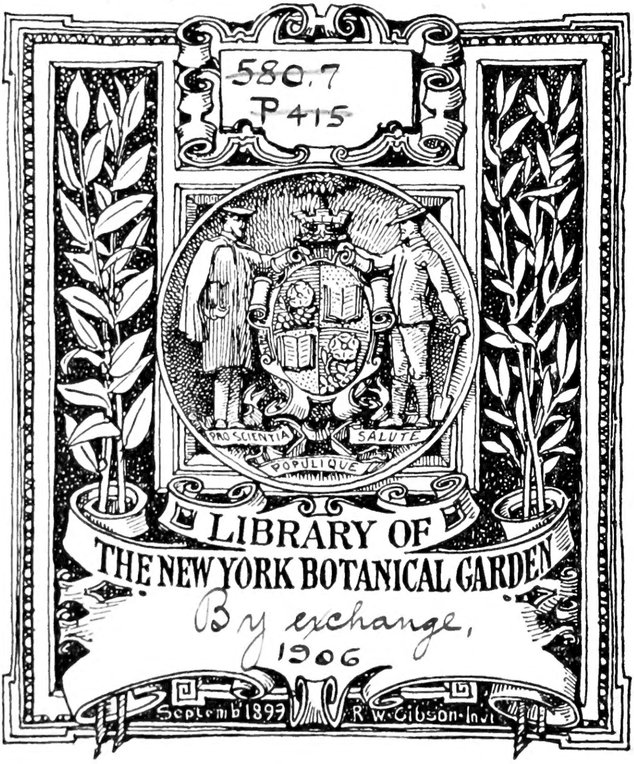
XC .E93 V.3



~~580.7~~
~~P415~~

LIBRARY OF
THE NEW YORK BOTANICAL GARDEN

By exchange,
1906

Vol. III., Pt. I. MARCH, 1906. Price Rs. 3.
4s. 0d.

ANNALS
OF THE
ROYAL BOTANIC GARDENS, PERADENIYA.

EDITED BY

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

CONTENTS.

Colombo:
GEORGE J. A. SKEEN, GOVERNMENT PRINTER, CEYLON.
London:
DULAU & CO., 37, SOHO SQUARE, W.

[*All rights of Reproduction and Translation reserved.*]

ANNALS OF THE ROYAL BOTANIC GARDENS, PERADENIYA.

NOTICE TO SUBSCRIBERS.

THE subscription rate is, for regular residents in Ceylon, Rs. 2·50 per annum, post free, payable in advance to the DIRECTOR, Royal Botanic Gardens, Peradeniya; for residents in other countries, Rs. 6 per annum, post free, payable in advance to the above, or eight shillings, payable to Messrs. DULAU & CO., 37, Soho Square, London, W.

The "Annals" will appear at irregular intervals, as matter is ready for publication, probably averaging 250 pages per annum, and when a volume of convenient size has been formed the Title Page and Contents will be issued. Individual Numbers or Papers may be purchased from the DIRECTOR, Royal Botanic Gardens, Peradeniya, or from Messrs. DULAU & CO., at prices marked upon them (considerably exceeding the subscription rate).

The "Circular" of the Royal Botanic Gardens, containing more popularly written articles on planting, agricultural, and botanical topics, may be received with the Annals by adding cents 50 to the Ceylon residents', and Re. 1·50, or 2s. to the foreign residents' subscription.

NOTICE TO CONTRIBUTORS.

All contributions should be addressed to the DIRECTOR, Royal Botanic Gardens, Peradeniya, Ceylon. They must be clearly written on one side of the paper only (Papers in French or German must be typewritten), and the figures must be ready for reproduction, and planned so as to properly fill a plate.

Each contributor is entitled to receive gratis fifty separate copies of his Paper, and may, by giving notice when returning proofs, purchase others at the rate, approximately, of two cents per page (including covers, if required), and 20 cents per full-page plate, for each copy, provided not less than 10 be taken.

ANNALS

OF THE

ROYAL BOTANIC GARDENS, PERADENIYA.

EDITED BY

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

VOLUME III.

March, 1906 — November, 1906.

LIBRARY
NEW YORK
BOTANICAL
GARDEN.

Colombo:
H. C. COTTLE, GOVERNMENT PRINTER, CEYLON.
London:
DULAU & CO., 37, SOHO SQUARE, W.

[All rights of Reproduction and Translation reserved.]

XC
.E93
V.3

ANNALS OF THE ROYAL BOTANIC GARDENS, PERADENIYA.

VOL. III., 1906.

Dates of Publication of Parts.

Part I. pp. 1–94	..	May 8, 1906
Part II. pp. 95–375	..	March, 1907

Dates given at the ends of certain Papers indicate the times at which they were handed to the Editor complete ; no alterations were made afterwards.

LIBRARY
NEW YORK
BOTANICAL
GARDEN.

CONTENTS.

Original Papers and Notes: PAGE

Reviews.

BRIEF SUBJECT INDEX.

Only those orders, genera, and species are mentioned here about which important notes are made.

Genera or species re-defined or transferred to other groupings are given in spaced type.

Descriptions of New Ceylon Fungi.

LIBRARY
NEW YORK
BOTANICAL
GARDEN.

BY

T. PETCH.

THE following diagnoses describe some of the fungi which have been observed on specimens submitted to the Department during 1905 from various districts in Ceylon. The majority are parasitic on the plants specified, but their occurrence has generally been confined to one locality, and their effect in most cases has been almost negligible.

Scarcely any descriptions of Ceylon fungi have been published since Berkeley & Broome's Paper on the Fungi of Ceylon in 1875, in which about 1,200 species (chiefly saprophytic) were recorded. Our knowledge of parasitic species is limited to those cases in which they have caused serious damage, though even here there are instances in which the fungus has never been described. Yet the number and variety of the cultivated plants of the Island postulates an equal abundance of parasitic, though not necessarily dangerous, fungi, and in order to arrive at a thorough knowledge of these it is intended to publish at intervals descriptions of such as have been investigated.

Asterina tenuissima.—Tenuissima, late effusa, maculam nebulosam in ramulis et fructibus formans; hyphis repentibus brunneis, 4–5 μ diam., glabris, a strato mucoso deinde junctis, multas erectas, septatas, olivaceas, acutas hyphas, 90–100 μ, gerentibus; peritheciis applanatis, nigris, 130–160 μ diam., ostiolatis; ascis clavatis, 30–40 × 9–12 μ;

JUN 18 1906

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. III., Part I., March, 1906.]

sporidiis uniseptatis, constrictis, hyalinis, fusoideis. 13 × 4 μ. An *Asterina nubecula*, B. et Br.?

Extremely thin, forming a blackish discolouration on branches and fruits, spreading indefinitely. Mycelial hyphæ brown, 4-5 μ diameter, smooth, united when old by a film of mucus, bearing numerous septate, erect hyphæ, 90–100 μ long, olivaceous, with acute tips; perithecia flattened, black, 130–160 μ diameter, ostiolate; asci, 30-40 × 9-12 μ, clavate; spores 13 × 4 μ, one-septate, constricted, fusoid, hyaline.

On green stems and fruits of *Hevea brasiliensis.*

Sphærella crotalariæ.—Maculas latas, pallidobrunneas, concentrice zonatas formans; peritheciis gregariis, atris, erumpentibus, circa ·2 mill. diam.; ascis cylindraceis, octosporis, 42 × 13 μ; sporidiis distichis, uniseptatis, fusoideis, hyalinis, 17–18 × 4–5 μ. Spermogoniis nigris, 90–130 μ diam., erumpentibus, cum peritheciis mixtis sed numerosioribus; sporulis ellipsoideis, hyalinis, continuis, 6–9 × 2–3 μ, in cirrum expulsis. Conidiis hyalinis, rectis vel subcurvatis, 53–75 × 3–4 μ, multiseptatis, apice vel latere hypharum fasciculatarum dispositis, in maculis brunneis minute papillatis.

Perithecia gregarious, black, erumpent, about ·2 mm. diameter, on large light brown patches marked with concentric, darker rings; asci 42 × 13 μ, cylindric, eight-spored: spores biseriate, one-septate, fusoid, hyaline, 17–19 × 4–5 μ.

Spermogonia black, 90–130 μ diameter, erumpent, mixed with the perithecia but more numerous; spores elliptical, hyaline, continuous, 6–9 × 2–3 μ, extruded in a tendril.

Conidia on minutely papillose, brown areas, 53–75 × 3–4 μ, hyaline, straight or slightly curved, multiseptate, borne terminally or laterally on clustered hyphæ.

On leaves of *Crotalaria striata.*

Diaporthe heveæ.—Peritheciis discretis, nigris. ·5–1 mill. diam., circinantibus, in ligno nidulantibus, in collum circa 1 mill. diam., ·5 mill. long., parum e cortice emergens. attenuatis ; ascis, anguste ovatis, octosporis, 40–45 × 6–8 μ : sporidiis oblique monostichis, hyalinis, fusoideis, uniseptatis, 10–13 × 4 μ.

Perithecia distinct, black, ·5–1 mm. diameter, in small groups, embedded in the wood ; neck about ·1 mm. diameter, up to ·5 mm. long, projecting slightly above the surface of the bark : asci 40–45 × 6–8 μ, linear oval, eight-spored ; spores obliquely uniseriate, hyaline, fusoid, one-septate, 10–13 × 4 μ.

In branches of *Hevea brasiliensis.*

Massaria theicola.—Peritheciis gregariis, in cortice omnino immersis, nigris, ·25–·3 mill. diam. ; ascis, anguste cylindraceis, 120–160 × 20 μ, octosporis ; paraphysibus paucis, septatis ; sporidiis oblique monostichis, hyalinis, continuis, deinde biseptatis, olivaceis, anguste ovatis, loculo medio sæpe nigriore, in gutta expulsis, 17–22 × 6–7μ.

Perithecia gregarious, totally immersed in the cortex, black, ·25–·3 mm. diameter : asci, narrow cylindric, 120–160 × 20 μ, eight-spored ; spores obliquely uniseriate ; paraphyses few, septate ; spores hyaline, continuous, becoming two-septate, olivaceous, narrow-oval, central cell sometimes darker than the terminal cells, extruded in a drop when ripe, 17–22 × 6–7 μ.

In main stems of *Thea viridis,* blackening the bark and making the wood the colour of walnut wood. The bush dies branch by branch as the mycelium advances.

