vicarton 19
Delwita 18
Mariawela
Mahale
Pathiragalla 87
Dea Ella
Liberia 39
Kandy 25
Rajawela
Hobonella
St Martins
Nawalapitiya
Nawalapitiya Hospital
Nittambuwa
Ambepussa
Nittambuwa Hospital
Colombo 89
Nuwara Eliya
Badulla 67
Passara Hospital
Maragalla
Bandarawela
Mupane
Ella
Ratnapura 57
Hambantota 37
Galle 91
Matara 70
Tangalla 41

Temperature Curves.

Average Monthly Mean Temperature

Fahrt.

Mean Annual Temperature

A. Mannar — 81·8.

B. Badulla — 73·2

C. Colombo. — 80·7

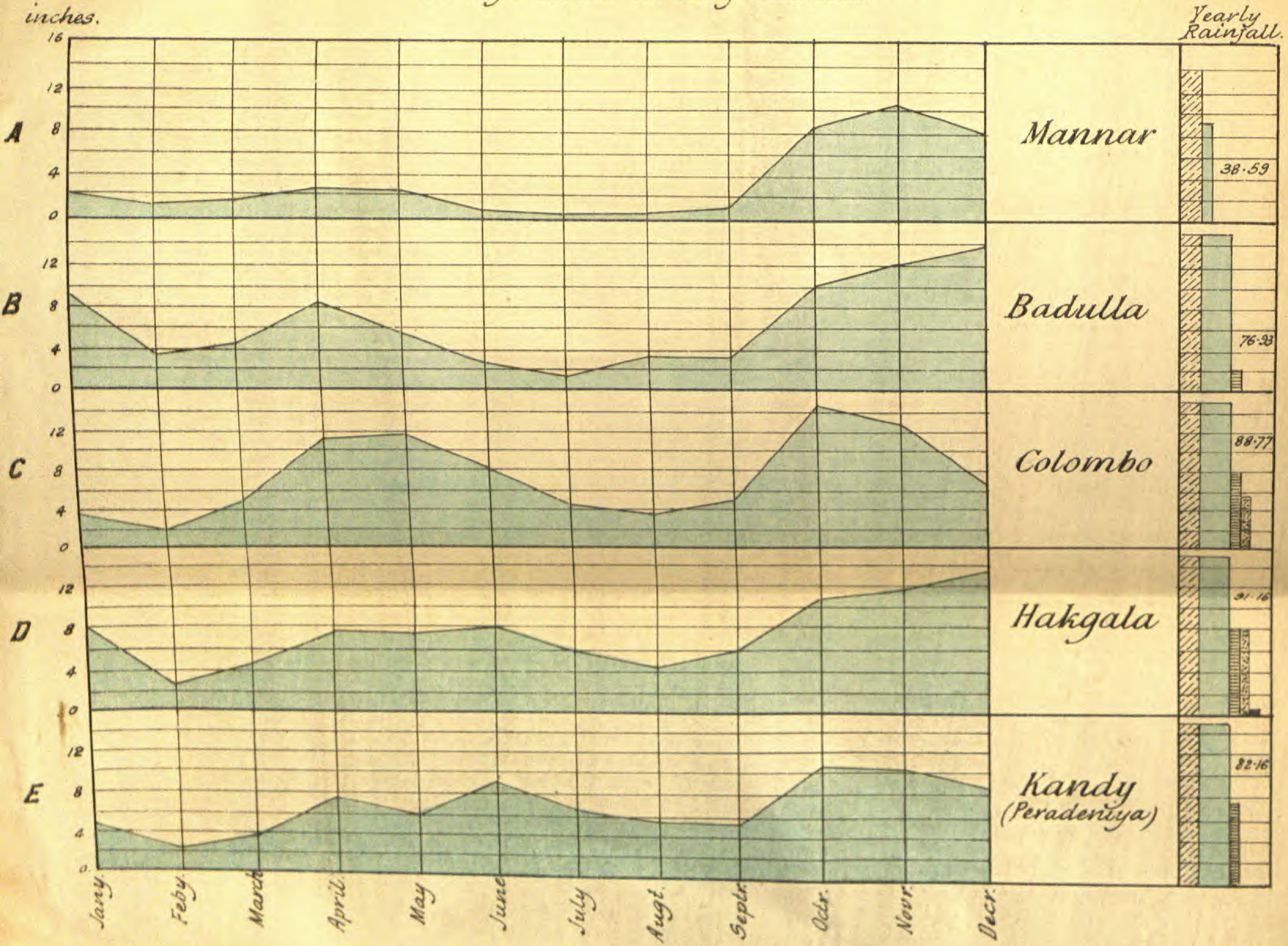
D. Hakgala — 60·3

E. Kandy (Peradeniya) — 75·5

Jany. Feby. Mar. Apl. May June July. Augt. Sept. Oct. Nov. Dec.

Rainfall Curves.

Average Mean Monthly Rainfall.



Humidity Curves.

Average mean monthly relative Humidity.

Average Yearly Humidity.

