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ANNALS

OF THE

ROYAL BOTANIC GARDENS,

PERADENIYA.

EDITED BY

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

DIRECTOR.

CONTENTS.

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Plates I. to V. will be issued later; they have not yet arrived owing to delays in France.

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, diœcious ; 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.

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* 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 margins are 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, diœcious, 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, diœcious, polygamous, and occasionally monœcious, 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 monœcious 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, Hiniduma, Hantane, Deltota, Matale, Kandy, Hewesse, Dambalagala, Pindeniya, Gangaruwa, Kadugannawa, 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 and along 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 1½ 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, diœcious ; 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, subglabrous 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 intersegmental 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, diœcious 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, diœcious ; 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 diœcious 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, diœcious 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, diœcious (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, diœcious, monœcious, 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 undersurface, 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 monœcious 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 undersurface, 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 membraneous, 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 corolla 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, diœcious, monœcious, 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, diœcious ; 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, diœcious 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 carpellary 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, (6½ 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, Kantalai, 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.**

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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.

Plate 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 ½); (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, ½ 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) monœcious 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.)

CONTENTS.

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.

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* *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.

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[*] 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

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* 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 13½ 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 until the 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.*

Inter-node.	*a.*	*b.*	*c.*	*d.*	Inter-node.	*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.

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* 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

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* 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 afternoon
	17	89	**2899**	143	132	76	—	Sunny
	18	95	—	157	167	75·5	3·0	Rain in afternoon
	19	95	—	157	167	75·5	4·5	Rain in afternoon
	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 afternoon
	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.

Inter-node.	Length. mm.	Differ-ence.	Inter-node.	Length. mm.	Differ-ence.	Internode.	Length. mm.	Differ-ence.
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.

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* 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.	Growth in mm. 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

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* 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

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* 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

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* *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.

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[*] 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

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* 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

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* *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

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* 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.

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[*] 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

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* 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

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* *Loc. cit.* p. 45.

† *Loc. cit.*, p. 14.

‡ Anzeiger d. Akad. d. Wissenschaften in Krakau, 1890, p. 292.

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

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[*] *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 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 with the different manner in which the pollination takes place in these two plants.

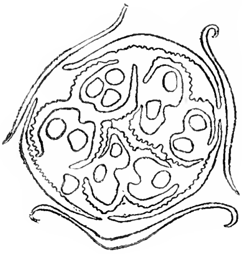

Fig. 1.—Transverse section of a male flower (15×1).

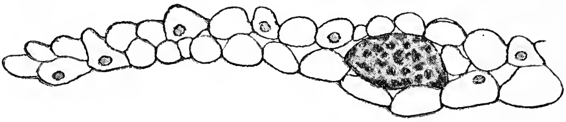

Fig. 2.—Transverse section of a male sepal with a tannin cell (225×1).

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

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* 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 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 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

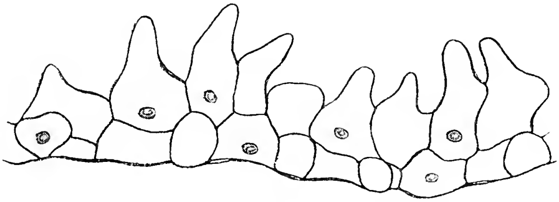

Fig. 3.—Transverse section of a male petal with papillæ (225×1).

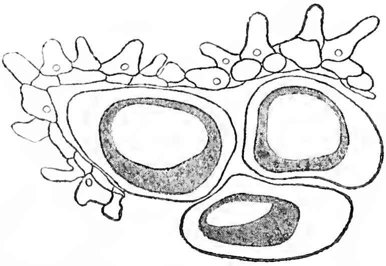

Fig. 4.—Transverse section of a microsporangium in an anther with a tetrad (112×1).

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

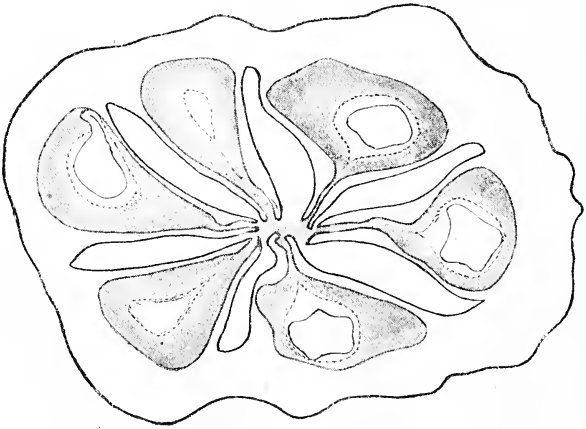

Fig. 5.—Transverse section of a young ovary; the ovules enclosed in mucilage and the placentæ split into air-chambers (15 × 1).

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 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 is drawn down by the spiral rolling up of the pedicel, the air-chambers between the split placentæ disappear.

Fig. 6.—Transverse section of a fruit with embryos. Nearly all mucilage gone and the air-chambers pressed together (15 × 1).

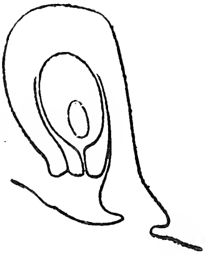

Fig. 7.—Ovule (35 × 1).

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 Ascherson 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 ½ 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.

Botanical Institute,
University of Upsala (Sweden), April, 1904.

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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. }
,, 5. } ♂—flowers (3·5 × 1).
,, 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.

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I.—INTRODUCTORY: THE WORK OF MENDEL AND AN ACCOUNT OF RECENT PROGRESS ON THE SAME LINES; WITH SOME NEW ILLUSTRATIONS.

CONTENTS.

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

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* 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 (extracted dominant)	Aa aA (heterozygotes, but looking like AA : on self-fertilization they each give)			aa (extracted recessive)
F_3	AA	AA (extracted dominant)	Aa aA	aa (extracted recessive)	aa
F_4	AA and so on breeding true	AA and so on breeding true	and so on	aa and so on breeding true	aa and so on 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 $A + 2Aa + a$, 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).

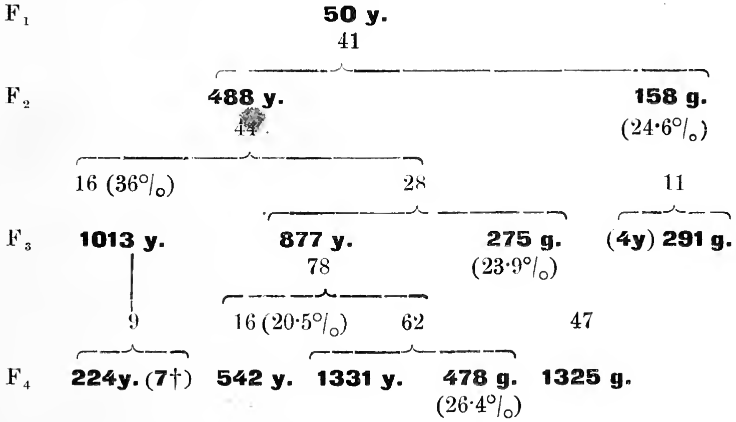
Sixteen plants from yellow seeds gave rise to 542 yellow seeds only.

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

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* 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:—

$$\left.\begin{array}{l}4\ \text{A}\\ 8\ \text{Aa}\\ 4\ \text{a}\end{array}\right\}\text{combined with}\left\{\begin{array}{l}1\ \text{B}+2\ \text{Bb}+1\ \text{b}.\\ 2\ \text{B}+4\ \text{Bb}+2\ \text{b}.\\ 1\ \text{B}+2\ \text{Bb}+1\ \text{b}.\end{array}\right.$$

or

$$\begin{array}{c}\text{AB}+2\text{ABb}+\text{Ab}.\\ 2\text{AaB}+4\text{AaBb}+2\text{Aab}.\\ \text{aB}+2\text{aBb}+\text{ab}.\end{array}$$

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

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* 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.

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* 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

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* 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

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* *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

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* 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

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* 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.

dimpled

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 dihybrid case the agreement is clear; thus:

$$\begin{array}{ccccccc} 9 & : & 3 & : & 3 & : & 1 \\ 9 & : & 3 & : & & 4 & \end{array}$$

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).

$$\mathrm{AB} \times \mathrm{ab} \qquad \text{gives—}$$

$$\mathrm{F_1} \qquad \mathrm{ABab}$$

(Gametes: AB; Ab; aB; ab.)

$$\mathrm{F_2} \qquad \begin{array}{r} \mathrm{AB} + 2\mathrm{ABa} + \\ 2\mathrm{ABb} + 4\mathrm{ABab} + \\ \mathrm{Ab} + 2\mathrm{Aab} + \end{array} \boxed{\begin{array}{l} \mathrm{Ba} \\ 2\mathrm{Bab} \\ \mathrm{ab} \end{array}}$$

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.)

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* 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";

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* *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

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* 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
IV.—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

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* 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.*

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* 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

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* 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
AN CN ... black
AG AJ
AG AN
AN AJ
AN AN } albinos
CJ AG
CJ AN } yellow
} 4 albinos
2 yellow
1 black
1 gray

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: $(A_1 + 2\,A_1a + a)\,(A_2 + 2A_2a + a)$, or :

$$\begin{array}{lll} 1\,A_1\,A_2 & 2\,A_1a\,A_2 & 1\,A_2a \\ 2\,A_1\,A_2a & 4\,A_1a\,A_2a & 2\,A_2aa \\ 1\,A_1a & 2\,A_1aa & 1\,aa \end{array}$$

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 :—

$$\begin{array}{ccccc} FD & + & 2\,FDFW' & + & FW' \\ 2\,FDWD & + & 4\,FDWW' & + & 2\,FW'\,WW' \\ WD & + & 2\,WDWW' & + & WW'. \end{array}$$