Aglaospora aculeata.—Peritheciis immersis, discretis. 1 mill. diam., vel in stromate nigro carbonaceo aggregatis, 3–5 mill. diam., in conico collo e cortice emergente ·75–1·5 mill. productis ; ostiolis discretis, rotundis ; ascis cylindraceis, apice truncato attenuatis, stipite curvato, quadrisporis, 180–210 × 30–35 μ : sporidiis in medio asco maturato aggregatis, cymbiformibus, 90–105 × 12–15 μ, primum viridi-hyalinis, continuis, plasmate angulata, in gutta alba expulsis, deinde fuligineis, 7–11 septatis.

Perithecia immersed, separate, 1 mm. diameter, or united in groups forming a black carbonaceous stroma, 3–5 mm. diameter, produced above into a conical neck which projects ·75–1·5 mm. above the surface ; ostiola distinct, circular : asci cylindric, narrowed towards the truncate apex, on a curved pedicel, four-spored, 180–210 × 30–35 μ ; spores collected in a bundle in the centre of mature asci, cymbiform, 90–105 × 12–15 μ, at first greenish hyaline, continuous, with the contents in large angular granules, extruded in a white globule, afterwards becoming fuliginous, 7–11 septate and producing up to six germ tubes on germination.

In branches of *Thea viridis*, forming black thorns arranged in almost straight lines along the branch.

Nectria diversispora. — Peritheciis ·25 mill. diam., solitariis vel agglomeratis, nullo stromate, rubris, subdiaphanis, granulatis ; ostiolis conicis, ochraceis ; paraphysibus linearibus ; ascis 80–100 × 10–15 μ ; sporidiis oblique monostichis, hyalinis, 11–13 × 4–5 μ, uniseptatis, medio constrictis, striatis, ovatis, apicibus obtusis, loculis sæpe inæqualibus, apicibus sæpe rotundatis.

Perithecia ·25 mm. diameter, solitary or in small groups, without any stroma, red, semi-transparent, rough with minute papillæ ; ostiolum conical, ochraceous ; paraphyses linear ; asci 80–100 × 10–15 μ ; spores obliquely uniseriate, hyaline, 11–13 × 4–5 μ, one-septate, constricted at the septum, oval, ends obtuse, wall striate, one cell often larger than the other, and one or both ends often rounded in a circular arc.

On dead bark of *Hevea brasiliensis* and on dead stems of *Thea viridis*.

Phyllosticta erythrinæ.—Peritheciis nigris, minutis, lenticularibus, prominentibus, epidermide excepto ostiolo tectis, 90–180 μ diam., 60–70 μ alt.; ostiolis circa 10 μ diam.; sporulis lineari-ovatis, hyalinis, utrinque acutis, 6–8 × 2 μ; basidiis circa 10 μ long.

Perithecia black, minute, lenticular, prominent, covered by the epidermis except at the ostiolum, 90–180 μ diameter. 60–70 μ high, diameter of ostiolum about 10 μ; spores linearoval, hyaline, sharply pointed at both ends, 6–8 × 2 μ; basidia about 10 μ long.

On yellow scaly patches on young branches of *Erythrina lithosperma*.

Phyllosticta ramicola. — Peritheciis ·1–·25 mill. diam., nigris, epidermide velatis, confertis, subprominulis, lenticularibus, 75–140 μ alt.: sporulis anguste ovatis, utrinque acutis, viridi-hyalinis, sæpe biguttulatis, 8–12 × 2–3 μ, cirro albido tenui expulsis.

Perithecia ·1–·25 mm. diameter, black, sub-epidermal, crowded, slightly prominent, lenticular, 75–140 μ high; spores narrow-oval with sharply pointed ends, 8–12 × 2–3 μ, greenish-hyaline, often two-guttulate, issuing in a fine, white, tendril.

On green stems of *Hevea brasiliensis*, causing dark brown patches which later become gray.

Phoma heveæ.—Peritheciis nigris, gregariis, immersis, subprominulis, semi-globosis, ·1–·2 mill. diam.; sporulis ellipticis, hyalinis, 4–5 × 2 μ, cirro viridi-flavo expulsis.

Perithecia black, hemispherical, gregarious, immersed, slightly prominent, ·1–·2 mm. diameter; spores, elliptical, hyaline, 4–5 × 2 μ, extruded in a greenish yellow tendril.

On branches of *Hevea brasiliensis*.

Sphæronæma album. — Peritheciis semi-immersis, globosis, hyalinis, 140–260 μ diam., in rostellum hyalinum, striatum productis; rostellis 250–800 μ long., basi 80–160 μ diam., apice 40–80 μ diam., apice fimbriato; sporulis ovatis, hyalinis, continuis, 7–11 × 4 μ.

Perithecia semi-immersed, spherical, hyaline, 140–260 μ diameter, produced above into a hyaline, longitudinally striate tube, 250–800 μ long, 80–160 μ diameter at the base, 40–80 μ diameter near the apex where it splits into linear, spreading teeth ; spores oval, hyaline, continuous, 7–11 × 4 μ.

On decaying fruits of *Hevea brasiliensis.*

Diplodia zebrina.—Peritheciis nigris, confertis, erumpentibus, ·25 mill. diam. ; sporulis olivaceis, ellipticis, 25–30 × 13–15 μ, virgis pallidis angustis striatis.

Perithecia black, crowded, erumpent, ·25 mm. diameter ; spores olivaceous, elliptical, 25–30 × 13–15 μ, longitudinally striate, showing narrow light and broader dark bands.

On dead fruits of *Hevea brasiliensis;* also on dead branches of *Thea viridis.*

Diplodia arachidis.— Peritheciis globosis, primum immersis, proimnentibus, deinde erumpentibus, nigris, gregariis, ·25 mill. diam. ; sporulis ellipsoideis, uniseptatis, atrobrunneis, 17–25 × 10–12 μ, pariete et septo crasso.

Perithecia globose, at first immersed, prominent, then erumpent, black, gregarious, ·25 mm. diameter ; spores ellipsoid, one-septate, blackish brown, 17–25 × 10–12 μ, wall and septum thick.

On stems of *Arachis hypogea.*

Chætodiplodia grisea.—Peritheciis minutis, nigris discretis, prominentibus, epidermide tectis, deinde erumpentibus, 250–400 μ diam., pilis erectis, olivaceis, septatis, 70–180 μ long. ornatis ; ostiolis circa 40 μ diam. ; sporulis primum continuis, hyalinis, cirro albido ejectis, deinde ellipticis, uniseptatis, 24–28 × 13–14 μ, fuscogriseis, pariete circa 3 μ crasso ; basidiis circa 10 μ long. ; paraphysibus internis 30–50 μ, linearibus.

Perithecia minute, black, distinct, prominent, covered by the epidermis, then erumpent, 250–400 μ diameter, rough with erect, olivaceous, septate paraphyses, 70–180 μ long ;

ostiolum about 40 μ diameter; spores ejected in a white tendril, at first continuous, hyaline, then elliptical, one-septate, dark gray, 24–28 × 13–14 μ; wall about 3 μ thick; basidia about 10 μ long; internal paraphyses, 30–50 μ, linear.

On pods of *Theobroma cacao*, causing brown areas rough with minute hemispherical papillæ covering the perithecia; also on dead seedlings of *Hevea brasiliensis*.

Botryodiplodia elasticæ.—Per corticem in acervulos lineares vel rotundatos, 1·5–2 mill. diam., erumpens; peritheciis ·25–·4 mill. diam. polygonatis; sporulis 25–30 × 14–15 μ, ovatis, uniseptatis, violaceo-brunneis, pariete et septo crasso; paraphysibus numerosis, linearibus, 40–80 μ.

Bursting through the cortex in linear or rounded masses, 1·5–2 mm. diameter, black; perithecia ·25–·4 mm. diameter, polygonal; spores 25–30 × 14–15 μ, oval, one-septate violet brown, wall and septum thick; paraphyses abundant, linear, 40–80 μ.

On roots of seedlings (stumps) of *Hevea brasiliensis;* also as a wound parasite on *Castilloa elastica* where the perithecial masses in the soft, decaying bark are flat. Apparently the same species occurs in the bark of dead *Hevea brasiliensis*, in which case, however, it is not erumpent and the white tendril of spores is the only outward indication of its presence.

Staganospora theicola.—Peritheciis minutis, gregariis, innatis, nigris, circa ·1 mill. diam.; sporulis triseptatis, viridi-hyalinis, oblongis, apicibus rotundatis, rectis vel leniter curvatis, 15-17 × 5 μ.

Perithecia minute, gregarious, innate, black, about ·1 mm. diameter; spores three-septate, greenish hyaline, oblong with rounded ends, straight or slightly curved, 15–17 × 5 μ.

On gray patches on leaves of *Thea viridis* with *Læstadia theæ*, Rac., and *Colletotrichum camelliæ*, Mass.

Glœosporium alborubrum. — Acervulis 150–200 μ diam., nigris, epidermidem irregulare lacerantibus ; conidiis hyalinis, oblongis, utrinque rotundatis, rectis vel leniter curvatis, 15–20 × 3–4 μ, cirro crasso albido vel puniceo ejectis.

Pustules 150–200 μ diameter, black, rupturing the epidermis irregularly ; spores hyaline, oblong, ends rounded, straight or slightly curved, 15–20 × 3–4 μ, issuing in thick pink or white tendrils.

On green stems of *Hevea brasiliensis.*

Glœosporium heveæ.—Acervulis pallido-brunneis, sparsis, erumpentibus, irregularibus, applanatis, epidermide rupta cinctis,·1–·25 mill. diam. amphigenis: conidiis oblongis, utrinque rotundatis, hyalinis, continuis, 12–17 × 3·5–5 μ, gutta pallido-brunnea ejectis; basidiis 20–34 × 2 μ.

Pustules light-brown, scattered, irregular, flattened, erumpent, surrounded by the torn epidermis, ·1–·25 mm. diameter, on both sides of the leaf ; spores extruded in a pale brown mass, oblong with rounded ends, hyaline, continuous, 12–17 × 3·5–5 μ ; basidia 20–34 × 2 μ.

On leaves of seedling *Hevea brasiliensis* which it defoliates.