A — Mannar — 82

B — Badulla — 79

C — Colombo — 79

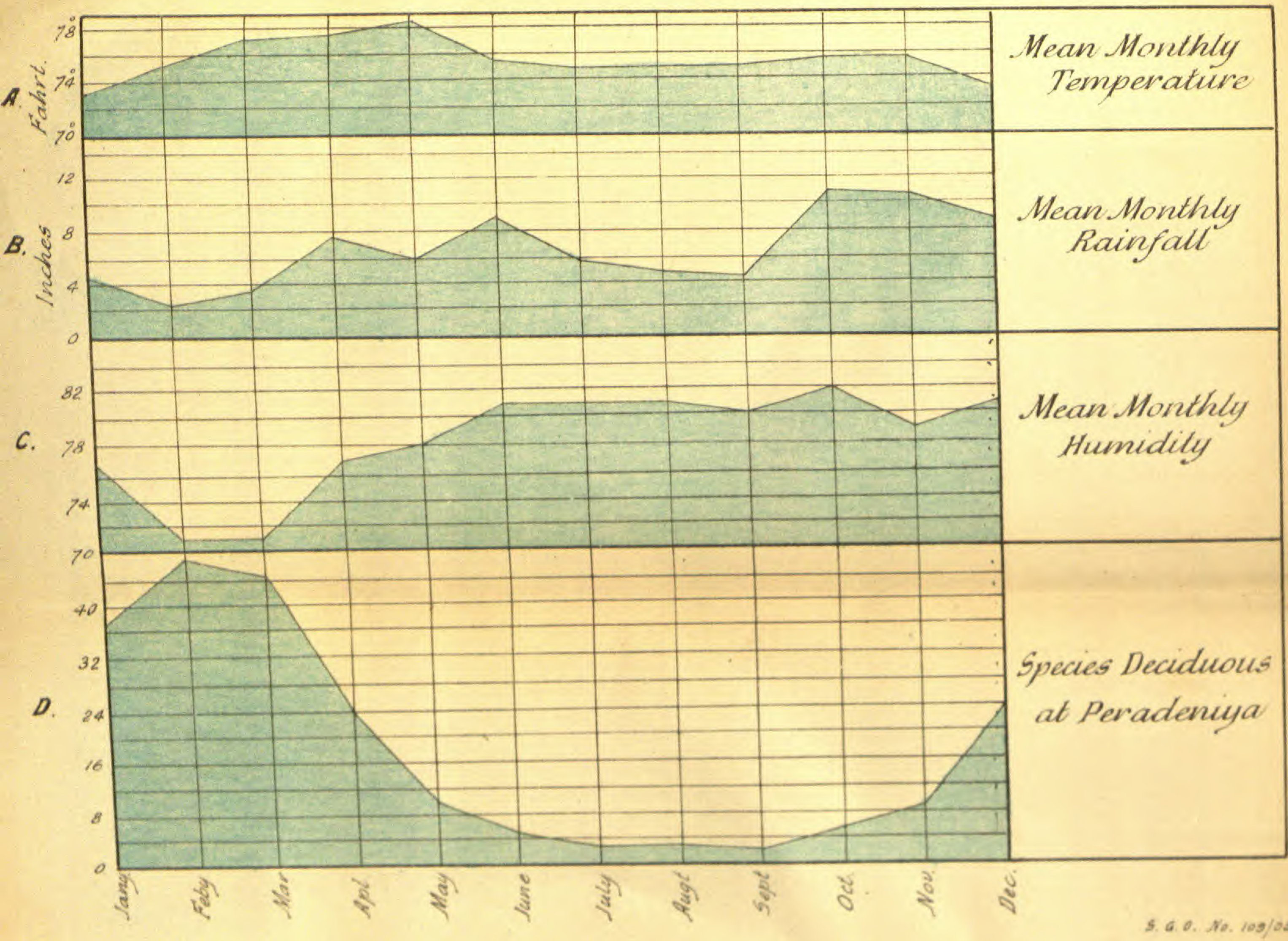
D — Hakgala — 87

E — Kandy (Peradeniya) — 78

Jany. Faby. Mar. April May June July Augt. Sept. Oct. Nov. Dec.