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 diœcious 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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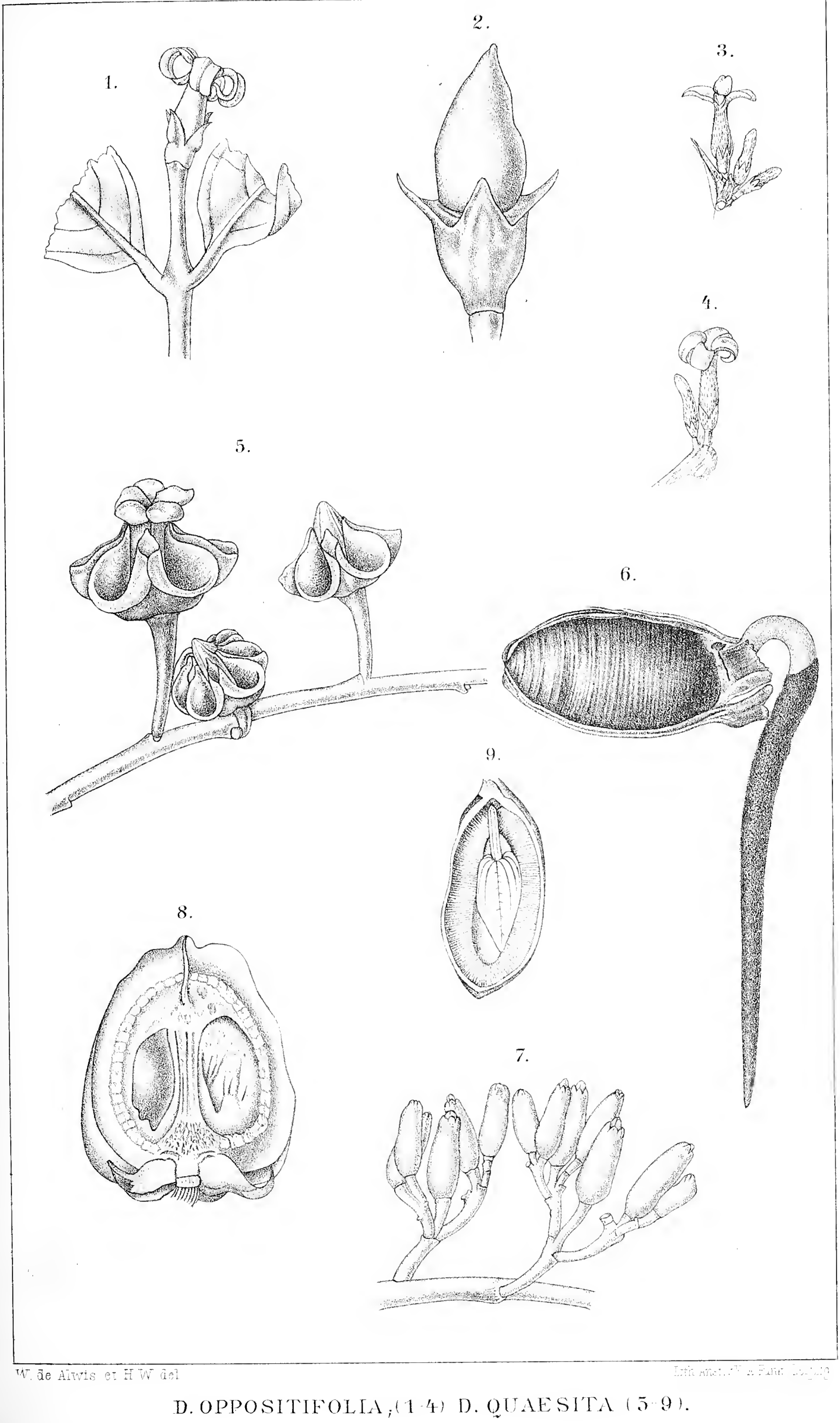
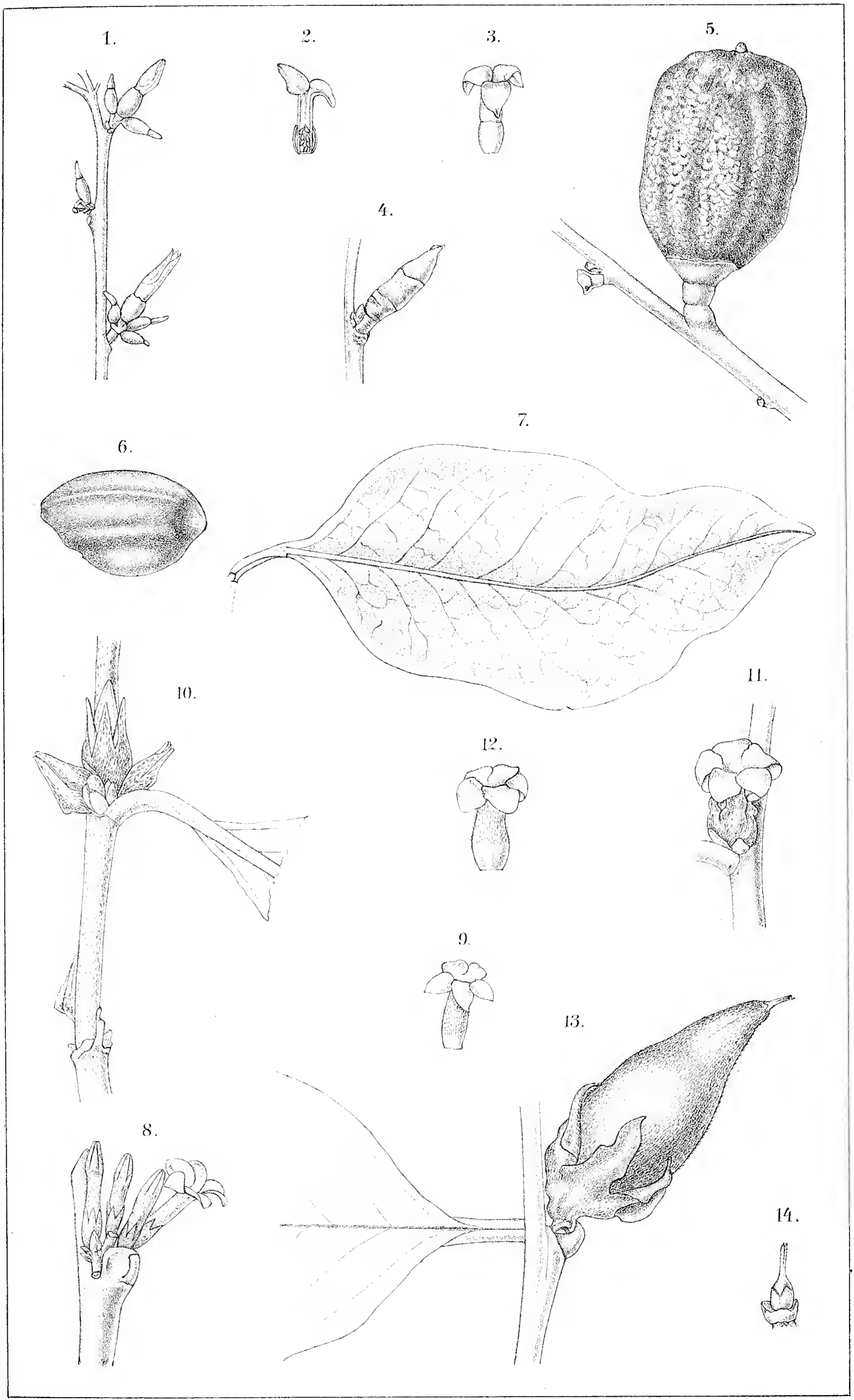


W. de Alwis et H W del
Lith. Anst. v. E. A. Funke Leipzig

D. OPPOSITIFOLIA, (1-4) D. QUAESITA (5-9).



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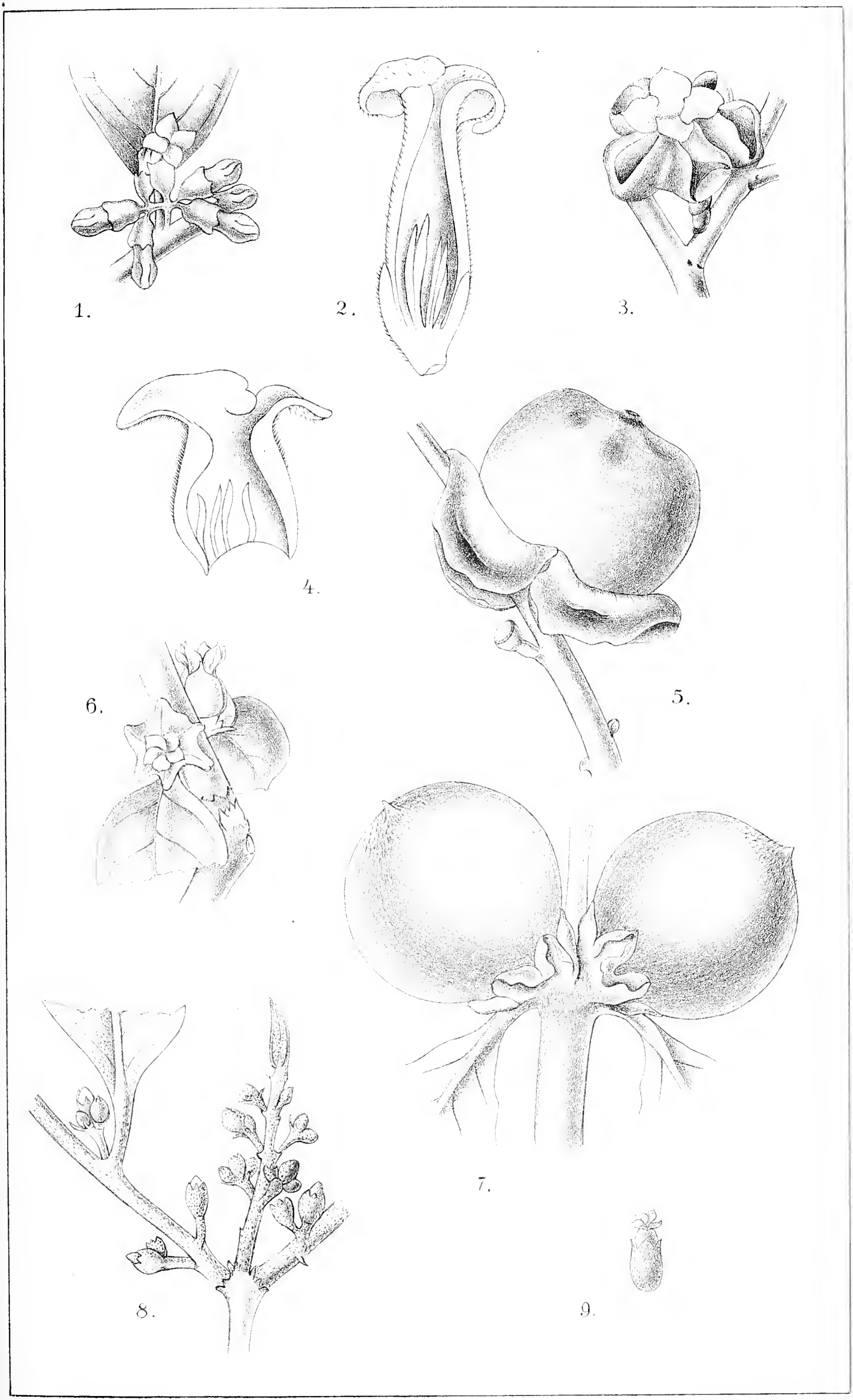
Lith. Anst. v. E. A. Funke, Leipzig

D. OOCARPA (1-7); D. ACUTA (8-14).



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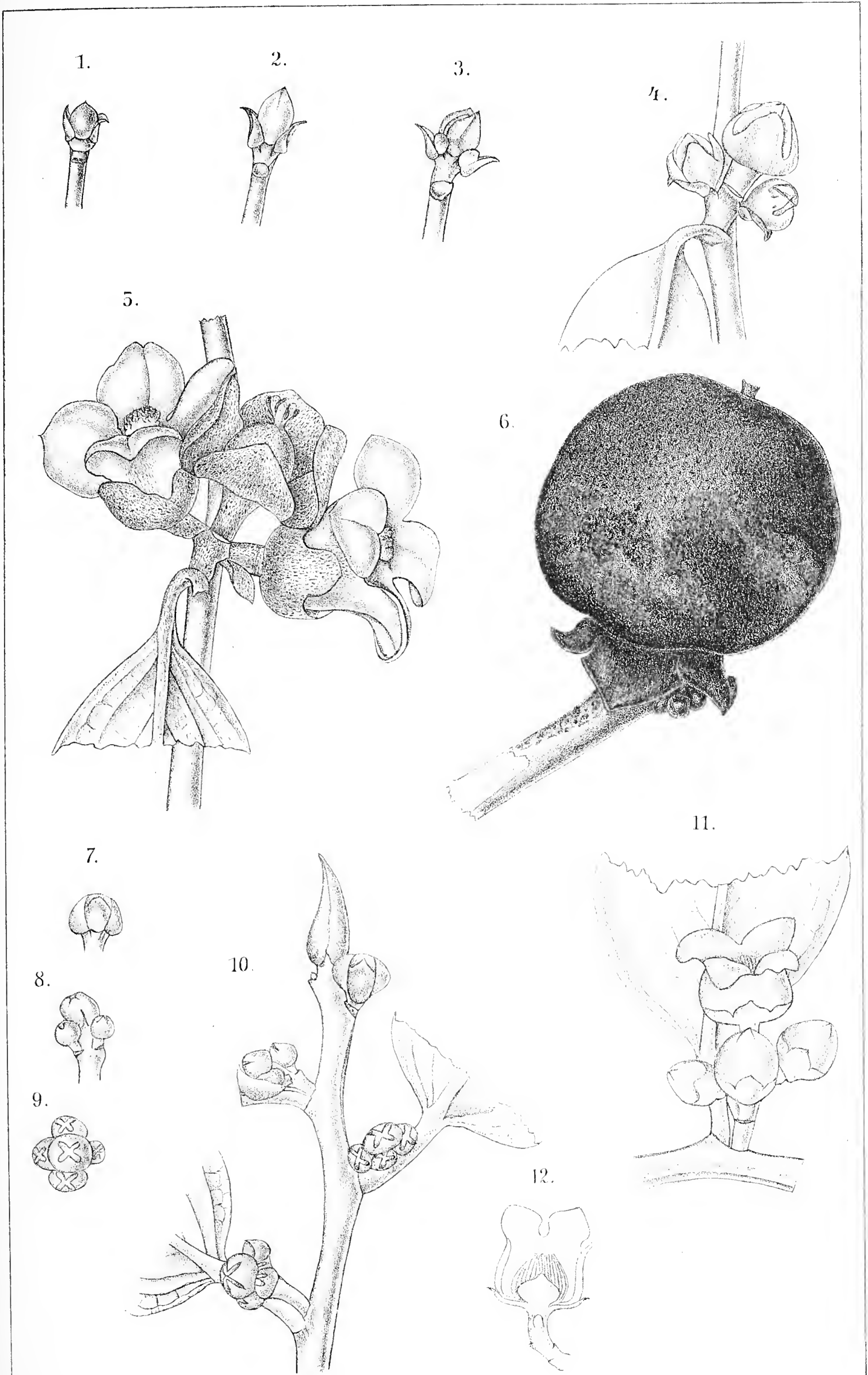
D. CRUMENATA (1-5), D. MELANOXYLON (6-9).