Colletotrichum heveæ.—Acervulis nigris, sparsis, epiphyllis, ·1–·25 mill. diam., setis violaceo-nigris, uni-vel bi-septatis, obtusis, ad 90 μ long., cinctis ; conidiis oblongis, utrinque rotundatis, hyalinis, granulatis, 18–24 × 7·5–8 μ ; basidiis 20–30 × 6–7 μ, apice incrassatis.

Acervuli black, scattered, epiphyllous, ·1–·25 mm. diameter, surrounded by violet black, one- or two-septate, obtuse setæ, up to 90 μ long ; spores oblong with rounded ends, hyaline, granular, 18–24 × 7·5–8 μ ; basidia, 20–30 μ × 6–7, swollen upwards.

On leaves of seedlings of *Hevea brasiliensis.*

Helminthosporium heveæ.—Epiphyllum, sistens maculas primum minutas purpureas deinde albidas, semi-translucidas, orbiculares, 1–5 mill. diam., brunneo-marginatas ; hyphis sparsis, olivaceis, simplicibus, 80–200 μ long. ; conidiis cymbiformibus, 8–11 septatis, brunneis, 100–120 × 15–18 μ.

On leaves of *Hevea brasiliensis*, causing minute purple spots which afterwards become white, semi-transparent, circular, 1–5 mm. diameter, surrounded by a brown line ; hyphæ scattered, olivaceous, 80–200 μ long ; spores cymbiform, 8–11 septate, brown, appearing dark brown and shining by reflected light, 100–120 × 15–18 μ.

Ceratosporium productum.—Hyphis repentibus olivaceis nitentibus, 4 μ diam. ; conidiis 2–4 fasciculatis, 9–13 septatis, non-constrictis, olivaceis, ad apicem pallidioribus, 130–200 μ long., 10–12 μ diam. basi, 5 μ diam. apice ; loculis basi quadratis, sursum attenuatis.

Creeping hyphæ olivaceous, shining, 4 μ diameter, bearing spores in groups of 2–4 ; spores 9–13 septate, not constricted, olivaceous, becoming paler towards the tip, 130–200μ long, 10–12 μ diameter at the base, 5 μ diameter at the apex cells, cubical at the base, increasing in length towards the apex.

On dead branches of *Hevea brasiliensis.*

Cercospora dilleniæ.—Maculis fusco-brunneis, demum griseis supra, areola fusco-brunnea cinctis ; hyphis sæpius epiphyllis, in cæspites nigros minutos congestis, brevibus, olivaceis ; conidiis obclavatis, rectis vel leniter curvatis, olivaceis, 5–9 septatis, 60–90 × 4–7 μ.

Forming dark brown spots, afterwards gray on the upper surface with a dark brown margin ; dying leaves remain green round the spot for two or three days after the unattacked parts of the leaf have become brown ; hyphæ generally epiphyllous, in minute black tufts, crowded, short, olivaceous ; conidia obclavate, straight or slightly curved, olivaceous, 5–9 septate, 60–90 × 4–7 μ.

On leaves of *Dillenia retusa*, Thunb.

Cercospora cearæ.—Maculis irregularibus, rubro-brunneis, deinde griseis, fusco-brunneo-marginatis, demum confluentibus; hyphis amphigenis, in cæspites minutos nigros, deinde griseis, congestis; conidiis cylindraceis, sursum leniter attenuatis, rectis, olivaceis, 42–78 × 6–7 μ, 5–10 septatis.

Spots irregular, red-brown, becoming gray with a dark brown margin, afterwards confluent forming large irregular patches extending from the edge of the leaf; hyphæ on both sides of the leaf, in minute black tufts, afterwards gray; conidia cylindric, tapering slightly towards the apex, straight, olivaceous, 42–78 × 6–7 μ, 5–10 septate.

On leaves of *Manihot Glaziovii*, Mull.

Fungi parasitic upon Scale - Insects (Coccidæ and Aleurodidæ): a general account with special reference to Ceylon Forms.

BY

JOHN PARKIN.

(*With Plates I. to IV.*)

CONTENTS.

I.—INTRODUCTORY AND HISTORICAL.

WHILE occupying the post of Scientific Assistant to the Director of the Royal Botanic Gardens, Peradeniya, in 1898–99, Mr. E. E. Green, author of "The Coccidæ of Ceylon" and Government Entomologist for the Island, brought to my notice various types of fungous growths on scale-insects, and desired me to take up their study. To him I am indebted for most of the material, and also for kindly naming the insects upon which the different fungi were growing. My thanks are also due to Mr. Macmillan, the

[Annals of the Royal Botanic Gardens, Peradeniya. Vol. III., Part I, March, 1906.]

Curator of Peradeniya Gardens, for two excellent examples found by him in the jungle around Pussella.

A number of specimens were briefly examined in the laboratory at Peradeniya during my sojourn in Ceylon. On my return to England the material brought home was investigated in greater detail, and the literature upon the subject consulted. The results were communicated to the British Association in 1900 in a paper* read before the Botanical Section.

Since then from time to time Mr. Green has sent me additional examples of these fungi as well as one or two new kinds. The publication of a full account of them has been delayed with the hope of obtaining further material for the elucidation of some of the more obscure forms, and also with the desire of incorporating the results of some culture and infection-experiments. However, as Mr. T. Petch, the newly appointed Mycologist to the Peradeniya staff, is proposing to take up the study of the group, it seems now desirable to place on record an account of the various forms that have passed through my hands, and at the same time to bring the subject up to date by referring in a general way to the species which have been described for other countries, hoping thereby to render some assistance to my successor.

The literature on the subject is not extensive, though it is necessary to go back as far as 1848 for the first reference. In that year Desmazières† described a new fungus in the conidial stage growing upon the scales of a coccid on young willow-stems in France. He proposed a new genus of the Fungi-imperfecti, *Microcera*, to receive this conidial form. Since then this fungus has been proved to be the conidial fructification of a species of Sphærostilbe, and has been shown to have an extensive distribution on scale-insects in both the old and new worlds.

Till comparatively recently no other papers of importance have appeared on the subject. Such a position for certain

---

* Report, Brit. Assoc. Bradford Meeting, 1900, p. 932. (Abstract.)

† Desmazières, Ann. des. Sc. Nat., 1848, p. 359.

species of fungi has been mentioned incidentally from time to time in systematic treatises. References to these occur in the descriptive part of this paper.

Within the last twelve years some of the Experiment Stations of the Agricultural Department of the United States of America have been interesting themselves in these fungi, especially from the economic standpoint. Webber* in 1897 in an important paper on the "Sooty Mold of the Orange and its Treatment" describes certain entomogenous fungi which indirectly can assist in the removal of "sooty mould" (Meliola) by attacking the coccids which excrete the honey-dew. It is upon this sugary excretion that the Meliola grows clogging the leaves and spoiling the appearance of the fruit. So not only does the scale-pest inflict direct damage on the orange trees by sucking its sap, but indirect harm as well by encouraging this unsightly Meliola. Webber chiefly deals with a fungus new to science and named by him *Aschersonia aleurodis*, parasitic upon the mealy wing or white fly (*Aleurodes*† *citri*) which is responsible for much sooty mould on the orange in Florida. Other species of Aschersonia are mentioned, as well as a sterile form named for the purpose of convenience, the "brown mealy wing fungus." This genus Aschersonia is largely represented on species of Aleurodes in Ceylon. Rolfs‡ in the same year published an account of fungous disease on the San José scale (Aspidiotus perniciosus) and shows that it can be used to check this great pest. The fungus appears to be the Microcera originally discovered by Desmaziéres. Two years later inoculating experiments carried out in Illinois with this fungus on the same insect are described by Forbes.§ He thinks,

---

* Webber: U.S.A., Depart. Agric., Div. of Veg. Physiol and Pathol, No. 13, 1897.

† The genus Aleurodes does not strictly belong to the family Coccidæ, but to the allied one Aleurodidæ. In this paper the term "scale-insect" includes members of both families.

‡ Rolfs, Florida Agric. Exp. Station, Bull. 41, 1897.

§ Forbes, Illinois do. do. 56, 1899.

however, the fungus will probably not be able to keep down the scale without the aid of artificial insecticides as well. Gossard* follows with a paper containing observations and experiments with this fungus on the San José scale in Florida. He says it has developed so vigorously in some localities as to render insecticides unnecessary. It is believed that at least during warm rainy weather the fungus is quite capable of keeping the insect in check. A point to be noticed is that kerosine and such like insecticides not only destroy the scale but its fungous parasite as well, while fumigation with hydrocyanic acid does not affect the latter. The same author† about a year later refers to the natural enemies of the white fly (*Aleurodes citri*), including *Aschersonia aleurodis* and the brown sterile fungus, originally brought to notice by Webber. Such are in brief the observations and experiments that have been made in the United States on fungi parasitic on scale-insects. The various publications demand close study from those who are interested in the economic aspect of the subject.

In Natal *Microcera coccophila* (ascus-stage *Sphærostilbe coccophila*) has been observed by Fuller‡ to be common on the red scale (*Aspidiotus aurantii*). In a wet summer, he says, it makes much headway against the coccid.

Quite recently McAlpine§ has described species of Microcera on scale-insects in Australia. He hopes to conduct inoculating experiments with those.

A different type of fungous parasite to the above was observed by Zimmermann in Java in 1897 on the green bug (*Lecanium viride*), one of the most dangerous enemies of the coffee shrub. In the following year he published a short paper‖ for the benefit of the Java planters, pointing

---

* Gossard, Florida Agric. Exp. Station Bull 61, 1899.

† Gossard, Florida do. do 67, 1903.

‡ Fuller, 1st. Report of Govt. Entomologist, Dept. Agric. Natal, 1901, p. 99.

§ McAlpine. J. Dep. Agric.; Victoria, vol. II., Pt. 7, 1904, p. 646.

‖ Zimmermann, Over eene Schimmel epidemie der Groene Luizen, Buitenzorg, Java, 1898.

out that cultures of this fungus might be employed as a check against this insect, and suggesting how experiments might be carried out. He refers the fungus to *Cephalosporium* and names it provisionally *C. Lecanii.* Numerous examples identical with this have been found in Ceylon. Since then the same author has described* systematically several Ascomycetous fungi belonging in the main to the group Hypocreales, parasitic on scale insects in Java; these will be referred to in detail under their respective genera.

Guégnen† in an exhaustive work on fungous parasites of man and animals published last year gives an account of a new conidial form, *Acrostalagmus coccidicola*, found by him on a coccid in a greenhouse in Paris.