S. G. O. No. 108/05.

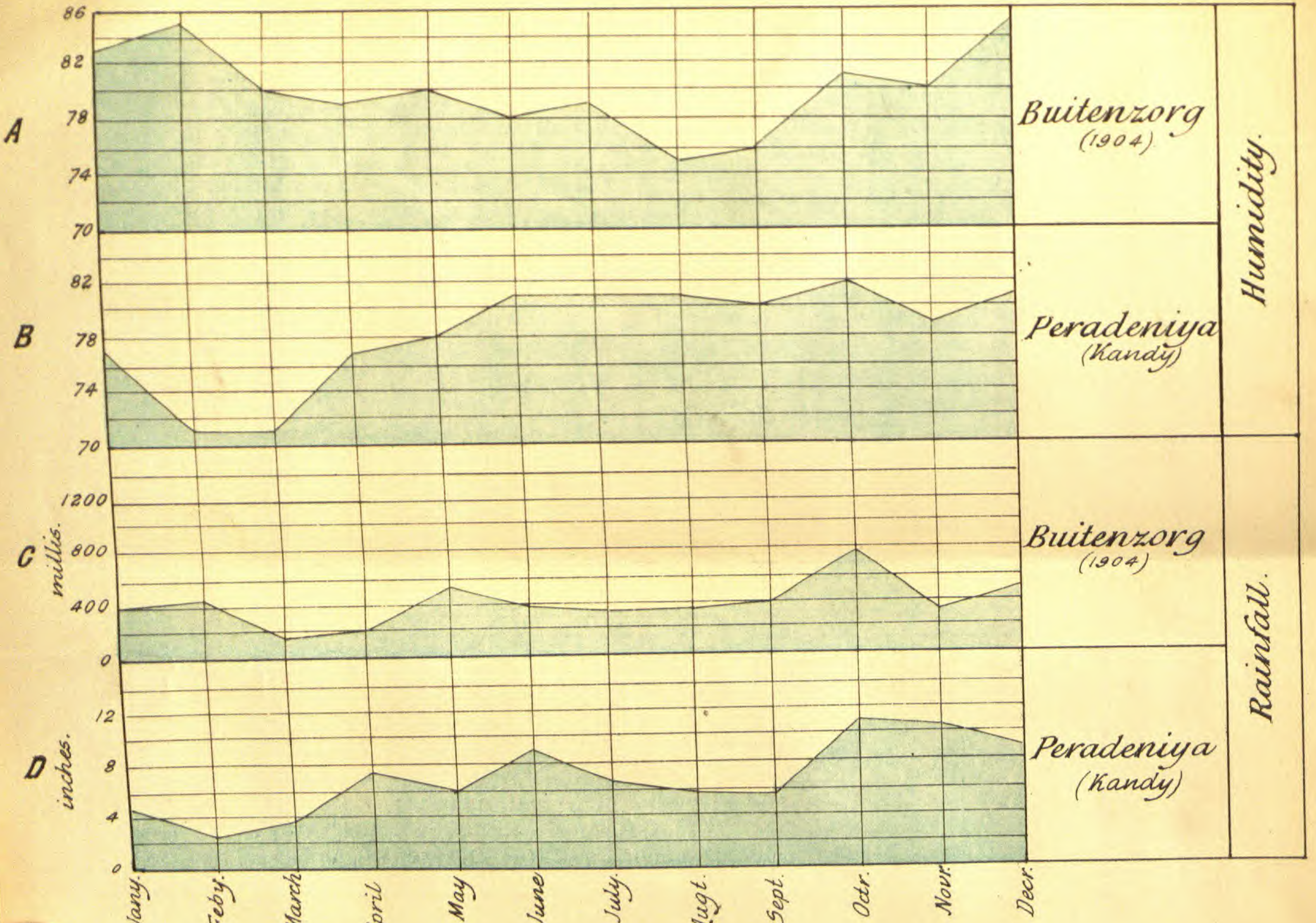
Relation between Humidity Rainfall and Temperature and the Number of Deciduous Species at Peradeniya