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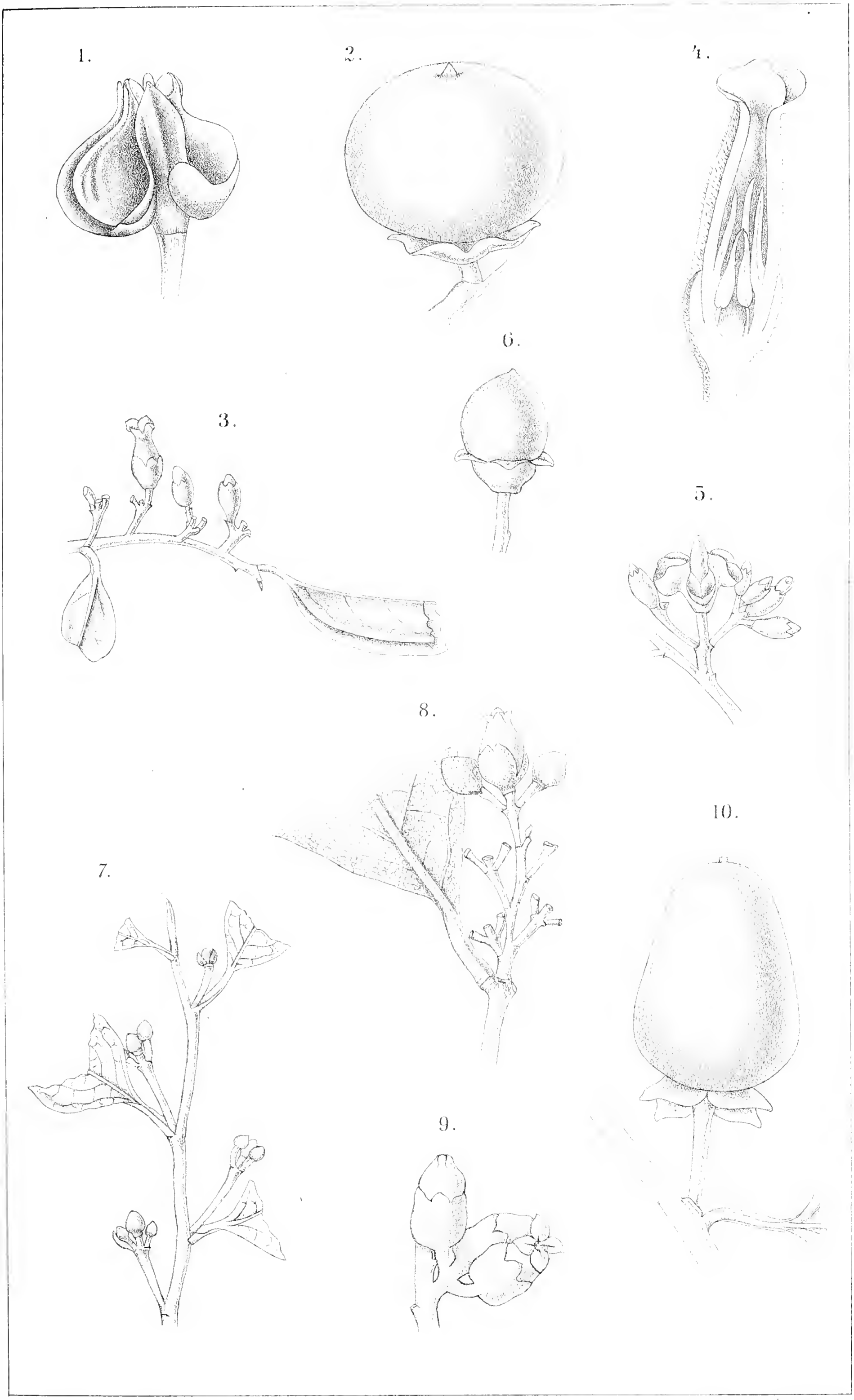
Lith Anst. v E. A. Funke, Leipzig

D. EMBRYOPTERIS (1–12).



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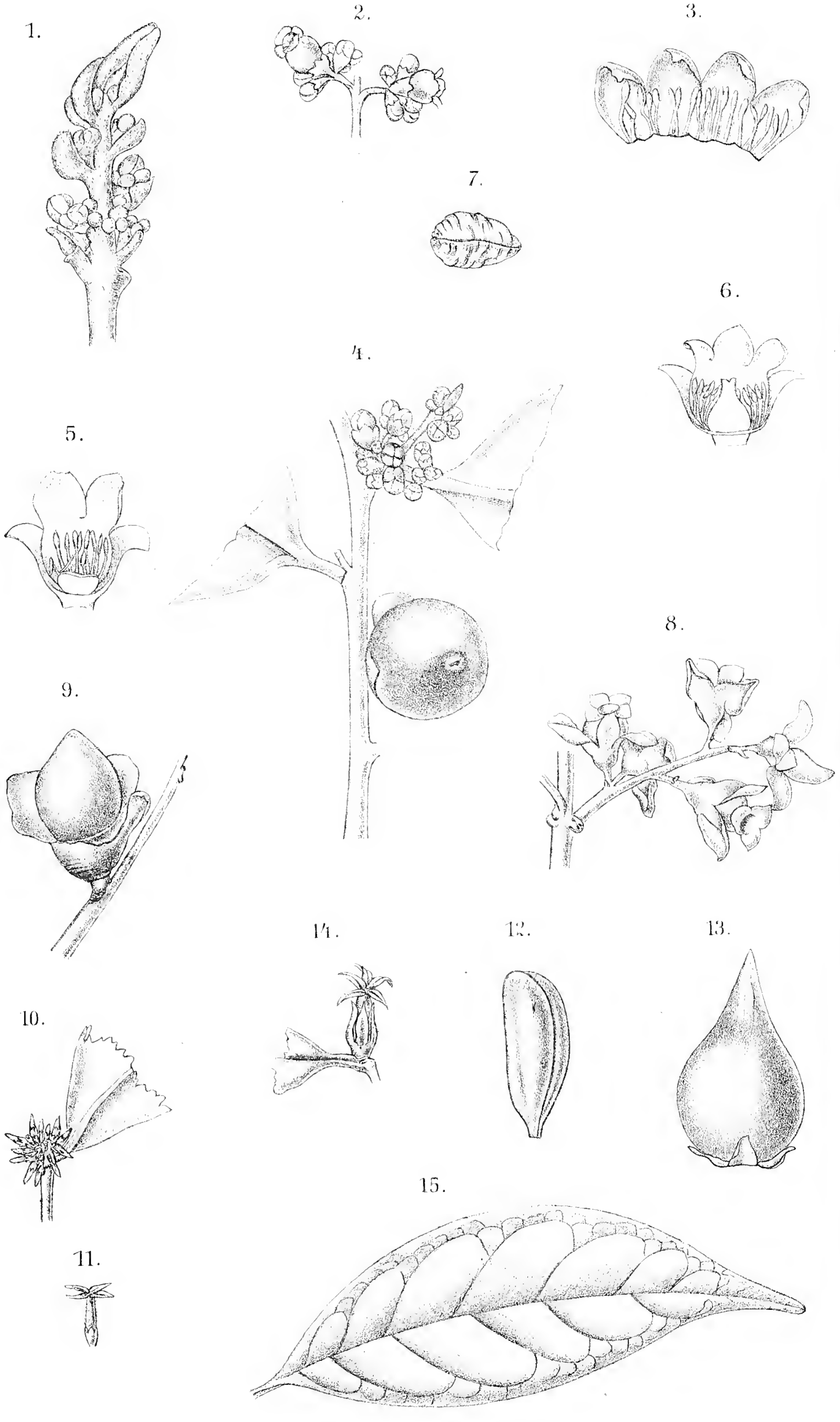
D. AFFINIS (1-6); D. TOPOSIA (7-10).



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Lith. Anst. v E. A. Funke, Leipzig

D. SYLVATICA (1-9); D. ATTENUATA (10-15).

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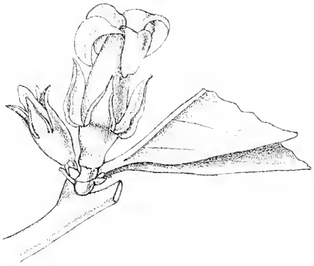

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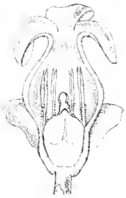

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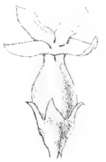

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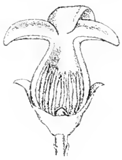

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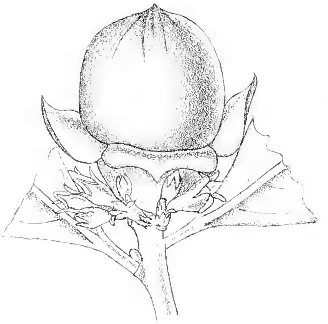

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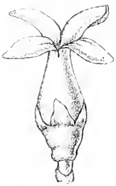

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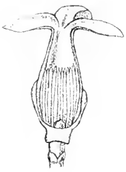

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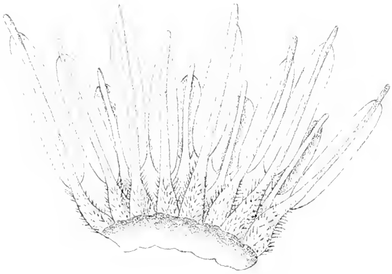

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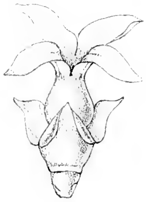

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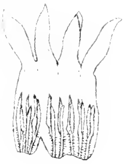

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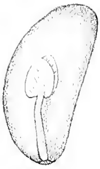

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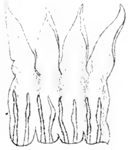
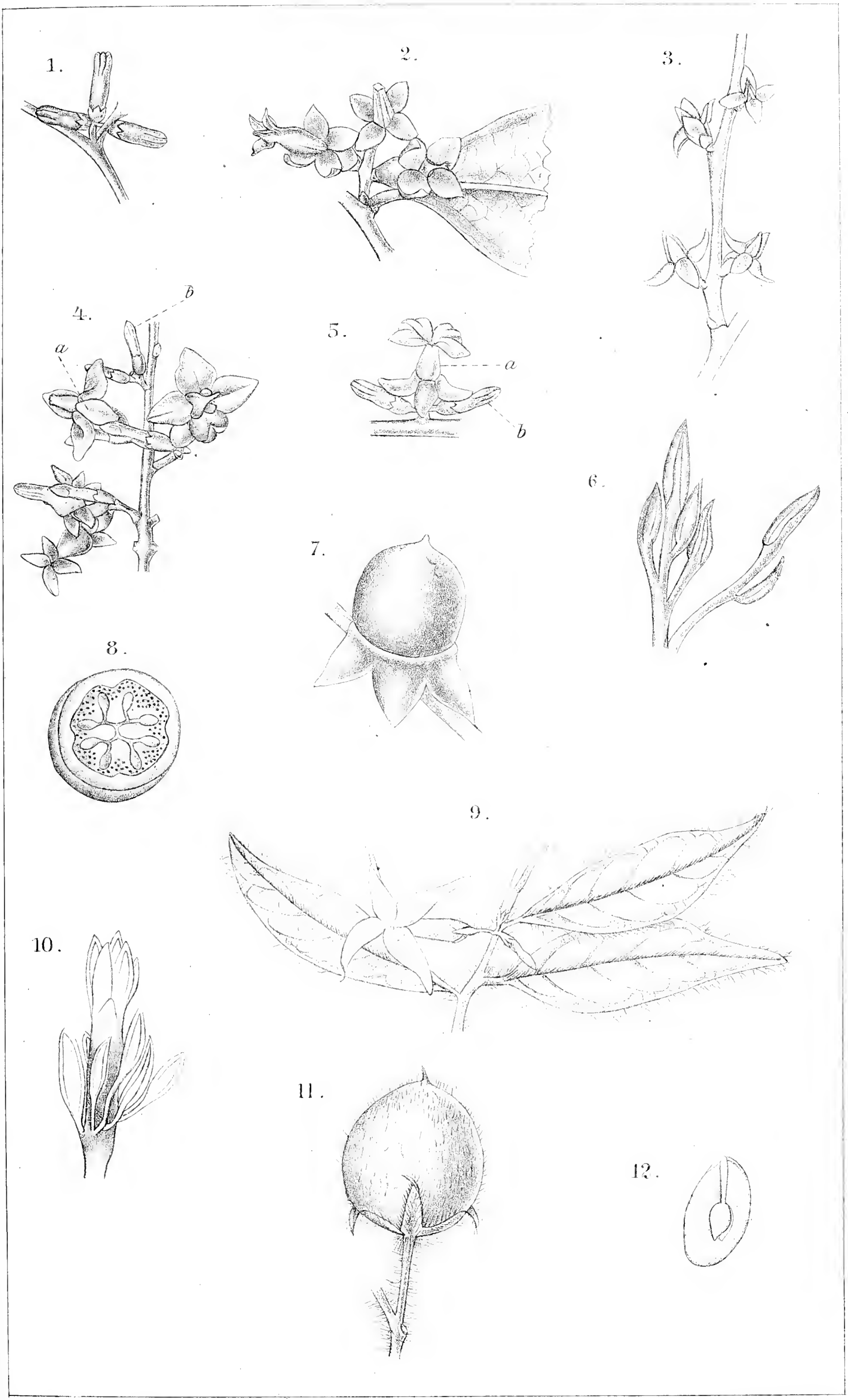