The most recent contribution to the subject is a paper by Dop‡ on a new fungus parasitic on Aspidiotus from Martinique. The advent of the fungus has practically saved the cocoanut palm cultivation in this Island. The author refers it to the genus Hyalopus; thus it is probably near akin to Cephalosporium.

Previous to the stimulus given by Mr. Green to the study of these fungi, the Ceylon forms had received no attention. The only mention of such a position for a Ceylon fungus occurs in a systematic paper by Berkeley and Broome§ on some fungi received from the Island. A species of Nectria is named as apparently growing from some coccus.

In the present paper the various fungi associated with scale-insects are taken in systematic order. The ones which have been described elsewhere by different observers are referred to briefly, and then the Ceylon forms similar to these are treated at some length and compared with them. Though an attempt is made to discriminate between species,

---

* Zimmermann, Centralb. f. Bakt., Abth. II., Bd. VII., 1901, p. 872.

† Guégnen, Les champignons parasites de l'homme et des animaux, Paris, 1904, p. 252.

‡ Dop, Bull. Scient. France et Belgique, XXXIX., 1905, p. 135.

§ Berkeley and Broome, Journ. Linn. Soc. XIV., 1875, p. 117.

no diagnosis of new ones has been undertaken, as this on the one hand is more the work of a specialist, and, on the other hand, their investigation is not sufficiently advanced to permit of this. A hasty formation of new species, specially of fungi, is to be deprecated. It seems preferable to err rather in the opposite direction, grouping together forms presenting slight differences, till further study warrants them being split into distinct species. Small deviations in size, shape, or colour, unless definitely shown to be constant, do not appear to be sufficient for the separation of species of taxonomic value. Colour as a systematic character should be used with caution, because it can alter with age, and has often faded in material, the examination of which has been postponed for some time after its collection. Then again no two observers are likely to describe the same tint in exactly the same words. So in order to arrive at uniformity in systematic colour descriptions a standard chromatic scale should be used as recommended by Guégnen.*

The recognition of what are called "biological species" amongst parasitic fungi renders still more difficult the separation of what should rank as taxonomic ones. To take a hypothetical case, the Microcera on Aonidia differs in certain external features from that on Aspidiotus; this is perhaps accountable for through a difference in the general structure of these coccids. If, however, the Microcera on Aonidia should be shown to be incapable of directly affecting Aspidiotus, would it be then justifiable to separate the two forms of this fungus as distinct taxonomic species?

All these scale-fungi are either complete Ascomycetous forms or incomplete conidial ones. The former are described first. The latter are provisionally placed in the Fungi-imperfecti, an artificial group the individuals of which are generally considered as conidial stages of various Ascomycetes. But as their ascus-fructifications are as yet unknown they cannot with any degree of certainty be classified with them.

* Guégnen. *loc. cit.*, p. 9.

The measurements recorded for the various parts of the fungi about to be described are given either in millimetres (mm.) or in micromillimetres* (μ).

The paper is illustrated by figures to aid the verbal descriptions. These have been either made directly from the specimens or copied from coloured drawings executed by Mr. Green and W. de Alwis, late draughtsman of the Royal Botanic Gardens, Peradeniya. It is to be hoped that these coloured drawings now in the possession of the author, with additions, may eventually be published with a complete account of the Ceylon coccidophagous fungi.

II.—SYSTEMATIC ACCOUNT.

(A) ASCOMYCETES.

Pyrenomycetes–Hypocreales.

Genus *Torrubiella*, Boudier.

This genus was founded by Boudier† in 1885 for a fungus named *T. aranicida*, discovered by him on spiders in France. Since then three other species have been added, viz.:—

T. tomentosa, Pat.,‡ 1892, on a spider (?) on a leaf of a tree, Ecuador, S. America.

T. rubra, Pat.,§ 1893, on the dead bodies of a coccid, on leaves of Melastoma sp., and Solanum sp., Ecuador, S. America.

T. luteorostrata, Zimm.,‖ 1901, on a coccid on a leaf of a jungle tree, Java.

This genus is characterized by forming a dense hyphal mat, upon the margin of which are borne several upright elongated perithecia. The ascospores are thread-like. Thus it is fairly sharply marked off from the rest of the

---

* A micromillimetre equals 0·001 mm.

† Boudier, Revue Mycol., 1885, p. 227 : and Saccardo, S. F. Addit. to vol., I.-IV., 1886, p. 220.

‡ Patouillard et Lagerheim, Bull. Soc. Mycol., France, VIII., 1892, p. 133.

§ Patouillard et Lagerheim : Bull. Soc. Mycol., France, IX., 1893, p. 154.

‖ Zimmermann, *loc. cit.*

Hypocreales with the exception of Globulina. The species so far discovered we see are entomogenous or rather restricted to spiders and coccids. The species for which the genus was originally founded possessed peculiar sterile hyphæ mixed with the asci, known as paraphyses. These are absent in the three species since added as well as in the Ceylon forms. The presence of paraphyses is given in "Die Pflanzenfamilien"* as a distinguishing character, separating it from Globulina. This now requires alteration.

Ceylon Forms.

The Ceylon specimens found on three occasions may perhaps be separated into two distinct species.

Type 1, resembling T. rubra *and* T. luteorostrata.

(*a*) On *Aleurodes*, sp.,† on the lower surface of leaves of Tetranthera, sp., found by Green in the jungle Pundalu-oya. February, 1899 (fig. 1).

The fungus forms over and around the insect a compact brown circular mat or pustule of hyphæ almost deserving the name of stroma. It is thickest in the middle and gradually thins out towards the periphery where it is succeeded by a fine white hyphal fringe extending for some distance over the leaf-surface. The brown pustules have a diameter of 1·5–2 mm. and the white part a breadth of about 1–1·5 mm. The long somewhat flask-shaped or conical perithecia are borne erect on the hyphal fringe and are conspicuously coloured objects. The lower bulbous part is bright pink; this colour then gradually deepens upwards, so that the apical part of the neck is nearly black. They stand separately; a few, such as five, around each pustule. The perithecium (fig. 2) measures 825 μ long; its lower bulbous part 225 μ and upper neck part 140 μ broad. The ascus (380 × 8–9 μ) contains eight thread-spores (300 × 2–4 μ) somewhat guttulate but not septate (figs. 3 and 4).

---

* Engler and Prantl, Teil I., Abtheil. I., p. 347.

† The Ceylon species of Aleurodes have not yet been classified. Mr. Green hopes to monograph the Aleurodidæ of the Island after he has completed the true coccids.

(*b*) On *Aleurodes*, sp., on lower surface of leaves of a jungle tree collected by Macmillan, Pussella, February, 1899.

This specimen was most likely an older stage of (*a*). The stroma-like mats covering the insects had here and there a distinct red colour. Some of them were as much as 4 mm. in diameter. The perithecia were similar to (*a*), but more numerous, while ascus and ascospore were identical.

Type 2, resembling somewhat T. tomentosa.

On *Aspidiotus destructor* on lower surface of leaves of a jungle tree, found by Green, Pundalu-oya, 1899 (fig. 5.)

This type differed from the foregoing chiefly in the colour of its perithecia. These were pale yellow-brown with gelatinous-looking apices. As many as nine were counted around a pustule, either occurring singly or in groups of two or three with coherent bases. The perithecia on the whole were smaller, measuring in length 525 μ and in breadth, lower part 225 μ, neck 75 μ. Ascus and spore similar. The whole fungus has a softer and whiter appearance to the preceding type and occurs on quite a different kind of scale-insect.

The differences between *T. rubra*, *T. luteorostrata*, and the red Ceylon form are very slight. Zimmermann says the Java species differs from *T. rubra* through its perithecia being smaller, having yellow ostioles and in many being grouped on one stroma.

No conidial stage has been found as yet associated with the Ceylon specimens, nor are any described by Patouillard and Zimmermann. Boudier* in 1887 discovered a conidial fructification (*Isaria cuneispora*) belonging to *T. aranicida.*

Genus *Nectria*, Fries.

The first material handed to me by Mr. Green consisted of scales of Aspidiotus attacked by a red fungus on twigs of a Citrus shrub. This was in the conidial condition and

---

* Guégnen, *loc. cit.*, p. 183.

referable to Fusarium. Later deep pink perithecia appeared, clearly revealing the fungus to be a Nectria. Further search has shown it to be one of the commonest of the Ceylon scale fungi, attacking exclusively coccids belong to the subfamily Diaspidinæ.

In a systematic account of some Ceylon fungi published in 1875 by Berkeley and Broome[*] a new species of Nectria, named *N. aurantiicola*, is mentioned incidentally as growing apparently from some coccus on orange twigs. This naturally suggests the possibility of *N. aurantiicola* being identical with the one first discovered by Green. It will be shown, however, that Berkeley and Broome's Nectria, judging from their description, does not agree in every detail with the one recently found. Still the disparity is perhaps hardly sufficient to separate the two forms as distinct species.

Two instances of Nectria occurring on coccids are recorded in Saccardo's "Sylloge Fungorum." The first *N. coccorum* Speg.,[†] was found in Brazil, and is described as growing on dead coccids situated on fallen leaves. No conidial fructification is mentioned. It is placed in the sub-genus Dialo-nectria and distinguished as having smooth solitary perithecia and no stroma, whereas Eu-nectria possesses one.

The second, *N. coccogena* (Eu-nectria), Speg,[‡] was also found in Brazil growing on dead coccids on living leaves of a species of Eugenia. No description of the fungus is given in Saccardo's work.

A more important instance of such a position for Nectria is that of Zimmermann. In his paper[§] of 1901 on Java forms of Ascomycetes parasitic on Coccidæ, he describes a species of Nectria, which he considers new and names *N. (Eu-nectria) coccidophthora*. He says it is closely related to *N. aurantiicola*, Berkeley and Broome, but differs in the

---

[*] Berkeley and Broome, *loc. cit.*

[†] S. F. additamenta to vols. I.–V., 1886, p. 203.

[‡] S. F. vol. IX., 1891, p. 959.

[§] Zimmermann, *loc. cit.*

colour of its perithecia and slightly in details connected with its conidial stage. It seems, however, identical in every way with the common Ceylon scale-Nectria. The Java examples were found on *Mytilaspis*, sp., on *Coffea arabica* and on *Parlatoria zizyphi* on Citrus, Buitenzorg.

1.—*Ceylon specimens considered identical with* Nectria coccidophthora, *Zimm.*

Conidial stage (Fusarium) fig. 6.