S. G. O. No. 109/05.

Humidity and Rainfall.

At Buitenzorg & Peradeniya.



Description of Plates.

Plate XXV.—Map of Ceylon showing the average annual rainfall and temperature in various parts of the Island. The isotherms are in red lines.

Plate XXVI.—Diagrams showing the monthly and yearly average temperatures in Fahrenheit at (E) Kandy (Peradeniya), (D) Hakgala, (C) Colombo, (B) (Badulla), and (A) Mannar.

Plate XXVII.—Diagrams showing the monthly and yearly average rainfall in inches at (E) Kandy (Peradeniya), (D) Hakgala, (C) Colombo, (B) Badulla, (A) Mannar.

Plate XXVIII.—Diagrams showing the monthly and yearly average humidity in degrees at (E) Kandy (Peradeniya), (D) Hakgala, (C) Colombo, (B) Badulla, (A) Mannar.

The data on which the curves on plates XXVI. to XXIX. are constructed have been obtained from the Administration Report of the Surveyor-General for the year ending December, 1902.

Plate XXIX.—Diagrams to show the relation between the monthly humidity, rainfall, and temperature, and the number of species deciduous during each month.

Plate XXX.—Diagrams to show the relative monthly humidity and rainfall at Buitenzorg (Java) and Peradeniya. Curve D. rainfall in inches; curve C. rainfall in millimetres.

8(9)05

REVIEWS.

The Dalbergias of S. E. Asia.

(The species of D. of S. E. Asia, by D. Prain ; Ann. R. B. G., Calcutta, X., Pt. 1, 1904.)

THIS is a splendidly illustrated and admirable monograph of this difficult genus of Leguminosæ. So far as the Ceylon Flora is concerned, our species are unaltered in scope or number, but the names of two are changed from those given in Trimen's Flora to earlier names, viz., D. Championii, Thw., to D. rostrata, Grah. (in Wall. Cat. No. 5,867, 1832), and D. monosperma, Dalz., to D. torta, Grah. (do. No. 5,873). All are figured (Plates 36, 76, 42) in Major Prain's monograph.

D. pseudo-Sissoo Miq. of Java, as suggested by Trimen, proves to be identical with D. rostrata. The distribution of this species should be given as found also in Borneo, Celebes, Java, Malay Peninsula, S. India. D. zeylanica, Roxb., proves as Trimen suggested to be the same as our D. lanceolaria, L. f. Major Prain gives this species, on the authority of a Thwaites's specimen, as "Central Province," whereas Trimen gives "dry low country." Thwaites's specimens are marked C. P. (Ceylon Plants), which, perhaps, explains the slip ; his localities include Deltota in the Central Province.