W. de Alwis et H.W. del. Lith. Anst. v E. A. Funke Leipzig

D. GARDNERI.



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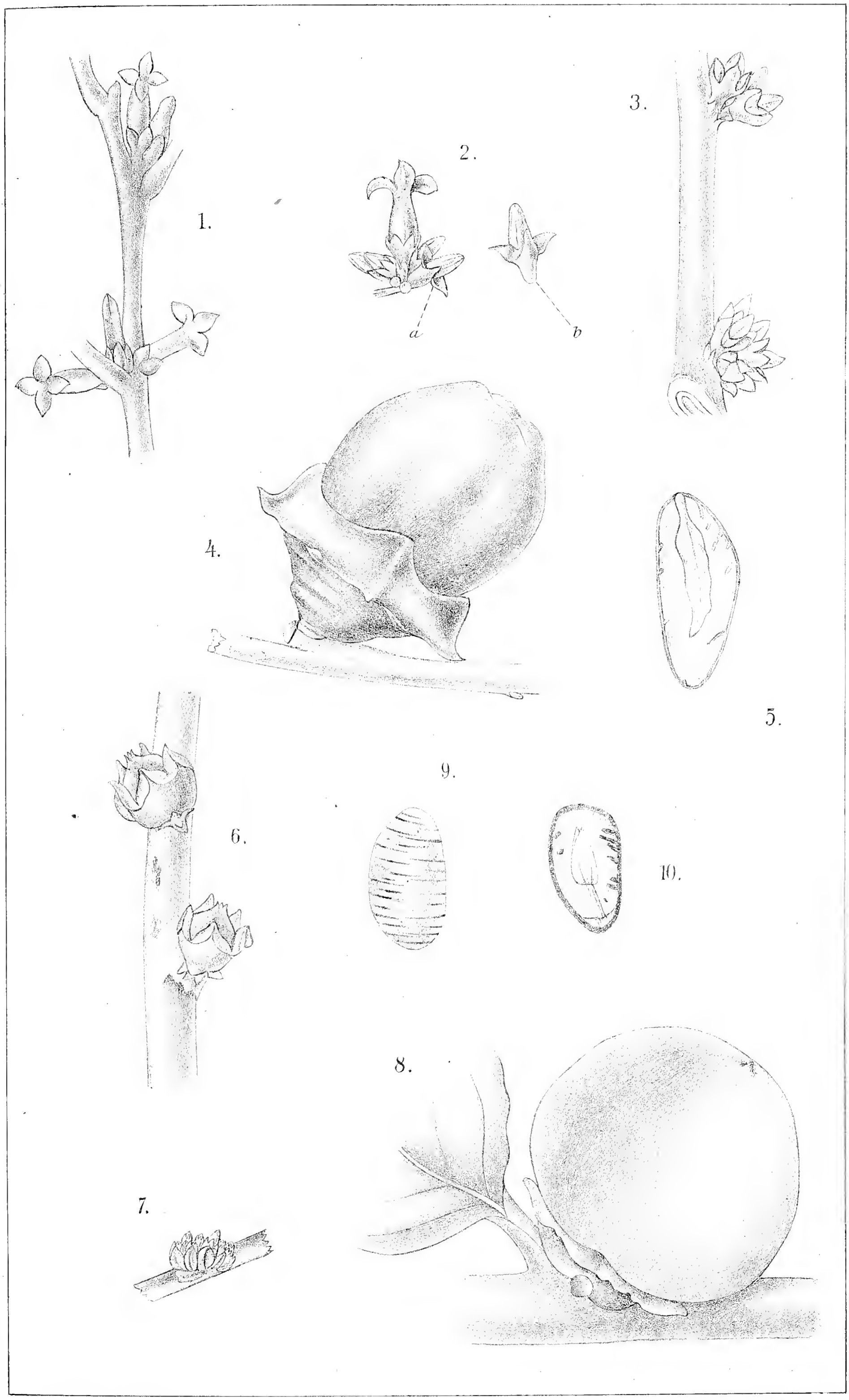
Lith Anst. v E. A. Funke Leipzig

D. EBENUM. (1-8), D. PRURIENS (9-12).



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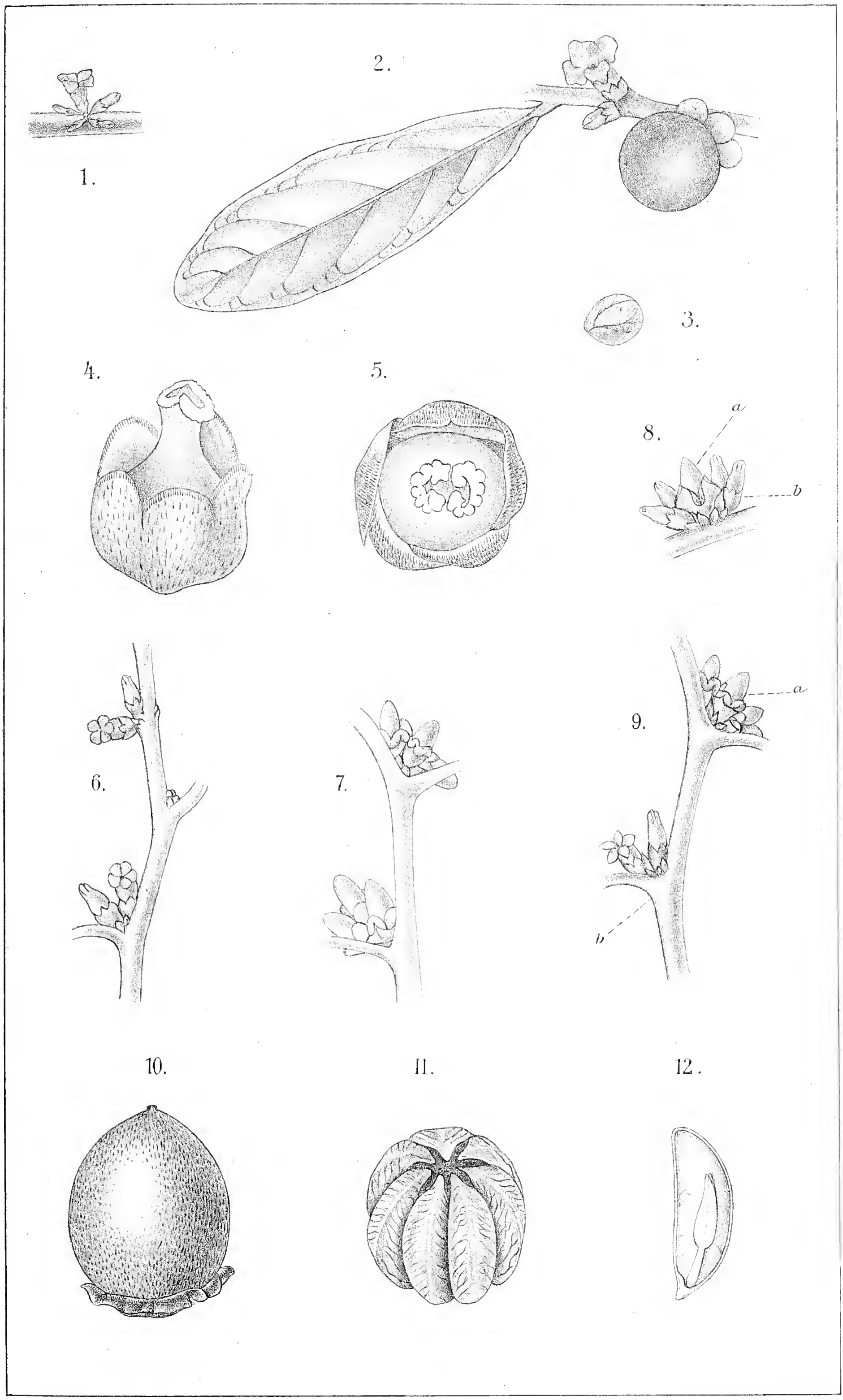
D. INSIGNIS (1-5). . D. MOONII (6-10).



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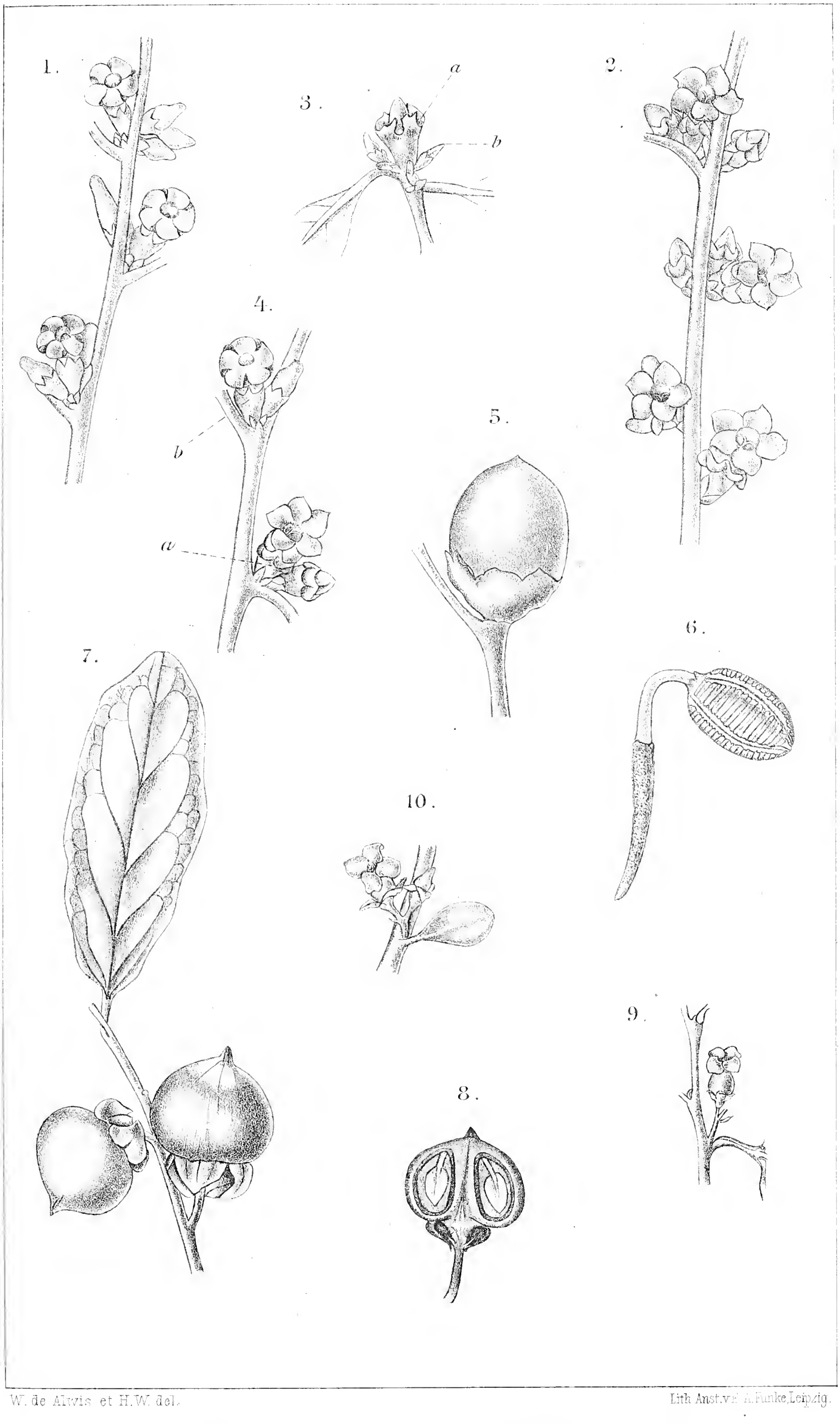
Lith Anst. v E. A. Funke Leipzig