Several bright orange-red club-shaped or columnar bodies appear standing up around the rim of the scale. Each consists of a short stout stalk and a conspicuous waxy-looking head (figs. 7 and 9). Sometimes the stalk is almost suppressed. It consists of hyphæ massed together, and is all that can be regarded as stroma. The head is composed of conidia and the special hyphæ (conidiophores) which bear them, arranged parallel to one another. The conidia are all held together in a compact mass by soluble mucilaginous matter. On treatment with water the head rapidly swells, releasing the conidia which float away (fig. 10).

Since the word stroma is sometimes employed loosely, it is well to be clear as to its meaning here. A lax irregular arrangement of hyphæ is termed a mycelium. Fructifications, *i.e.*, special spore-producing structures, may be borne directly on the mycelium ; but often the hyphæ first become thickly massed together and much septated to form a compact tissue often pseudoparenchymatous in structure—the stroma—upon or within which the fructifications appear. In the case of this Nectria little of this special compact tissue or stroma is developed. It is merely represented by the stalks of the conidial cushions.

Conidiophores may occur separately or be joined together into compound bodies. In this fungus they are conglutinated into a wax-like head, to which the name sporodochium* has been applied.

---

* Massee, British Fungus Flora. vol. III., 1893, p. 270.

Neither stroma nor to any extent has mycelium been noticed covering the external surface of the scale. Zimmermann* speaks of the stroma of *N. coccidophthora* as being shortly stalked, using the word here evidently as equivalent to sporodochium.

The stalk of the sporodochium varies considerably in length; the extremes met with were 1·2 and 0·15 mm. Very commonly the length is 0·2 to 0·3 mm. with a breadth of 0·15 to 0·3 mm. Zimmermann* gives the length of the stalk from 0·3 to 0·4 mm.

The head is more constant in its proportions, about 0·4–0·5 mm. long by 0·25–0·4 mm. broad, agreeing closely with Zimmermann's figures for length, viz., 0·4–0·45 mm. He says the head is enveloped in a sheath of sterile hyphæ connected together sideways by ladder-like cross-pieces. In the Ceylon specimens this sheath is also present. It can easily be overlooked, as it adheres closely to the conidial mass and is not readily distinguished from the conidiophores themselves. It consists of parallel septate hyphæ, stouter than those bearing the conidia (3μ compared with 2μ). At long intervals hyphæ adjacent to one another are connected by narrow and extremely short cross-pieces ($1{\cdot}3 \times 1{\cdot}4\mu$). A distance of 70μ may occur between two successive connections (fig. 13).

The conidiophores are filiform; at any rate they do not bifurcate in the upper part (fig. 12). They may branch a little near the base.

The conidia are long, multiseptate, and slightly curved with somewhat falcate ends (fig. 11). The septa vary in number; extremes met with were 5 and 10, 9 is about the average, though 7 is very common. This variation may be partially accounted for through differences in age. Average length 90μ. Some measured as much as 104μ, and others as little as 68μ. Breadth 6–9μ. Zimmermann's numbers for septa are 7–9, and for measurements 110–$120\mu \times 6\mu$. Thus the conidia of the Java form appear to

---

* Zimmermann, *loc cit.*

be somewhat longer. Berkeley and Broome's species, *N. aurantiicola*, is described as having multiseptate conidia 94μ[*] long, very near the above average for the Ceylon *N. coccidophthora*. A smaller variety of conidium is also mentioned by these authors, only 3-septate and 20μ in length. Such have not been found as a distinct feature of any of the sporodochia examined by me. There is the possibility of these shorter and less septated conidia being immature.

Ascus-stage.

The perithecia appear later grouped around the stalks of the old and disappearing sporodochia. Thus both types of fructification may be considered as borne on a feebly developed stroma (fig. 8). As many as seven perithecia have been counted clustered round the stalk or base of a sporodochium. They are deep pink nearly spherical bodies with an average diameter of $200–225\mu$. The ascus is of the usual Nectria pattern ($120 \times 9\mu$) (fig. 15). The two-celled oval ascospore measures $12–15 \times 7–9\mu$ (fig. 16). The perithecia described by Zimmermann are very similar. His measurements make the perithecium rather bigger and the ascospore somewhat longer. Those of *N. aurantiicola* are also very similar, except in colour which is given as orange.

This Ceylon Nectria has been collected by Mr. Green and the author on five species of coccids belonging to three genera, all included in the Diaspidineæ. Further details respecting these specimens are to be gathered from the Table at the end of the paper.

Till a comparison can be made with fresh examples of the Java species it does not seem at all advisable to make a new species or even variety of this common Ceylon Nectria. My own observations and measurements differ so little from those of Zimmermann that at present I am

---

[*] In their paper (*loc. cit.*) the measurements are given in fractions of the inch. They have been converted into the metric scale for the sake of comparison.

inclined to regard the two as identical, especially as they both occur on the same type of scale-insect.

Relative to *N. aurantiicola* it is a point of some significance to remember that it was formed on orange twigs and appeared to be on a coccid. The above Nectria first discovered by Green has often been found on stems of Citrus spp., trees largely frequented by the Diaspidineæ. It thus seems possible that *N. aurantiicola* described by Berkeley and Broome may have been the same fungus. A difference in colour of the perithecia is not to be trusted if the material was examined some time after it was collected. The deep red of such perithecia may have faded.

As regards the Brazilian species, *N. coccorum* and *N. coccogena*, enumerated in Saccardo's Sylloge Fungorum, the first one is described as having orange-red perithecia, a point of distinction if this was the colour of the fresh specimens; its ascospores are also considerably longer. No conidial fructification is mentioned. I have not been able to see a description of the second one.

Before passing on to the next genus, a form of Nectria found on one occasion only and differing somewhat from the above deserves some notice.

2.—*Nectria, sp., differing slightly from 1.*

A bamboo bush growing in the nursery of the Royal Botanic Gardens, Peradeniya, in December, 1898, was infested with scale, upon which were growing two kinds of fungi. The scales on the upper surface of the leaves were attacked by a Nectria, and those on the lower side by a gray mould (Verticillium).

Some uncertainty existed as to the exact species of bamboo. The Curator informed me that it was perhaps *Bambusa Oliveriana*, Gamble. He thought it had come along with others from Calcutta, and as it always had a sickly look it had not been removed from the nursery. Mr. Green identified the scale as *Asterolecanium miliaris*, and was surprised to receive it, as he had not come across this insect in the Island before. Hence it is just possible that this coccid with its fungous parasites had been imported from India upon the bamboo.

The Nectria as already pointed out occurred invariably on the upper surface of the leaves. Some of the scales thus situated were covered with a thin white mycelium. From beneath them protruded light red bodies, the sporodochia. On older leaves deep pink nearly spherical bodies, the perithecia, were found similarly placed, instead (fig. 17).

Conidial stage (Fusarium).—The pale red sporodochia had practically no stalk (stroma). They did not stand erect, but grew out horizontally for a short distance (about 0·18 mm.) from the rim of the scale. Two or three were usually the number to a single scale, but as many as five were seen. Often one, resembling a fish-tail, protruded from the posterior end of the insect (fig. 18).

The conidia were similar to those of *N. coccidophthora* already described, and measured $100\text{–}110 \times 5{\cdot}5\text{–}7{\cdot}5\mu$. Their septa varied from 5–9.

Ascus-stage.—The perithecia occurred solitary or in groups of 4 or 5. They were broadly ovate in shape and bright pink in colour, measuring 255μ in height and rather less in breadth. The ascus of the usual type measured $115 \times 13{\cdot}5\mu$; the ascospore,elliptical and somewhat pointed, $22\text{–}27 \times 9\text{–}10\mu$ (fig. 19).

In no marked feature except in general appearance does it differ from the common Ceylon form. Its sporodochia are not so prominent, do not stand erect, and have no stalk; but the conidia themselves are almost identical. The perithecia and asci are also very similar, but the ascospore is distinctly larger. In this latter respect it agrees more closely with the description of *N. coccorum** which has ascospores measuring $22\text{–}25 \times 5\mu$. It also corresponds with this species by having its perithecia solitary or in small groups, and by the absence of stroma.

---

* Saccardo, S. F. Addit to vols. I.–IV., p. 203.

The subgenera Eu-Nectria and Dialo-Nectria, as already indicated, are distinguished from each other according to the presence or absence of a fleshy stroma, and as to whether the perithecia occur in clusters or solitary. This is a somewhat arbitrary distinction, at any rate as far as these scale Nectrias are concerned. One and the same species might be placed with equal justification, in either subgenus. Lindau, in "Die Pflanzenfamilien"* says the genus requires monographing, since the alleged subgenera are insufficiently marked off from one another.

It is to be noted that this bamboo Nectria was growing on a scale belonging to a different sub-family, the Lecanodiaspidinæ.

As already pointed out, a curious feature about the scales on this bamboo was the restriction of the Nectria to those on the upper surface of the leaves. On those of the lower side occurred a Verticillium. This will be referred to in detail under the Fungi-imperfecti. It may possibly be connected with the Nectria. Verticillium is known as a conidial stage of a Nectria.†

Genus *Lisea*, Sacc.

This genus differs from Nectria in having blue or violet perithecia instead of red ones. A new species, named *L. Parlatoriæ*,‡ has been described by Zimmermann, parasitic on a scale-insect. It was found at Buitenzorg, Java, on *Parlatoria zizyphi* on Citrus leaves. No conidial stage is mentioned. The genus is known to have one of the Fusarium type. Lisea has not yet been found on scale-insects in Ceylon.

(?) Genus *Calonectria*, de Not.

On two occasions Mr. Green has supplied me with leaves infested with scale, on which were situated perithecia agreeing closely with those of Calonectria.

---

* Teil I., Abtheil. I., p. 358.

† Saccardo, S. F., vol. II., p. 511.: Nectria solani.

‡ Zimmermann, *loc. cit.*

1.—*On* Mytilaspis citricola *on orange leaves.*

The perithecia occurred in groups, each resting on a small mat of hyphæ proceeding from the scale. No stroma was seen. They were pale brown in colour, globular in shape with a wort-like ostiole (pore), and measured 217μ in diameter. The ascus (70–84 × 12–14μ) contained 8 spores somewhat irregularly arranged (fig. 20). The spindle-shaped ascospore (fig. 21) was conspicuously biseptate and less so 4-septate perhaps owing to immaturity and measured 30–46 × 6·5–7μ. Its lower end, as situated in the ascus, tapered with a blunt point, the upper end being acute and sharp.