J. C. W.

A Revision of the Genus Pisonia.

(G. Bargagli-Petrucci : Le specie di Pisonia della Regione del Monsoni ; Lavori eseg. nel R. Orto Bot. di Firenze, Fasc. 1, p. 73, 1901.)

A REVISION of the eastern species. No change is made in the arrangement or name of the Ceylon forms (Trimen, Flora, III., p. 391).

J. C. W.

Localization of Thein in the Tea Plant.

(A. Nestler : Untersuchungen uber das Thein der Theepflanze : Jahresb. D. Vereinig. d. V. d. angewandten Bot. I., 1903, p. 54.)

USING the method described in vol. 1, p. 252, of the Annals, Nestler now shows that the tea plant contains thein in the seed, cotyledons, stem-bark, flower, and leaf. In the leaf it is found in the mesophyll, and possibly in the epidermis.

J. C. W.

Essential Oils.

(Semi-annual Report of Schimmel & Co., Leipzig, April, 1902.)

THE useful half-yearly report of this well-known firm contains as usual much that is of interest to Ceylon. In the introduction mention is made of the growing feeling against the adulteration of essential oils—a practice only too common here, and one which is largely responsible for the depression of our citronella oil industry and the successful competition of Java. Of the Java oil Messrs. Schimmel & Co. remark: "we have obtained extraordinary results.....this product shows clearly what can be obtained by rational, expert cultivation and distillation of the crude material, for the species of plant used in Java is the same as in Ceylon. And yet what a vast difference between these two oils!

"..... it is sincerely hoped that the excellent product may constantly increase in favour.....so that the manufacture may be continued on a large scale." Further interesting details of the chemistry of this oil are given in the report. There is also a valuable account of the chemistry of Ceylon cinnamon oil.

Among other items of interest attention may be drawn to the article on champaca oil, in which it is stated that the oil distilled from the fresh flowers of the sapu, Michelia Champaca, has not been obtainable for years, in spite of a strong demand.

J. C. W.

Violent excretion of Water from the Leaves of certain Aroids.

(Hans Molisch: Hervorspringen von Wassertropfen aus der Blattspitze von Colocasia nymphæfolia (Caladium nymphæfolia Hort) Ber. d. Bot Ges. XXI., 1903, p. 381.)

IN the case of Colocasia antiquorum a rapid excretion of drops of water from the young leaves, with such force as almost to resemble a tiny fountain, was observed by Muntingh as early as 1672. Molisch has closely examined the phenomenon in the case of C. nymphæfolia.

The excretion is most marked in young leaves, blades of which are not yet expanded, and takes place most actively at night, when as many as 163 drops per minute were observed by Molisch to spring from a single leaf tip. The drops of water escape from a special water-pore situated near the apex of the leaf.

R. H. L.

Observation on Growth in the Tropics.

(M. Burgew : Einige Wachsthumsbeobachtungen aus den Tropen. Ber. XXI., 1903, p. 435.)

THIS paper deals with the rates of growth of a species of Costus, of the young shoots of Brownea grandiceps and of Albizzia moluccana—all plants well known to residents in Ceylon. The Costus was observed to excrete large quantities of water by night from the inner surface of the leaf bases, and the evaporation of this water by day left a series of high water marks from which the daily rate of growth of individual internodes could be ascertained. Growth was rapid at night, but very slow by day. The average growth of a whole shoot during fifteen days in November was 5·4 cm. in twenty-four hours.

R. H. L.

Anatomical and Physiological Investigations in the Tropics.

(Anatomisch-physiologische Untersuchungen in den Tropen. Von Dr. Carl Holtermann.)