D. OVALIFOLIA (1-5). D. HIRSUTA (6-12).



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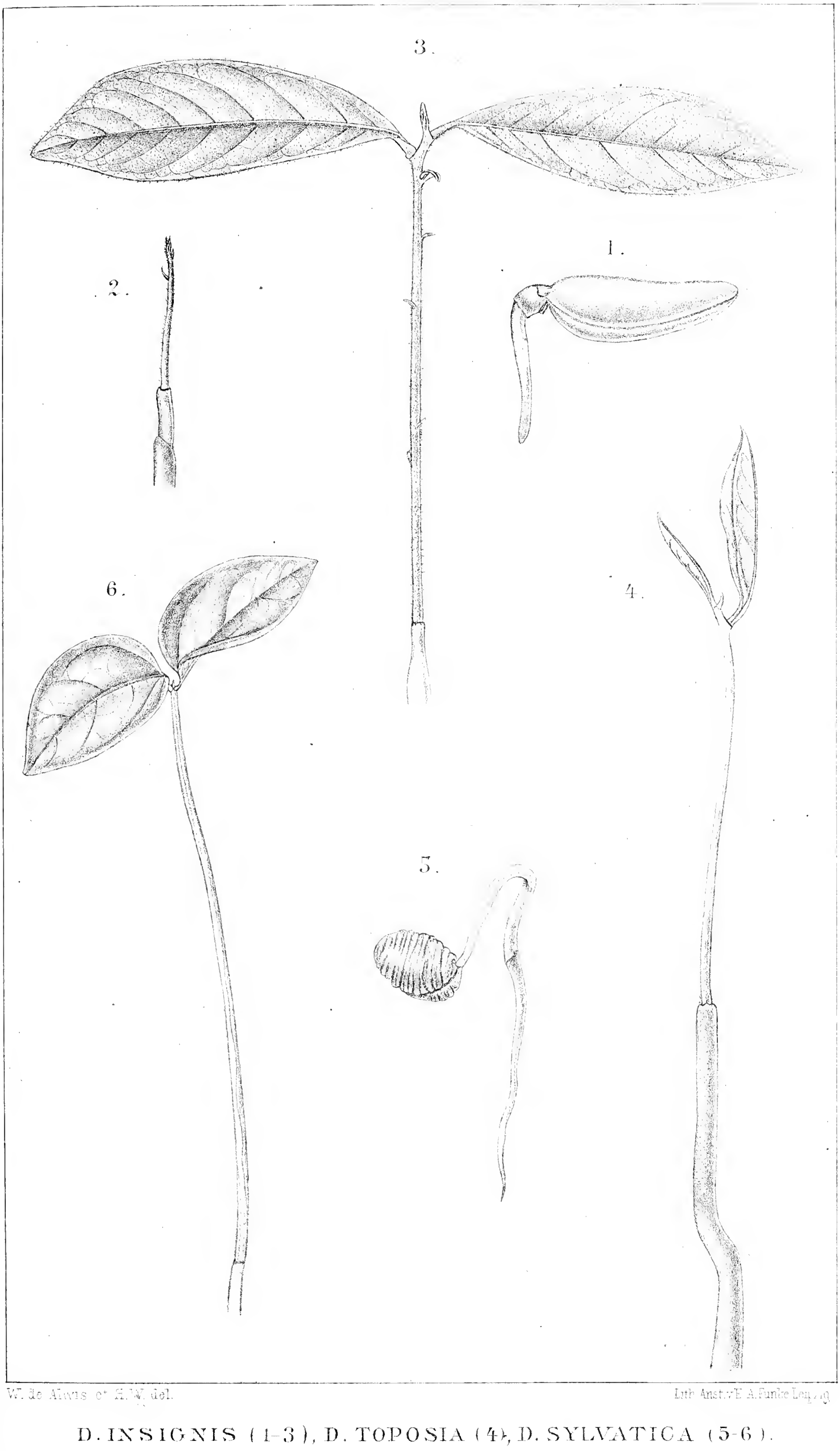
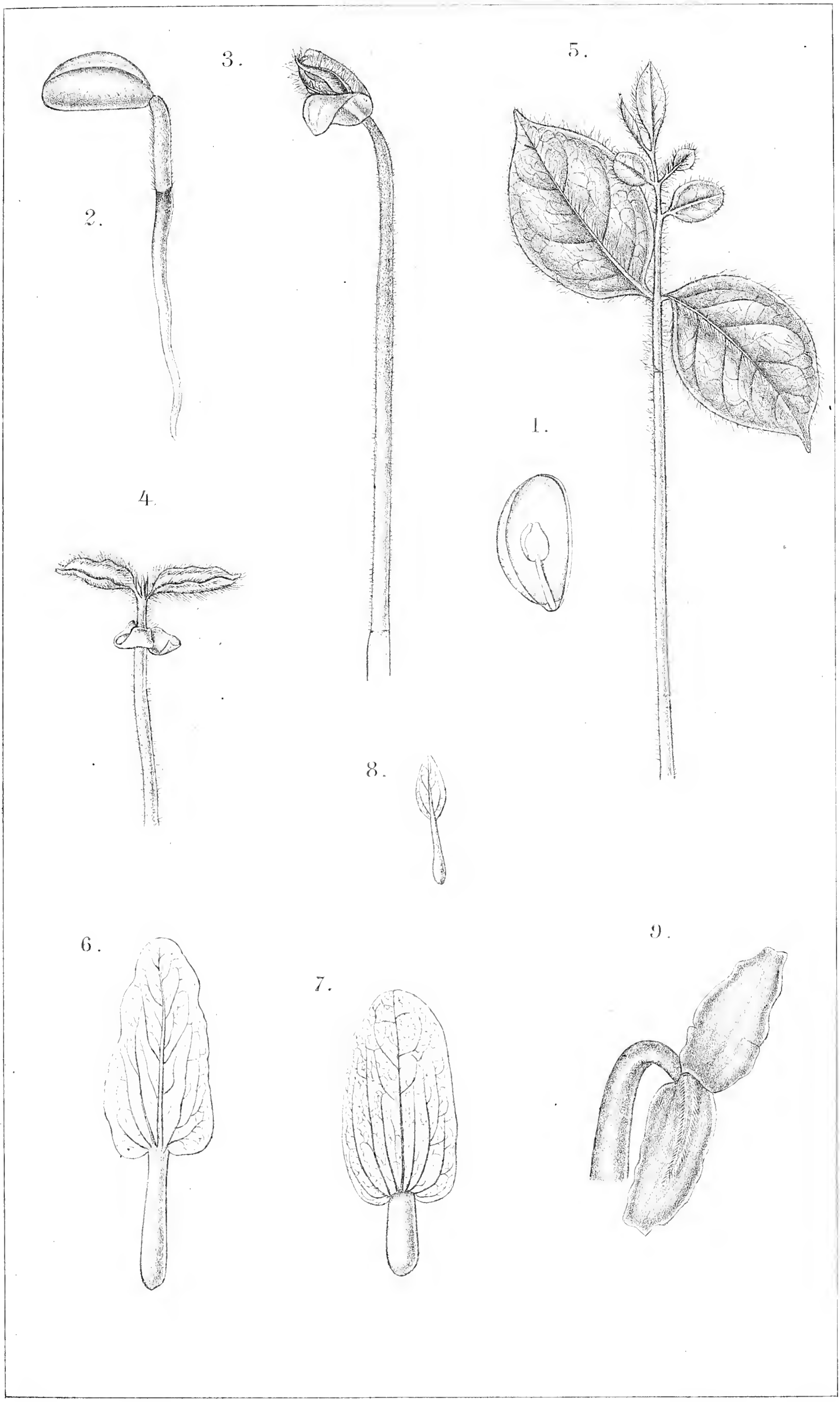
D. THWAITESII (1-6), D. MONTANA (7-10).



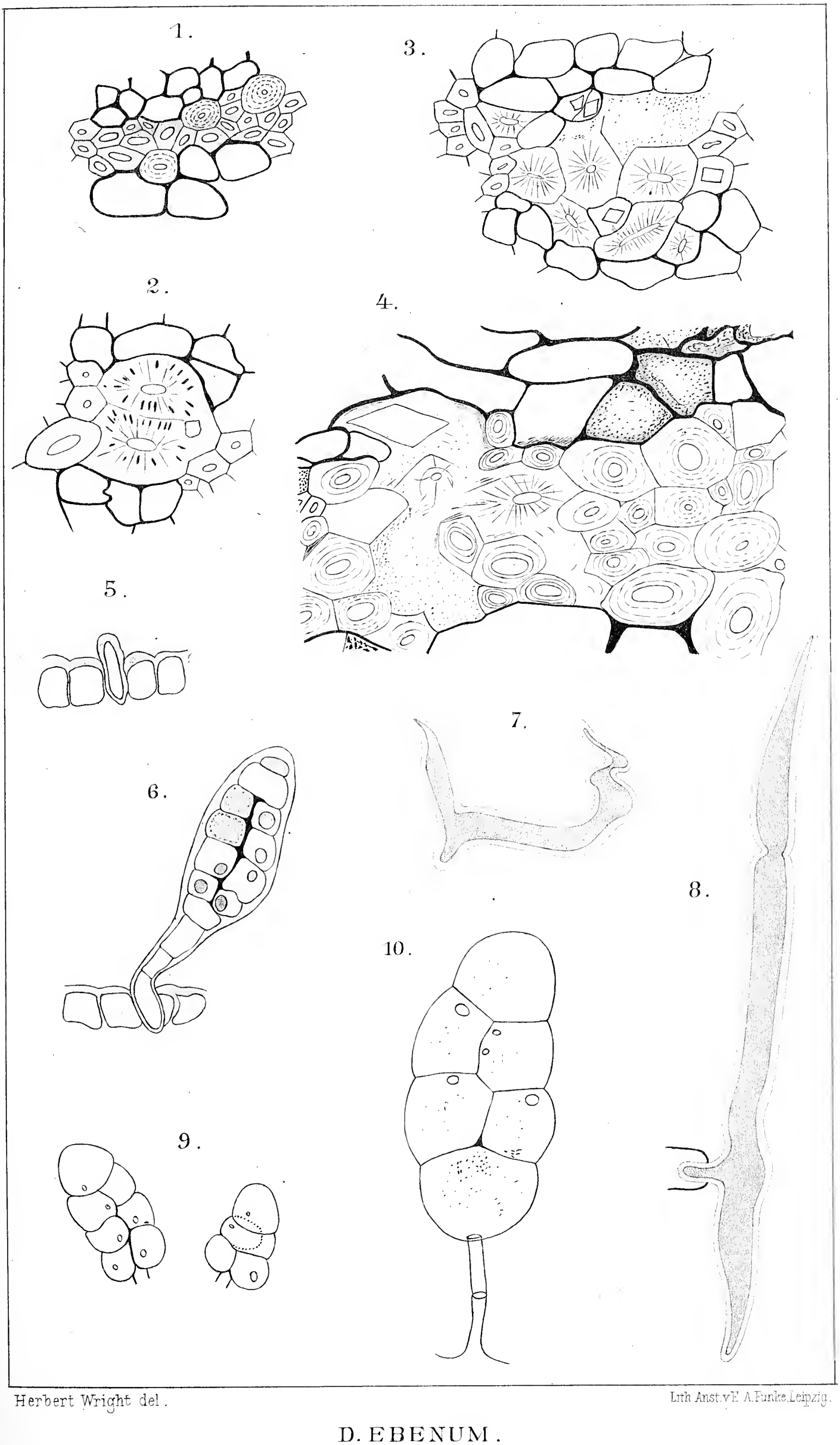
W. de Alwis et H. W. del. Lith. Anst. v. E. A. Funke Leipzig.

D. INSIGNIS (1-3), D. TOPOSIA (4), D. SYLVATICA (5-6).



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).



Herbert Wright del.
Lith Anst. v F. A. Funke, Leipzig.