2.—*On* Chionaspis vitis *on leaves of Loranthus, sp.*

Similar to 1, but the perithecia were dark brown and seemed old ; 320μ in diameter. The ascus measured 85 × 16μ, and the spore 55 × 7·5μ ; it was 5-septate (fig. 22).

No conidial fructifications were found in connection with either of these supposed Calonectriæ.

Genus *Ophionectria*, Sacc.

A fungus allocated to this genus and named *O. coccicola* (Ell. and Ev.) Berl. and Vogl.* was found on a living coccid on the leaf of Citrus in Florida. Zimmermann† has discovered it in Java on *Parlatoria zizyphi*, and suggests the possibility of its having been imported from America. He describes the conidial stage of it for the first time. It has not been found as yet in Ceylon.

Genus *Sphærostilbe*, Tul.

The perithecia of *Microcera coccophila*, a conidial form first discovered on scale-insects by Desmazières,‡ were described by Tulasne§ in 1865 and named *Sphærostilbe coccophila*. Since then similar perithecia have been found connected with this Microcera in the United States. Though the conidial form is common in Ceylon, perithecia have not yet been found.

---

* Saccardo, S. F., vol. IX., p. 996.

† Zimmermann, *loc. cit.*

‡ Desmazières, *loc. cit.*

§ Tulasne, Carpologia, vol. III., p. 105.

There seems to be some ambiguity as to the characters of the genus Sphærostilbe. In Lindau's scheme of classification of the Hypocreales (Die Pflanzenfamilien, Teil I., Abth. I., p. 347) the tribe Nectrieæ is divided into two main divisions, viz., genera which have Stilbum-like conidial fructifications and those which have not. The former contains amongst several others the genus Sphærostilbe, while the latter includes Nectria. In other respects these two genera are alike. On this basis how can the above species be reckoned a Sphærostilbe, when it has the Microcera form of conidial fructification? Should it not be rather put in the genus Nectria? It seems to me in any case hardly justifiable to separate Ascomycetous genera merely on differences in their conidial fructification, especially as the same species may possess more than one type of conidiophore. To me it would be sounder policy to construct genera only on distinctive features in the ascus-stage and to use differences in the lower kind of fructification for subdivisions within the genus. Consequently I should be inclined to refer the species in question to the genus Nectria, and at the same time to incorporate with it the other species of Sphærostilbe as well, provided that no common feature can be found in the perithecium and its contents to distinguish these forms from those of Nectria. The scale-insect fungi of the conidial genus Microcera will be described in detail in the part devoted to the Fungi-imperfecti.

Genus *Broomella*, Sacc.

This genus is characterized by having its perithecia partially sunk in a fleshy stroma, but its ascospores are not thread-like as in Hypocrella and Cordiceps. A new species named *B. Ichnaspidis*, has been found by Zimmermann* on a scale-insect, *Ichnaspis filiformis*, on leaves of *Coffea liberica* and *Elæis*, sp., at Buitenzorg, Java. Its ascospores are many celled (up to 16).

---

* Zimmermann, *loc. cit.*

A larger form of this fungus has also been collected in Java and is described as a separate variety by this author.

Fungi referable to this genus have not yet been discovered on scale-insects in Ceylon.

Genus *Hypocrella*, Sacc.

This genus is one which may eventually be shown to be of common occurrence on scale-insects. It is characterized by having disc-shaped or hemispherical stromata in which the perithecia are sunk. Its thread-like ascospores often break up into sporules.

The species so far described have been found on leaf and stem surfaces in the tropics. Quite possibly in some of these cases a scale-insect is the real host and not the plant.

The conidial fructification, as far as is known, belongs to the genus Aschersonia—one which occurs frequently on scale-insects.

Zimmermann in his paper* describes for the first time a new species of Hypocrella (*H. Raciborskii*), having as its host a scale-insect. It was found by Raciborski in Central Java on a coccid fixed to a Citrus leaf. It possesses a conidial fructification of the Aschersonia type. The conidial chambers (pycnidia) are situated in the lower part of the stroma whereas the perithecia are formed in the upper part.

A Hypocrella distinct from the above has been collected in Ceylon, showing no conidial fructification.

Though numerous examples of Aschersonia have been found in Ceylon, only in one have the stromata possessed perithecia as well as pycnidia.

A third example of a probable Hypocrella had a stroma not strictly referable to Aschersonia.

Ceylon Forms.

1.—On *Lecanium expansum* on the upper surface of leaves of *Schumacheria alnifolia*, Maskeliya, Sept., 1901 (fig. 23).

---

* Zimmermann, *loc. cit.*

The bright orange stromata consisted of a thickened rim and a raised central crown, thus somewhat hat-shaped. The largest measured as much as 7·5 mm. in diameter: the medium ones 4·5 mm., and some of the small ones 2·5 mm. The rim is dotted over with dark brown spots, the openings of the perithecia; sometimes these spots may extend a short way up the crown. The colouring is not quite uniform, the rim being nearer red, and the crown nearer yellow. The interior of the stroma is light yellow.

The flask-shaped sunken perithecia measure 400–440 μ in depth and the narrow asci 103 × 7·3 (fig. 24).

The ascospores were perhaps thread-like, but they had split up in short rods 6–7 × 1·5μ.

No pycnidia could be observed in the stroma, so this latter was solely in the ascus-stage.

This Hypocrella is evidently quite distinct from the Java one, *H. Raciborskii*, Zimm., as the perithecia are just in the reverse position; if new to science, as it appears to be, it might receive the name of *Hypocrella coccophila* or *Lecanii*.

2.—On *Chionaspis vitis* on leaves of Loranthus, sp., Horton Plains, Sept., 1900.

The material was scanty, consisting in all of seven pale buff or whitish stromata. Only one of these possessed perithecia. The others were in the conidial (Aschersonia) condition. The somewhat flask-shaped perithecia measured 500μ deep and 160μ in the broadest part. The asci were apparently immature with thread-like spores forming in them.

3.—On *Lecanium*, sp., on lower surface of leaves of *Gelonium lanceolatum*, Pundalu-oya, Nov., 1898.

The conidial stages of this distinct and peculiar fungus are described under the Fungi imperfecti.

Sunk in the upper part of an old black stroma occurred flask-shaped perithecia with slender asci full of sporules quite small and cylindrical, resulting most likely from the breaking up of thread-like ascospores (figs. 46, 47, 48).

This fungus with black hemispherical stromata is apparently a species of Hypocrella, but its conidial stage can hardly be included in Aschersonia on account of the colour and other peculiarities.

(?) Genus *Drussiella*, Pat.

The fungus, supposed to belong to this genus, has not been examined by the author. It is only referred to Drussiella on account of its external resemblance and habit to *D. tuberiformis*, Pat., the only member of the genus, found on the haulm of a bamboo (Arundinaria) in tropical America.*

The specimen in question has been found several times by Mr. Green on Arundinaria at Pundalu-oya, Ceylon. He considers it to always originate on a coccid. It commences beneath the leaf-scale of the bamboo and swells out into a large black tuber (stroma). The scale–insect, apparently associated with it, is *Aclerda distorta*.

Pyrenomycetes-Perisporiales.

Genus *Apisporium*, Kunze (*Capnodium*, Mont).

This genus consists of black fungi often found growing on "honey dew," deposited upon leaves by aphides and some kinds of scale-insects. It appears under several conidial forms, which are much commoner than the ascus stage.

An instance of Capnodium growing on the sugary excretion emitted by a coccid (Monophlebus) is recorded in a paper by Stebbing.† But it may also be parasitic on certain scale-insects as well. This, at any rate, is possible from a paper by Britton‡ on the natural enemies of the San José scale (*Aspidiotus perniciosus*). He mentions a fungus, probably a species of Capnodium, as causing a reduction in the number of scales on infested trees. If he is

---

* "Die Pflanzenfamilien." Teil I., Abtheil, I., p. 367.

† Stebbing. Journ, Linn. Soc., XXIX., 1904, p. 154.

‡ Britton. U.S.A. Exp. Sta. Connecticut, Report Entom. pt. II., 1902.

correct in his identification of the fungus, it is an interesting fact, for the Diaspidinæ, to which the San José scale belongs, do not secrete "honey dew;" thus the fungus can hardly in this case be growing upon such excretion.

Plectascineæ.

Genus *Myriangium*, Mont. and Berk.

A black fungus referable to this genus has often been observed in Ceylon on the surface of leaves and stems associated with Coccidæ.

Zimmermann[*] has come across a similar fungus at Buitenzorg in Java on leaves of *Coffea liberica* and *Elæis*, sp., and associated with the scale *Ichnaspis filiformis*. He names it *Myriangium Duriæi*, Mont. and Berk.

The genus in "Die Pflanzenfamilien[†]" has a special tribe to itself, the Myriangiaceæ, which is attached to the Plectascineæ, one of the main divisions of the Ascomycetes. Three species are mentioned there. Others have been added since.[‡]

The fungus consists of a moderate amount of hard pseudoparenchymatous black stroma situated on the surface of leaves or stems. From this the perithecia grow out as circular protuberances compressed together. It has no ostiole like the true Pyrenomycetes, but when ripe its hard wall breaks away scattering the spores. The asci are not borne on a special hymenium in the perithecium, but irregularly distributed through a ground tissue filling the receptacle. The inner part of the wall of the ascus is mucilaginous, and by the swelling of this it bursts and the spores are released. The ascospore is hyaline, multicellular, muriform with slight constriction in the middle.

The Ceylon form has perithecia measuring in height 300–375 and in breadth 420–675 μ, asci ovate to globular

---

[*] Zimmermann, *loc. cit.*

[†] Teil I., Abth. I., p. 319.

[‡] Hennings, Hediwigia, XLI., Beiblatt 2, 1902, p. 54. McAlpine, "Australian fungi, two new species of Myriangium," Linn. Soc. N.S.W. April 27, 1904.

40 × 30 μ (fig. 26) and ascospore 20-30 × 8–11·5 μ (fig. 27).

It agrees very closely with Zimmermann's description. His measurements are for the ascus 35 μ long and for the spore 25×10.

It has been chiefly studied on *Aspidiotus camelliæ* on the stem of Osbeckia (fig. 25), and on *Chionaspis biclavis* on Tabernæmontana.