PROFESSOR Dr. Carl Holtermann worked at Peradeniya from November 29, 1900, to April 27, 1901. The paper under review should be regarded as a preliminary to a more detailed work describing the results of Holtermann's observations on the leaf-fall and transpiration of plants in Ceylon.

After describing the meteorological conditions and general characters of the flora prevailing in wet and dry districts in Ceylon, the author proceeds to dwell on the leaf-fall of tropical trees. He points out that in Ceylon there are no forests, the trees of which completely lose their leaves for a long period, and contrasts this with the forests of Tectona grandis (Teak) which he has seen in Java. He was particularly struck with the fact that with very few exceptions Ceylon possesses evergreen trees. He states that the flora of Ceylon contains, perhaps, 10–15 deciduous trees, and that none of them are endemic to the island; subsequent observations, which appear in this number of the "Annals of Peradeniya," will perhaps lead to a slight modification of this statement, though the impression which Holtermann describes is certainly correct. There are very few deciduous trees in Ceylon, and only a small proportion of the species which are periodically leafless are endemic. In the paper on Foliar Periodicity I intend to show that there are about 770 endemic species in Ceylon, over 280 of which belong to the arborescent class. About 17 of the endemic species and 78 indigenous species are deciduous and undergo a leafless phase for varying periods of time. Holtermann briefly describes the nature of the defoliation or foliar renewal in Tectona grandis, Odina Wodier, Melia dubia,

Bassia longifolia, Ficus Trimeni, Ficus religiosa, Meliosma Arnottiana, Gyrocarpus Jacquini, Schizolobium excelsium, and species of Bombax, Spondias, Cochlospermum, Terminalia, Erythrina, &c. He points out that different species may pass through their leafless phases during the wettest or the driest months. He also makes a few observations on the relation of the annual rings of growth to foliar periodicity.

His observations on the transpiration of plants in Ceylon are of particular interest. He points out that at Peradeniya on ordinary days with a clear sky, evaporation commences after sunrise and remains feeble up to 10 A.M., but from this time it increases, until between 12 and 3 it reaches its maximum and then decreases until sunset, and subsequently dew is formed. Transpiration stops nearly or completely after sunset when saturation point is being approached. Microscopical examination of the plants convinced Holtermann that at Peradeniya during the moist warm period the stomata are closed during the night.

At Peradeniya, from January to March there is a dry north-east wind, and during this period transpiration is greater than at any other time and may even continue all through the night. The evaporation on damp days, when the air is saturated, is very slight or scarcely perceptible. In order to emphasize the great difference between the transpiration during hot dry and wet days, he states that Asplenium Nidus on misty days lost only from 0·00 to 0·21 gram of water per day, but on sunny days it transpired 3·50 grams.

Holtermann worked with various plants. Cymbidium bicolor, a common epiphytic orchid, was selected among others. This plant possesses thick stiff leaves (which are protected by a strong thick cuticle and a layer of cells running under the epidermis on the upper surface of the leaf) and narrow stomata. He proved that the transpiration from one plant of this species was, from the 23rd to the 27th January, both days inclusive, only 0·457 gram, or at the rate of about one gram in ten days. This means approximately one pound of water in thirteen years, a very small quantity indeed. Alstonia scholaris was also experimented with. The leaves of this commonly occurring tree are not xerophytic ; they possess normal stomata and internal tissues and a cuticle of average thickness. One shrub of this plant possessing 100 leaves lost during the 13th and 14th February, when the sky was cloudless and the temperature high, 1·24 grams ; but during the 15th and 16th, when rain was falling, only 0·06 gram of moisture was lost by transpiration.

Discussing the value of these and other observations Holtermann proceeds to state that there is between 12 and 2 o'clock on clear days in the tropics a much greater loss of water by transpiration than in Europe.