D. EBENUM.

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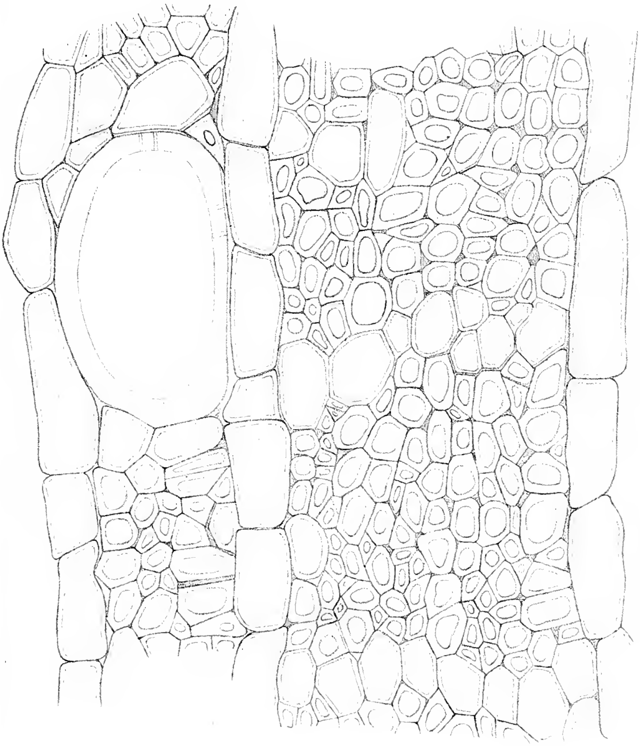

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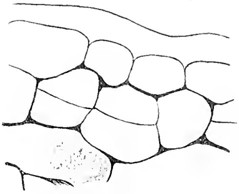

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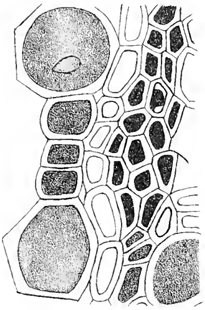

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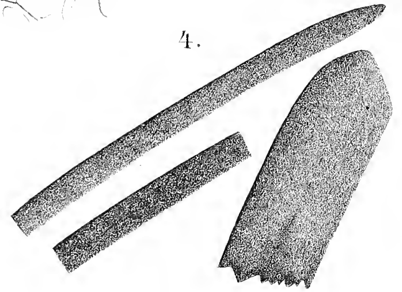

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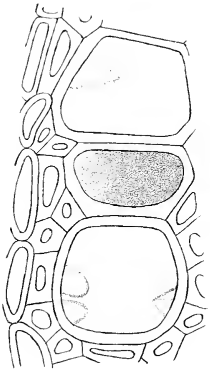

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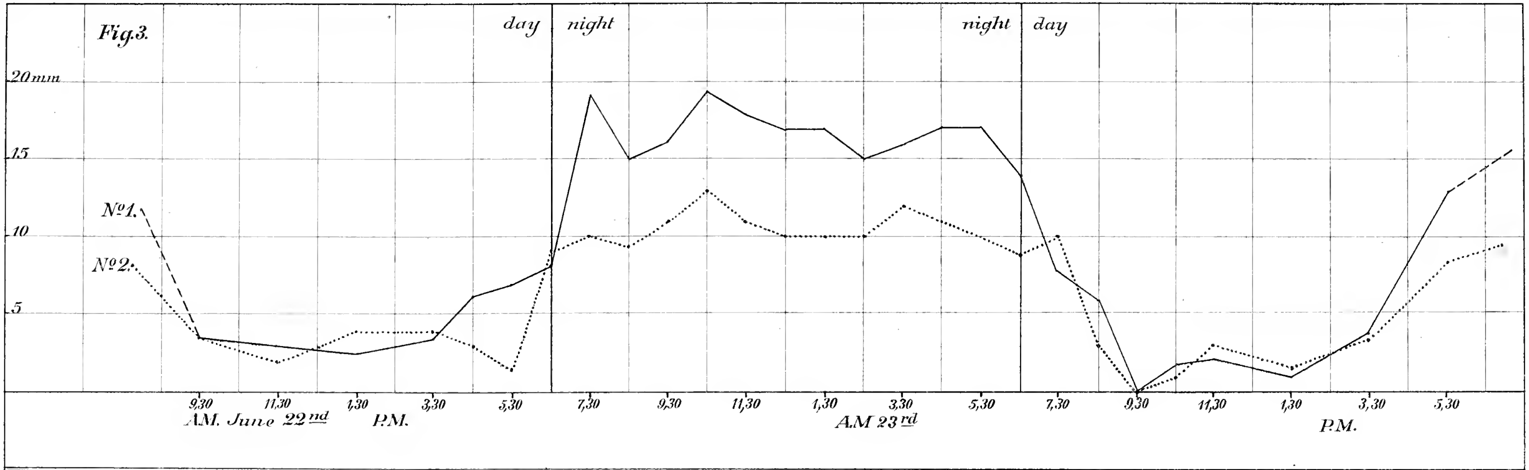
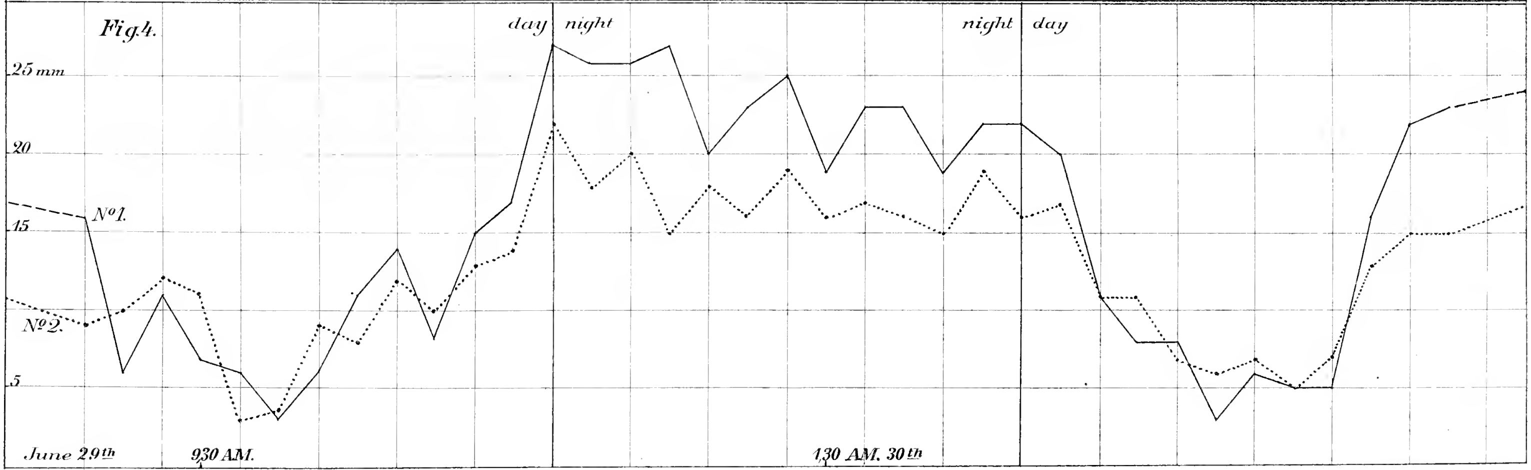
Herbert Wright del.

Lith Anst. v E. A. Funke, Leipzig.

D. EBENUM.





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Lith. Anst. v. F. A. Funke, Leipzig.

DENDROCALAMUS

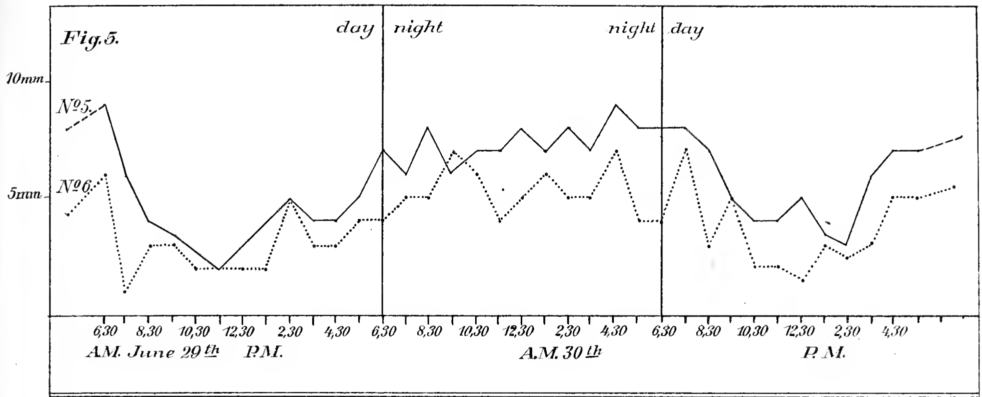


Fig. 5.

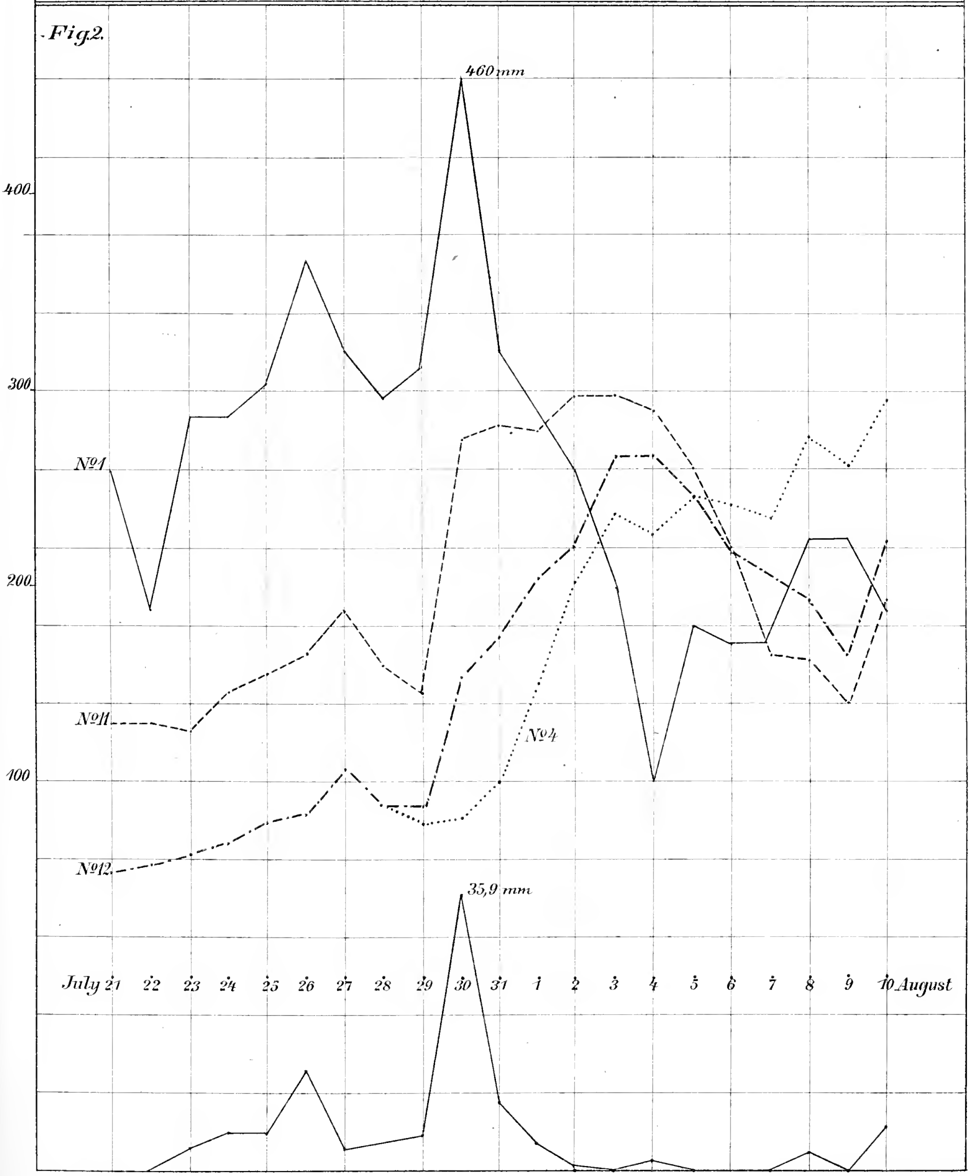


Fig. 2.

R.H.L. del.

Lith. Anst. v. E.A. Funke, Leipzig.

DENDROCALAMUS and GIGANTOCHLOA

Fig. 6.