A curious point is that it has almost invariably been found associated with scales attacked by the Nectria already described, suggesting the possibility of the one fungus being in some degree dependent on the other. Myriangium being a black fungus and not unlike in external appearance and habit to Meliola and Capnodium, which follow "honey dew," it might be thought to be connected with such coccid excretion. This, however, cannot be the case here as it has only been found associated with scale-insects which do not excrete "honey dew." Notwithstanding I have always had a doubt of its parasitism. Zimmermann expresses a similar doubt. He says the fungus is not bound to the presence of the coccid and perhaps penetrates dead scales only. On account of its association with the Nectria it may follow this fungus as a scavenger feeding on the remains of the scales and possibly on the Nectria itself; thus it is probably only a saprophyte. Further observation together with inoculating experiments should explain its share in the destruction of the coccid.

A black conidial form similarly situated as the above has been found on two occasions in connection with *Mytilaspis citricola* on Citrus, and *M. lasianthi* on Codiæum, both scales being at the same time attacked by Nectria. It possessed receptacles (pycnidia) holding pale brown oval conidia produced by a hymenial lining and measuring 4×3μ Most likely this is the conidial stage of the Myriangium, but direct proof was not obtained. No conidial fructification is mentioned for the genus in "Die Pflanzenfamilien."

(B) FUNGI-IMPERFECTI.

Sphæropsidales-Nectrioidaceæ.

Genus *Aschersonia*, Mont.

This genus* was founded in 1848 by Montagne for certain conidial stages of fungi collected in the tropics on the surface of leaves. It is characterized by possessing brightly coloured hemispherical, turbinate, or pulvinate stromata, the surface of which is sprinkled over with darker coloured dots, the openings to the sunken conidial receptacles (pycnidia). The conidia are very small, fusiform, and hyaline, and are borne singly on short filiform hyphæ, which line the pycnidium and which have interspersed amongst them, as a rule, longer sterile ones, paraphyses.

In 1893, in Florida, Webber found on orange leaves badly infested with a scale-insect known as the mealy wing or white fly (*Aleurodes citri*), highly coloured pustules of a fungus. The insects and the pustules were mingled together on the surface of the leaves. Finding the fungus similarly associated on several subsequent occasions, he was led to regard it as most likely parasitic on the insect. A preliminary account of the fungus was published in 1894,† when it was provisionally referred to *Aschersonia tahitensis*, Mont. Since then the fungus has been examined by Patouillard and compared with the original specimens of *A. tahitensis*, with the result of making this fungus of the orange groves of Florida a distinct species, *A. aleyrodis*, Webber. It appears to differ, however, only slightly from *A. tahitensis*. A full account of the fungus is given in Webber's paper "On the Sooty Mold of the Orange and its Treatment."‡ In this treatise are mentioned four other kinds of Aschersonia parasitic on scale-insects, but a full description of them is reserved for a future occasion.

---

* Hennings, "Die Gattung Aschersonia, Mont." Festschrift für P. Ascherson, 1904, p. 68.

† Webber, Journ. of Mycol., VII., p. 363.

‡ Webber, U. S. A. Depart. Agric., 1897. No. 13.

Thus Webber was the first to discover Aschersonia to be parasitic on insects. He considers his observations to strongly indicate the general entomogenous nature of the genus. Though its members have in the past been described as growing (presumably parasitic) on leaves, yet it is quite possible that a coccid might be the true host. The fungus in its mature state so completely envelopes the scale, that the remains of the latter can only be made out by examining sections with a microscope. Thus unless suspicion was aroused, systematists might easily be deceived and imagine that the fungus was growing directly on the leaf. The whole genus requires fresh study from this point of view.

Till 1900 the genus consisted of some twenty species. Recently Hennings* has added five new ones from specimens received from Java. They are described as usually associated with different kinds of Lecanium, which they resemble in shape and colour. One of them, *Aschersonia sclerotioides*, P. Henn., is definitely mentioned as being situated upon a Lecanium on *Castilloa elastica*. It seems to me that here again the fungi have probably developed on the scale-insects rather than at the expense of the leaf-tissue.

Numerous forms of Aschersonia have been found in Ceylon on species of Aleurodes and Lecanium. In all cases their stromata were readily detached from the foliar surface, and no hyphæ have been seen penetrating the leaf.

The specimens to be described are separated into three groups. Each group may represent one species or perhaps more than one. The differences between forms are often so indefinite, that much more study of the whole genus is required before a useful separation into species can be attempted.

These conidial forms grouped under Aschersonia very likely belong to the genus Hypocrella. Direct evidence for this view has been given previously (see p. 29).

---

* Hennings, Hedwigia, XLI., 1902, p 140. For a recent enumeration of the species and an account of the genus, see Hennings, Festschrift für P. Ascherson, 70 Geburtstages, 1904, p. 68.

Ceylon Forms.

A.—*Forms resembling Webber's* Aschersonia aleyrodis.

Seven different lots of material collected in Ceylon have been examined, as well as a specimen from Sumatra. These have been compared with some of Webber's own material, kindly sent by him to Mr. Green and passed on to me.

Without more examples and further investigation it is impossible to claim all these forms as identical with *A. aleyrodis*. Some seem to resemble *A. tahitensis* more closely. But no sharp line of demarcation between the several forms could be made.

The conidium (fig. 30) in all is very similar, measuring 9–13 × 1·5–2μ ; it may be 3-guttulate. Paraphyses are uniformly present, but I have not been able to detect in them the peculiar darkened cells (segments) mentioned by Webber as being quite characteristic of *A. aleyrodis.*

The stromata as a rule have the flattened hemispherical shape. The pycnidial orifices are either arranged in a circle or else dotted irregularly over the surface.

The colour of the stroma varies from creamy white to bright orange-yellow, and that of the orifices may be brick-red, orange-red, or dull green. A membranous border, termed the hypothallus, surrounding the stroma and closely adherent to the leaf surface, may be present or absent. *A. aleyrodis* possesses one about a millimetre wide, while *A. tahitensis* does not.

1.—On a black *Aleurodes*, sp., on the lower surface of the leaf of *Andropogon muricatus* (cuscus grass) figs. 28 and 29.

Stroma creamy-yellow, pycnidial orifices red-brown, fairly numerous and scattered, hypothallus present.

Some stromata kept for a short time in a closed vessel showed columns of conidia rising from the pycnidial orifices in a similar manner as described by Webber.*

This form closely resembles *A. aleyrodis.*

2.—On a black *Aleurodes*, sp., on the lower surface of the leaf of *Hedyotis verticillaris.*

---

* Webber, *loc. cit.*, p. 22.

Stromata small, pinkish white; pycnidial orifices conspicuous, coral red, few in number and often arranged in horse-shoe fashion; only slight development of hypothallus. Similar to 1, except as regards hypothallus.

3.—On a black *Aleurodes*, sp., on the lower surface of the leaf of *Ochlandra*, sp. (a bamboo). figs. 31 and 32. A fine lot of material collected by Macmillan at Pussella, Feb., 1899.

Stroma creamy white, much flattened with irregular surface, large, as much as 4·5 mm. in diameter, 0·5–0·75 mm. in thickness, neighbouring ones often fused together owing to the scales being so numerous; pycnidial orifices yellow brown or greenish, inconspicuous, numerous, often crowded on the central raised part of the stroma; no definite hypothallus; pycnidium 180μ deep, very definite in shape being oval in longitudinal section with a very short neck.

This form differs from 1 and 2 in the paler and flatter stroma and in the smaller and more numerous pycnidial orifices. However some of little and perhaps younger stromata more nearly resemble 1 and 2.

4.—On a pale *Aleurodes*, sp., on the lower surface of the leaf of *Memecylon capitellatum* (figs. 33, 34, and 35).

Stroma bright yellow, fades with age; pycnidial orifices deep orange, conspicuous, often arranged in a circle or horse-shoe; a very marked hypothallus present as a rule. This Aschersonia in all essential features, except colour, resembles *A. aleyrodis.*

Interspersed with it on the same scale were plentiful flat brown circular pustules resembling Webber's sterile "brown mealy-wing fungus." It is described in a later section of this paper.

5.—On a pale *Aleurodes*, sp., on the lower surface of the leaf of *Flemingia strobilifera.*

Stroma buff-yellow, averaging 1 mm. in diameter; pycnidial orifices conspicuous, orange, few in number and often arranged horse-shoe fashion; hypothallus present, extending 0·5 to 1 mm. from stroma.

Resembles 4 very closely. A few of the stromata were old and shrunken without hypothallus, and brown or olive green in colour.

6.—On a pale *Aleurodes*, sp., on the lower surface of the leaf of *Diospyros Toposia*.

Very similar to 5, but the hypothallus not so wide, about 0·32 mm.

7.—On a pale *Aleurodes*, sp., on the lower surface of the leaf of *Filicium decipiens*.

Stroma olivaceous, without hypothallus; pycnidial orifices arranged more or less in a circle.

Most likely old stromata, similar to the old ones mentioned under 5.

The presence or absence of a hypothallus appears to me of doubtful taxonomic value. Stromata on the same leaf may or may not have it markedly developed. Atmospheric conditions perhaps have something to do with its development.

Of course such a character as to whether the fungus is epi-or hypo-phyllous is of no value, as naturally the position varies with that of the insect. Coccids usually frequent the lower surface of leaves, no doubt for protection.

B.—*Forms with rich brown unflattened stromata without paraphyses.*

This type has only once been found in Ceylon, but Mr. Green has passed on to me three apparently identical examples he has received from India.

The stromata are large, hemispherical, or even two-thirds of a sphere in shape. The surface is irregularly furrowed. The pycnidial orifices are inconspicuous and fairly numerous. There is no hypothallus. The conidia appear less fusiform, more lenticular than those of Group A., measuring 6–12 × 4–5μ (fig. 38).

They are all perhaps identical with one another and distinct from those of Group A. It is significant that they occur on Lecanium and not on Aleurodes.

1.—Ceylon example on *Lecanium psidii* on stems and midribs of *Myristica moschata* (figs. 36 and 37).

Stroma buff coloured; pycnidial orifices scattered; pycnidia regular in shape and rather shallow. A fine specimen.

Indian examples.

2.—On *Lecanium hemisphæricum* (var. *coffeæ*) on tea leaf and stem, Upper Assam.

Stroma fulvous or clay-coloured; pycnidial orifices of a darker shade and scattered.