There are in the tropics a large number of plants which, though exposed to the full rays of the sun, only lose a small quantity of moisture by transpiration, *e.g.*, Euphorbia antiquorum, Cereus triquetra,

and others. The leaves of these plants are small, and the green stems often carry on the greater part of the work of transpiration and assimilation. The stems of such plants are provided with a thick epidermis and deeply-sunk stomata. On a very hot day and in a very exposed place, Cereus triquetra lost by transpiration from 8 A.M to 6 P.M. 0·01 gram per quadratdecimeter. Holtermann also carried out experiments which proved that the tobacco plant lost twice as much moisture at Jaffna as at Peradeniya, and that the transpiration in the drier districts of north Ceylon is considerably greater than in the moist climate in the south-west of the Island. He also states that though a change of external conditions did not lead to any great difference in the transpiration from Cyanotis zeylanica, yet other plants which had been transplanted into pots transpired more than those cultivated under natural conditions, and showed striking changes in the anatomy of their roots.

H. W.

Periodicity of Growth in Thickness of Stems in the Tropics.

(Zur Periodicitat des Dickenwachsthums in den Tropen, von A. Ursprung, Botan. Zeit., Heft X., 1904.)

THE paper under review is an interesting contribution to our knowledge of the periodicity of plants in tropical areas and the relationship of foliar periodicity to anatomical differentiation. Ursprung regrets the absence of definite information regarding the periodic behaviour of most trees in the tropics, and points out the necessity for such knowledge before the zones of growth in the stem can be interpreted.

In the introduction Ursprung points out that the differences between spring and autumn wood depend upon the periodic formation of certain types of cambial products, and suggests that the relationship of the latter to foliar periodicity requires special consideration.

In discussing the origin of the periodicities of leaf activity he states that a knowledge of the climatic conditions which existed at the time of the origin of the species referred to would be valuable. He traces the foliar periodicity and zone formation in trees growing in uniform climates to internal forces, but allows that where the periodic climatic differences are great the external forces are of vital importance.

A description of the characters of the rings of growth of several trees common in Ceylon is given, and the differences of these when the tree is grown in the relatively equable climate of Buitenzorg and unequal climate prevailing in East Java, are described. Every species dealt with provides material sufficient for a separate paper, but space prevents my giving more than a summary of Ursprung's conclusions.

Tectona Grandis, L.—This species, in Buitenzorg, is never completely leafless, but retains a crown of leaves, though in East Java it passes through a leafless phase. The rings of growth in trees grown in East Java are more complete and distinct than those of trees grown in Buitenzorg. The climatic periodicity in East Java leads to a definite leaf-fall and zoned formation in the xylem. The rings are not necessarily annual, and when not complete are due to local activity of the cambium. The zone formation increases in sharpness in a centrifugal direction, probably on account of the defoliation in the early years being less complete than in the latter years. Observations in Ceylon have shown that certain species do not become defoliated annually until they have attained a certain age, and this may prove to be the case with teak.

Poinciana Regia, Boj.—Trees of this species are never, according to Smith, entirely leafless in Buitenzorg, though they are conspicuously so in East Java, and the rings of growth in trees grown at the latter place are more complete and distinct than those grown in Buitenzorg. I may add that at Peradeniya young trees are completely leafless every year, though old trees are sometimes only partially so.

Eriodendron anfractuosum, D.C.—Trees of this species are leafless at Buitenzorg and East Java, though the rings of growth are more distinct in the latter than the former place. At Peradeniya the trees drop their leaves in the first year.

Albizzia moluccana.—This is practically an evergreen tree with a definite foliar periodicity, and at Buitenzorg and East Java is never leafless, though at the latter place the rings of growth are more conspicuous than at Buitenzorg.

These observations prove—(1) that in Java the effect of a dry period is to make the zone formation in the wood sharper and more complete; (2) that defoliation is not necessarily the only phenomenon, which will lead to the production of zones in the xylem, (3) in the same climate at Buitenzorg the sharpness of the rings of growth varies, and putting them in order, with the sharpest first and weakest last, we have the following: Tectona grandis, Poinciana regia, Eriodendron anfractuosum, Odina gummifera, Melochia indica, and Albizzia moluccana.