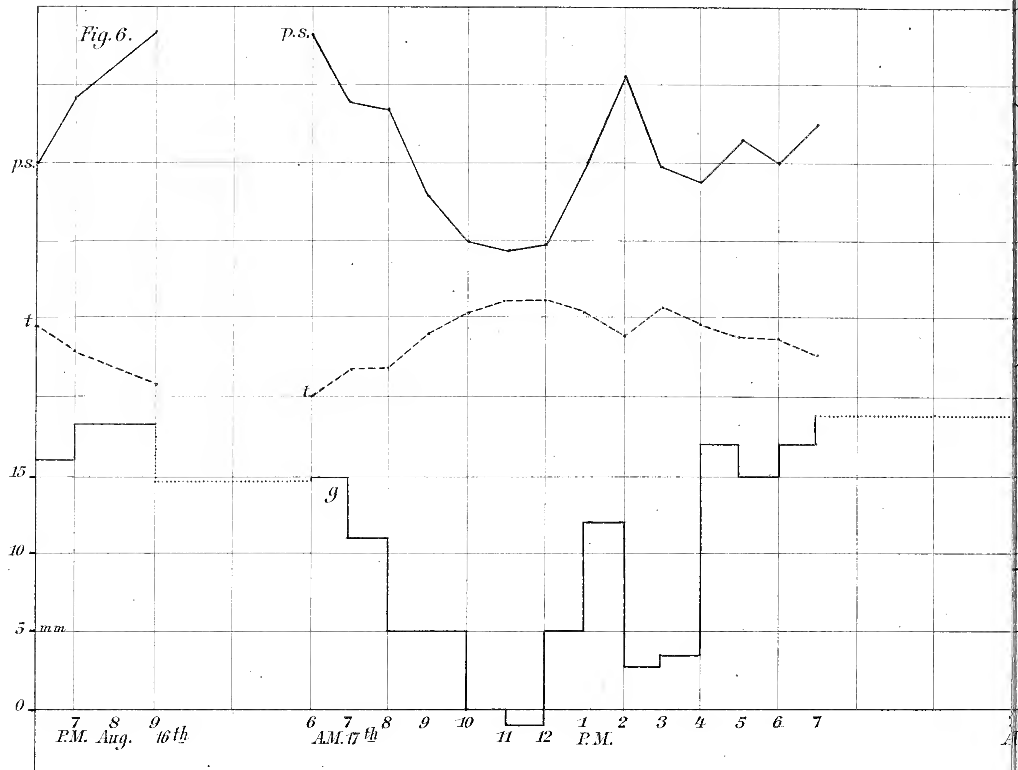
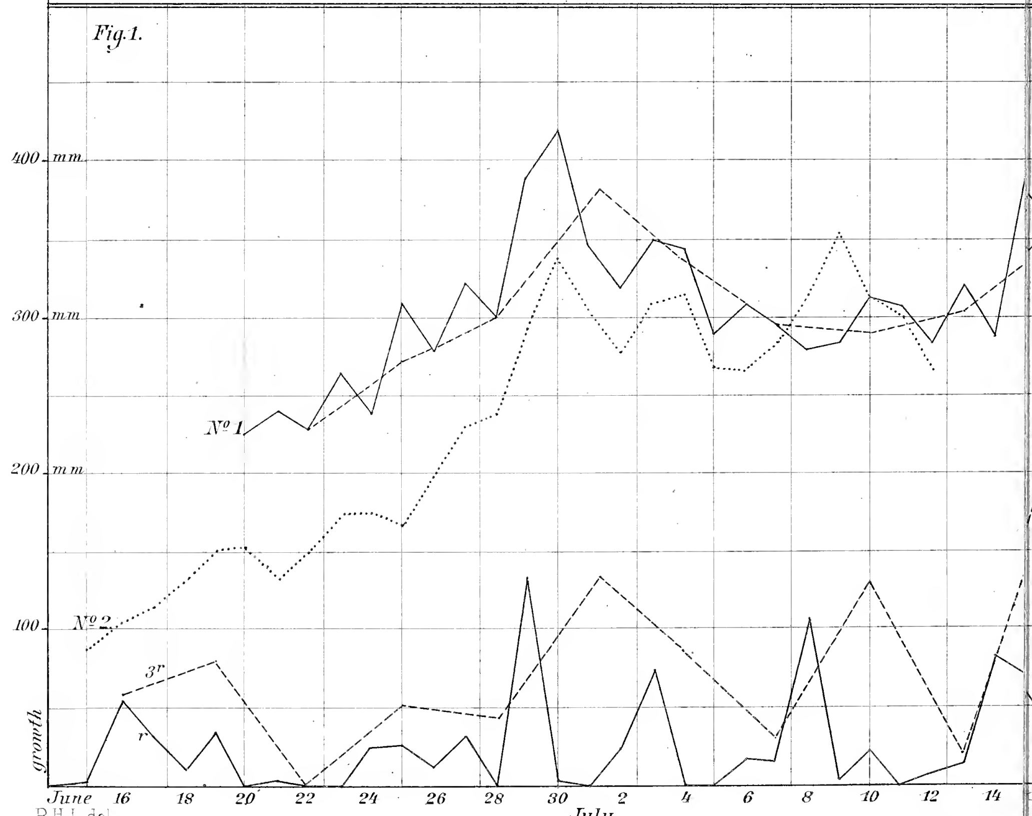


Fig. 1.



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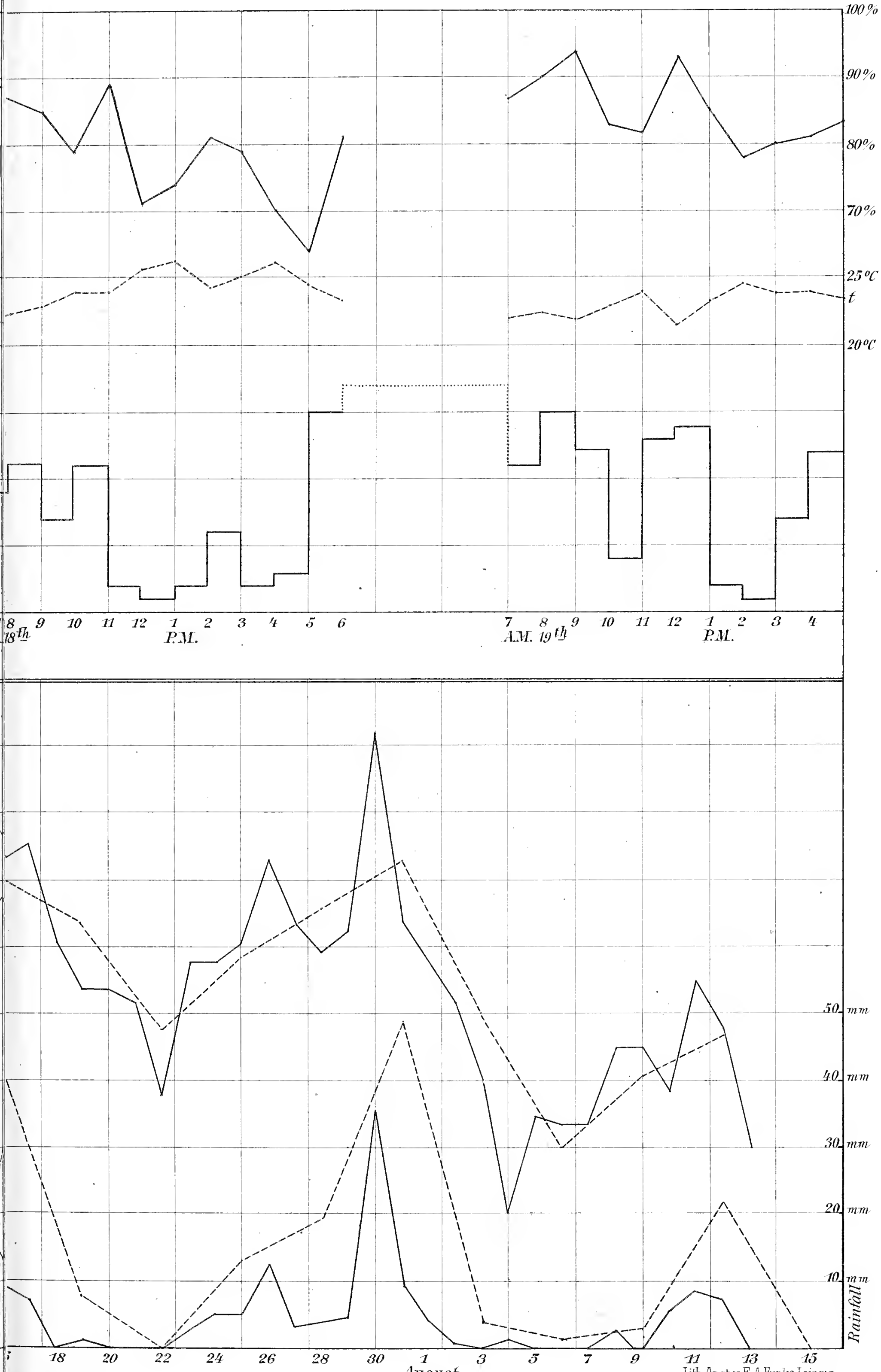
DENDRO



ALAMUS.

Lith. Anst. v. E. A. Funke Leipzig

Fig. 6.

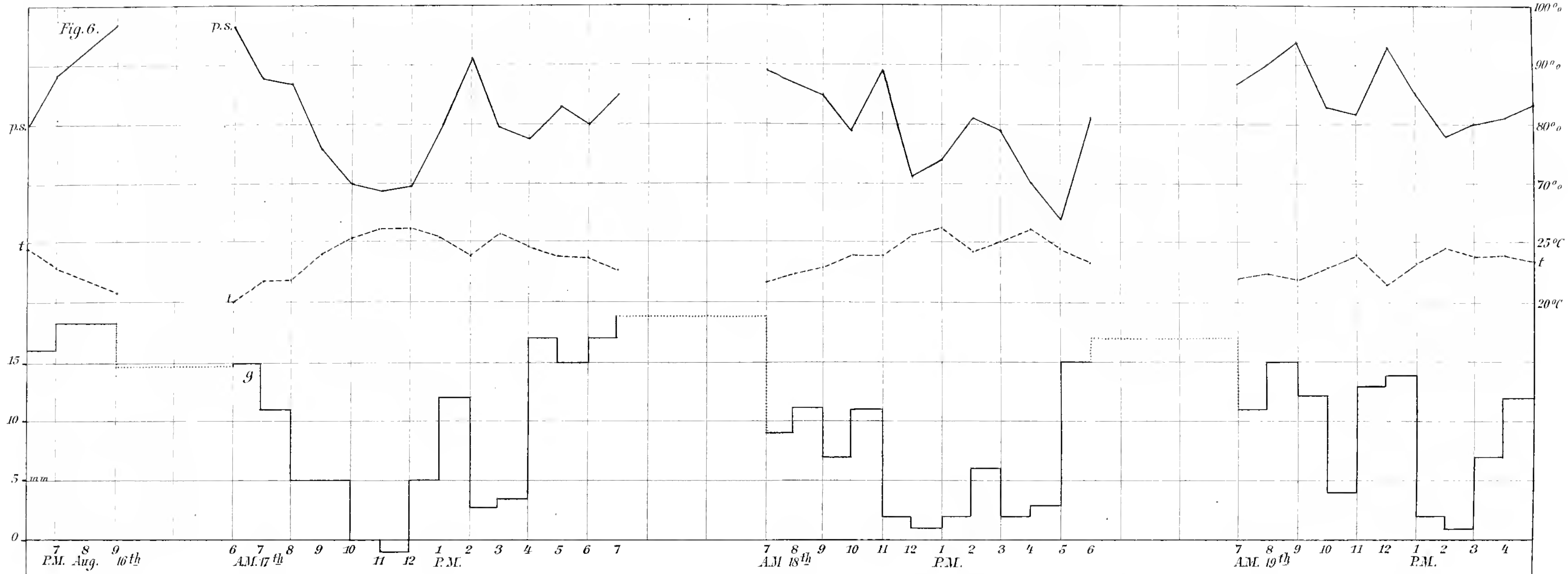
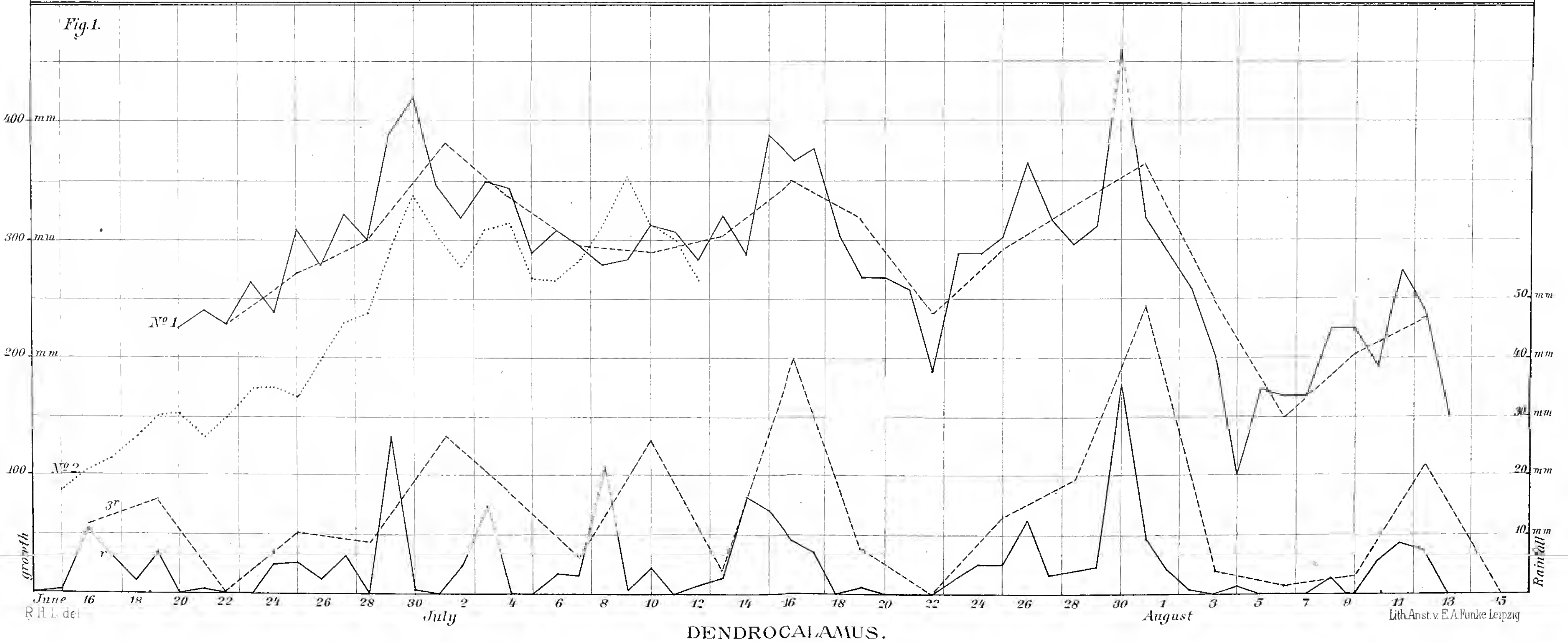


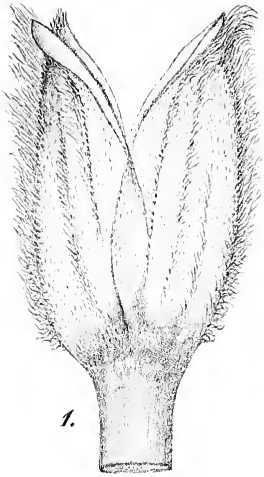
Fig. 1.