H. W.

Manual of the Trees of North America.

By Charles Sprague Sargent. (University Press, Cambridge, 1905.)

This book deals mainly with the characters of temperate zone trees. A map of North America (exclusive of Mexico) showing the regions into which the country is divided according to the prevailing character of the trees, and a glossary of technical terms are given. An analytical key based on the character of the leaves has been made, and the book is well illustrated on almost every page.

H. W.

The Flora of the Ceylon Littoral.

(A. G. Tansley and F. E. Fritsch: New Phytologist, Vol. IV., Nos. 1, 2, and 3, 1905.)

THIS is an account of the coast and mangrove flora of Ceylon by Messrs. Tansley and Fritsch, who recently worked at Peradeniya. The coast flora is divided into the Pes-capræ-Formation which extends to a few feet of high tide mark, and the Barringtonia-Formation or Beach Jungle, the characteristic plants in these sections being figured and described. The photographs of mangrove plants, Bruguiera gymnorhiza, Rhizophora conjugata, Sonneratia acida, Chrysodium (Acrostichum) aureum, and others are given, as well as accounts of the vegetation of the river at Matara and Balapitiya.

H. W.

Morphology of Angiosperms (Morphology of Spermatophytes, Part II.).

By John Merle Coulter and Charles Joseph Chamberlain.

(London, 1904.)

THIS work is issued in the form of a book of nearly 350 pages, profusely illustrated. It deals with the general classification of the Angiosperms, geographic distribution, fossil forms, phylogeny, and comparative anatomy of this group. Separate chapters are devoted to fertilization, the endosperm, and the embryo; and the information given should be useful to students of flowering plants.

H. W.

The Comparative Anatomy and Phylogeny of the Coniferales, Part II., Abietineæ.

By Edward C. Jeffrey.

(Boston, January, 1905.)

A CONSIDERABLE amount of attention has been given to the resin canals in the different genera and the transfusion tissue. The Abietineæ should, according to the author, be regarded as a very ancient order of the Coniferales, and may even be the oldest living representatives of this group. The occurrence of resin ducts in the woody tissues and the cortex is regarded as primitive for the group. The group is divided into—(1) the Pineæ (Pinus, Picea, Larix, Pseudotsuga) and (2) the Abieteæ (Abies, Pseudolarix, Cedrus, Tsuga).

H. W.

On the Anatomy of the Roots of Palms.

By E. Drabble, D.Sc.

(Trans. Linn. Soc., II. Series, vol. VI., 1904.)

This paper deals with the internal characters of over sixty species of palms. The roots of more than seventy species were sent from Peradeniya to Dr. Drabble, and the work before us presents many new ideas, and is a comprehensive treatise on the anatomy of the roots of an interesting group of plants. Many of the species examined can be seen in the living state in the Gardens at Peradeniya.

H. W.

Publications.

The following publications have been issued since the last volume of the Annals :—

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15 }
16 }
17 } ... Administration Reports for 1903.
18 }
19 }

20 ... A Report on some Ceylon Timbers ... H. Wright
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25 ... Castor Oil Plant in Ceylon ... H. Wright
26 ... Plant Breeding (Part 2) ... R. H. Lock
27 ... Plant Breeding (Part 3) ... R. H. Lock
28 ... Branch Canker in Tea ... J. B. Carruthers
29 ... Canker (Nectria) of Para Rubber ... J. B. Carruthers

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1 ... Notes on Dioscoreas (Yams) ... H. F. Macmillan
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4 ... Climbers ... ... H. F. Macmillan
5 ... Zea Mays in Ceylon ... ... H. Wright
6 ... Para Rubber in Ceylon ... H. Wright and A. Bruce

7, 8, 9, 10, and 11, Administration Report, Royal Botanic Gardens, 1904.

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