R. H. L. del.

Lith. Anst. v. E. A. Funke Leipzig

DENDROCALAMUS.



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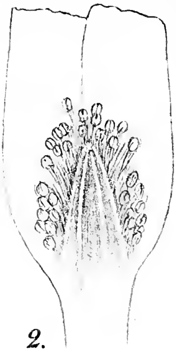

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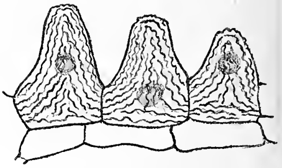

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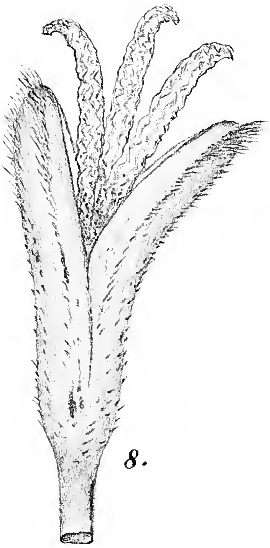

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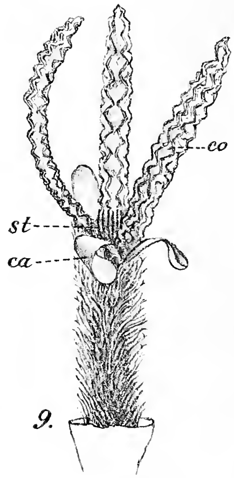

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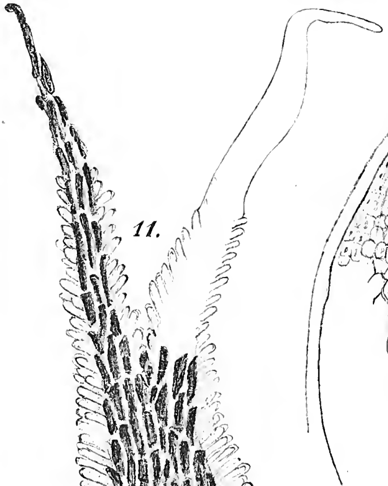

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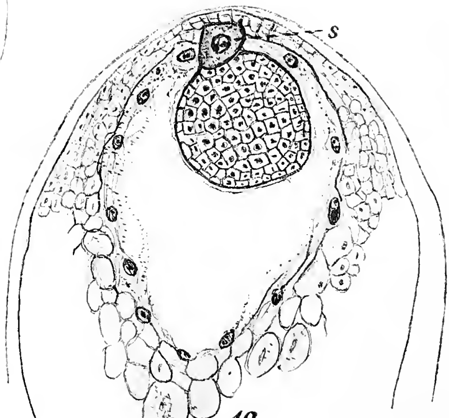

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Ljunggren et Svedelius del.

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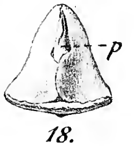

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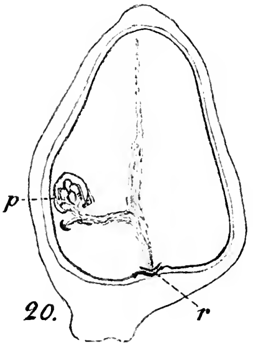

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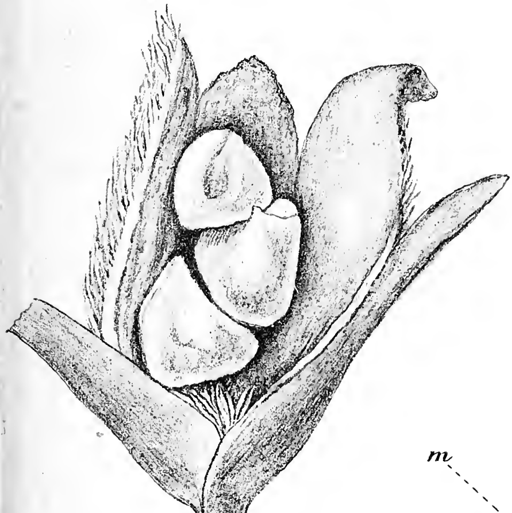

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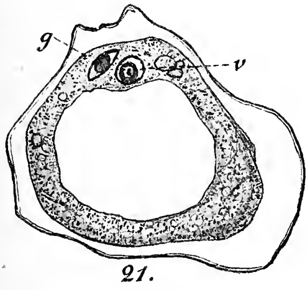

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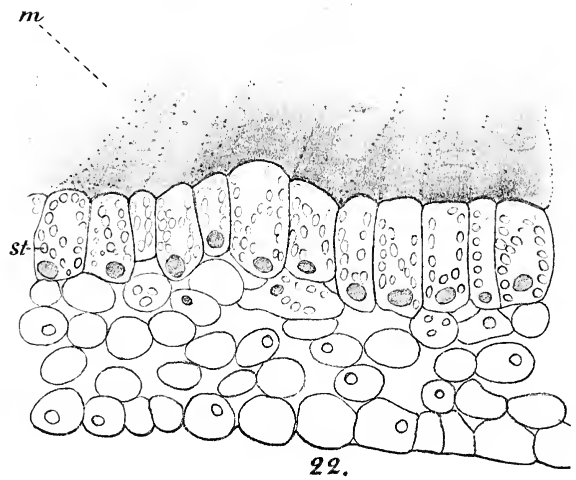

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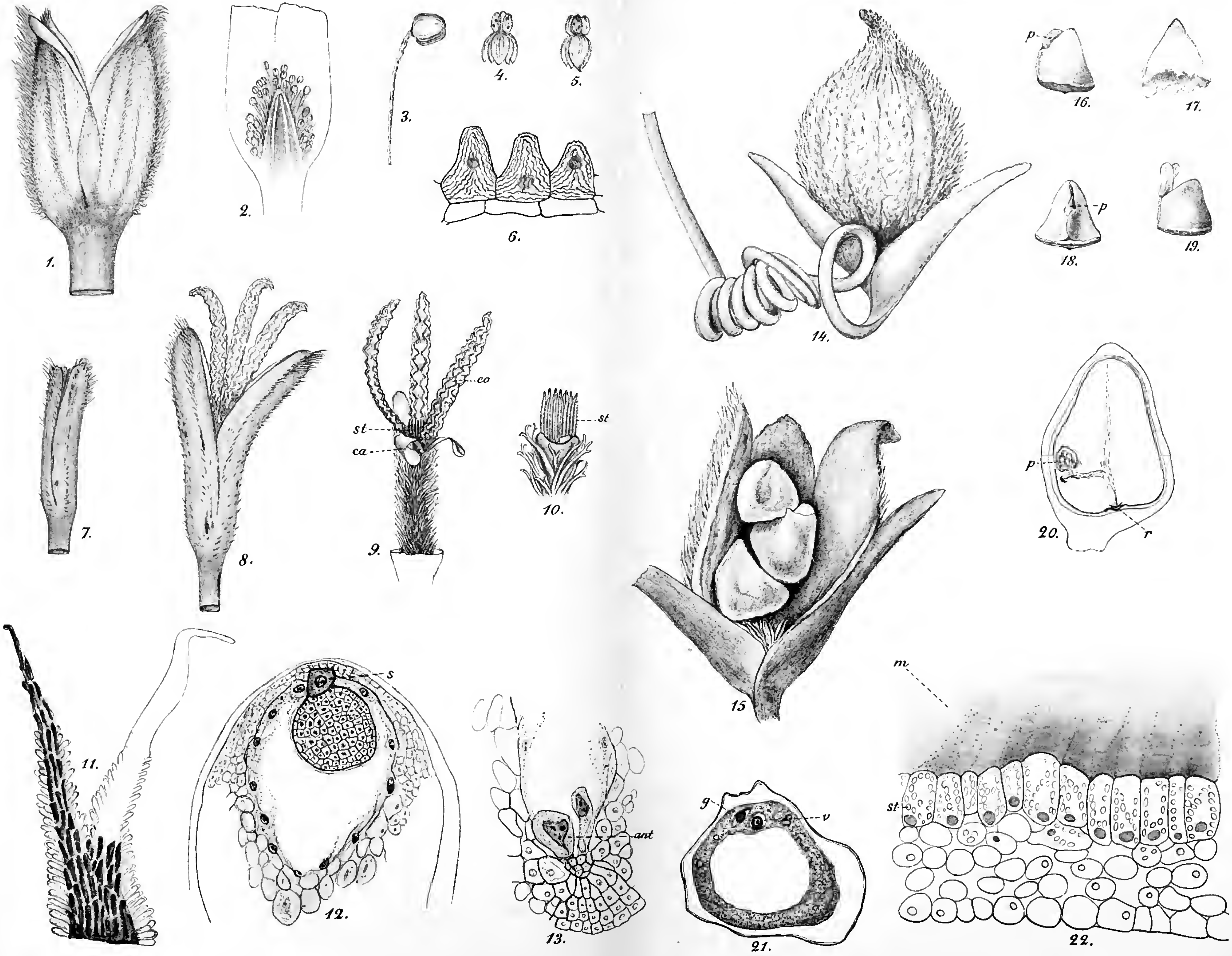

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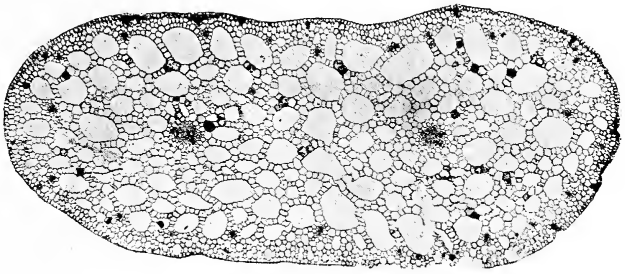

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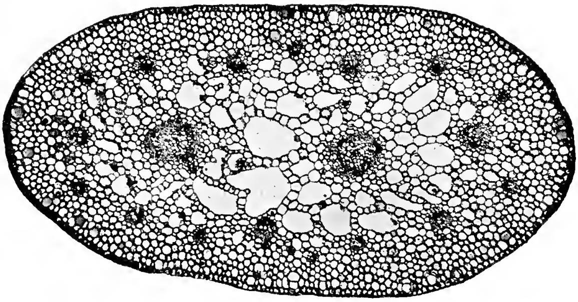

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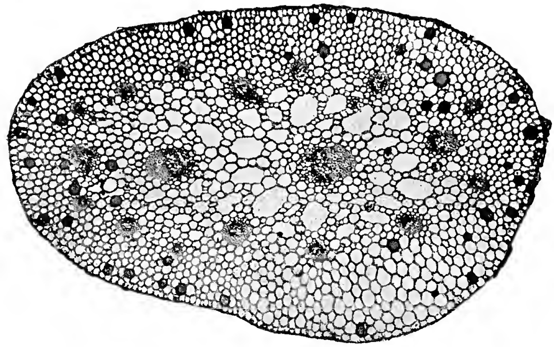

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