3.—On *Lecanium*, sp., on tea stem, Kurseong.

Stroma orange to brick-red, basal part yellow; pycnidial orifices irregularly arranged.

4.—On *Lecanium*, sp., on tea leaf and stem, Darjeeling.

Stroma clay-coloured with lighter tinted base.

C.—*Form with large pycnidium, only 1-3 to a stroma.*

Quite a different type of Aschersonia to the preceding was found on a single occasion in the jungle, Horton Plains, Ceylon, by the author. Only a few stromata were obtained. The fungus was formed on a species of Aleurodes on the lower surface of the leaf of *Eugenia revoluta* (fig. 39).

The mature stroma possessed a hypothallus, surrounding a slightly raised yellow cushion from which projected upwards a short column. This bifurcated at the top into two short processes each ending in a large opening, the pycnidial orifice (fig. 40). One stroma had only a terminal orifice; and another had three. The pycnidium is deep and somewhat lobed at the base (fig. 41).

The orifices were plugged with yellow-brown or olive-green gelatinous masses of conidia. These latter, of the usual Aschersonia type, measured $10 \times 2\mu$ (fig. 42).

A Fungus with Aschersonia-like Stromata but black.

A distinct fungus resembling Aschersonia in shape and habit, but black, was found in 1898 by Green in the jungle, Pundalu-oya, Ceylon, and handed to me for examination.

The dark pustules occurred on the lower surface of leaves of *Gelonium lanceolatum* and were not at all abundant—never more than two or three on a leaf and those bearing them were scarce. The evidence for their position on a scale was not conclusive.

Two or three months later while on a visit to Horton Plains, I found a few similar pustules on the upper surface of leaves of *Calophyllum Walkeri*. In this case there was no doubt of the fungus being on a scale-insect, as sufficient remains were there to allow Mr. Green to identify it as a species of Lecanium.

A third example, probably identical with the above, was sent to Mr. Green from Java. It was on a *Lecanium*, sp., on the leaf of *Jambosa aqua*.

Description of the Fungus.

The dark brown or black pustules (stromata) are hemispherical in shape with an even surface and with usually a swollen basal collar. The colour of the interior is orange, only the exterior is black. They measure from 1–2 mm. in height.

Some, apparently the younger ones, were covered (especially the upper part) with a gray bloom, easily rubbed off revealing the shiny black surface beneath. This bloom is composed of conidia. In fact nearly the whole surface of such a stroma is covered with a conidia-bearing hymenium, similar to what lines the pycnidia of Aschersonia. The conidia resemble those of this genus being fusiform, hyaline, and guttulate, and measuring $8 \times 2\mu$ (fig. 45).

Some stromata possessing this bloom revealed, with the aid of a lens, minute pores arranged in a circle around the lower part; these are the openings of pycnidia, likewise lined with a hymenium bearing conidia similar in size and shape to the superficially borne ones. The pycnidium is somewhat lobed or branched (figs. 43 and 44).

In what was most likely a still older stroma, which had lost its bloom and looked shrunken, were flask-shaped perithecia with asci. These occurred sunken in the upper part of the stroma. Reference has already been made to this example under Hypocrella (see p. 30).

Hence it is probable that all the above black pustules belong to a species of Hypocrella.

The conidial stroma though suggesting Aschersonia differs from all hitherto described species; if it is to be admitted, then the characters of the genus will require to be somewhat modified.

By searching the up-country jungles of Ceylon more of this fungus might be procured and thus permit its systematic position to be definitely settled.

Hyphomycetes–Mucedinaceæ.

Genus *Cephalosporium*, Corda.

As was pointed out in the introduction to this paper, Zimmermann named a fungus which he found attacking the green bug (*Lecanium viride*) on the coffee in Java, *Cephalosporium Lecanii.*

The short account* he wrote about it was intended more for the benefit of the Java planters than as a botanical treatise. Beyond this pamphlet I have come across no further allusion to such a type of fungus in connection with scale-insects.

In Ceylon a fungus similar to this Java one has repeatedly been observed by Mr. Green and myself on species of Lecanium. In fact he has been aware of it in the Island for some years on the green-bug. To particularize, four separate lots of material have been collected on *L. viride*, three lots on *L. hemisphæricum*, and two on *L. nigrum*. For details see Table at the end.

The fungus shows itself to the naked eye as a white or pale yellow powdery bloom around, and to some extent over the scales (figs. 49 and 50). The powdery or mealy appearance is due to innumerable conidial heads covering the

---

* Zimmermann, "Over eene Schimmel epidemie der groene Luizen," 1898, Biutenzorg, Java.

hyphæ. The external part of the fungus develops as follows:—Hyphæ radiate out on all sides from below the scale for a millimetre or more over the leaf surface. Each hypha produces at frequent intervals short lateral branches, the conidiophores, 16-20μ in length. Each conidiophore bears on its apex a spherical head of conidia, enveloped in mucilage (fig. 53). This head with a diameter of 4μ appears when dry as a glistening globule, the individual conidia not being distinguishable. On treatment with water the mucilaginous matter dissolves and the conidia are dispersed; sometimes the last one produced remains attached to the tip of the hypha. In order to examine the conidia *in situ*, the fungus should be mounted in dilute acetic acid, which prevents the mucilage from dissolving and renders the conidia visible fig. 54). Five to seven are usually present in one head. They are really abstricted from the conidiophore in succession, but instead of remaining in a chain become aggregated together into a spherical mass by the mucilage which is secreted. Some infected scales kept in a damp atmosphere showed conidiophores bearing conidia in short curved chains, owing perhaps to mucilage not being able to mass them together.

The colourless conidia are minute measuring $3{\cdot}5\text{–}4 \times 1{\cdot}4\mu$, figures almost identical with those given by Zimmermann for the Java form. They are shortly cylindrical or nearly oval or slightly sausage-shaped.

The conidiophores may be so numerous that here and there the mucilaginous heads, which touch one another, fuse to form larger masses of conidia.

The lateral short branches of the main hyphæ, which here are termed conidiophores, may even branch themselves, so as to produce two to four heads of conidia (fig. 52).

If a scale from affected material, but with no external fungus visible, be removed from a leaf and placed on a microscopic slide in a damp chamber, the development of the conidial part outside the insect can be readily followed. After one day the radiating hyphæ proceeding from the margin of the scale were just visible ; after two days the first conidiophores appeared, and after four to five days the whole insect was surrounded by a fringe of hyphæ bearing numerous conidial heads (fig. 51).

An example of Cephalosporium parasitic on *Lecanium hemisphæricum* var. *coffeæ* on the stem of *Jussiæa suffruticosa* possessed a few perithecia. These were resting on the peripheral part of the fungus, and were globular in shape and pale yellow in colour. The long asci within unfortunately showed no definite spore formation, and so were most likely immature. However, their presence points to the probability of this Cephalosporium being a conidial stage of some genus of the Hypocreales, to which group nearly all the other Ascomycetous scale-fungi described belong.

Before leaving this genus a remark is needed upon its systematic position in the Fungi imperfecti. According to the synopsis given in "Die Pflanzenfamilien"* Cephalosporium is placed in a small group of genera characterized by the conidia *not* being enveloped in mucilage, whereas the neighbouring genus Hyalopus has its conidia so held together. The Ceylon forms and the Java one, according to Zimmermann, possess mucilage, so on this classification they should both be referred rather to Hyalopus.

Genus *Hyalopus*, Corda.

A new scale fungus has quite recently been described by Dop† who refers it to the genus Hyalopus.

About 1902 the cocoanut palms of Martinique were severely attacked by a scale-pest, a species of Aspidiotus very closely allied to the San José Scale (*A. perniciosus*). In fact the pest assumed such alarming proportions as to threaten the cultivation of these palms. Suddenly the insect received a check, and in a comparatively short time disappeared. Dop has shown this to be due to the rapid spread of a fungus

---

* Teil I., Abtheil, I., pp. 417-418.

† Dop, Bull. Scient. France et Belgique. XXXIX., 1905, p. 135.

disease. He names the species *Hyalopus Yvonis*, in honour of M. Saint-Yves of Martinique. He says it differs from *Acrostalagmus coccidicola* referred to below, in slight details, chiefly in having simple and not branched or whorled conidiophores. It forms little gray patches over and around the scales. The fertile hyphæ (conidiophores) are upright, and are each terminated by a mucilaginous sphere containing several conidia measuring 4 × 1–1·5μ. These readily bud like yeast in water.

The investigator has tried various culture and inoculation experiments. In a 5 per cent. sugar jelly the fungus increases wholly in the yeast fashion, hyphæ only appearing as the nutritive material becomes exhausted. In broth made of scale-insects the conidia form a mycelium. Hence the fungus may either assume a mycelial or a yeast form, according to the medium, in which it is grown. In the body of the coccid it appears to increase yeast-like, but externally it forms a mycelium bearing the above mentioned conidiophores.

His inoculations have only been partially successful. He has tried them on *Aspidiotus Nerii*, and finds that success only attends inoculations with the yeast form. He has not been able to obtain by artificial infection a mycelium bearing conidia.

This fungus is evidently near akin to the Ceylon and Java Cephalosporium, though hardly identical. Its great capacity of budding like yeast is a difference. It is a point also of some significance to note that this fungus occurs on Aspidiotus, whereas Cephalosporium has so far been only found on Lecanium.

Genus *Acrostalagmus*, Corda.

This genus differs from Cephalosporium in having upright conidiophores, branched in a verticillate manner. Guégnen* describes in his recent work "On Fungi Parasitic on Man and Animals," a new species which he found growing on the scales of a coccid on a shrub in a green-house

---

* Guégnen, *loc. cit.*, p. 253.

in the Paris Exhibition of 1900. He names it *A. coccidicola*. The mycelium formed around the body of the insect is of a deep yellow colour.

The fungus is easily cultivated upon various artificial media. The mucilaginous heads usually contain 10–12 conidia, occasionally as many as 16. The conidium is cylindrical 4–5 × 1μ.

This fungus is evidently distinct from the Java and Ceylon Cephalosporium just described, though perhaps somewhat allied. The species of scale-insect, upon which it was found, is not mentioned in the account.

Genus *Sporotrichum*, Link.

Guégnen* in his account of the species of this genus found growing on insects, mentions one, *S. Lecanii*, discovered by Peck in North America on a Lecanium. This is the only instance of this habit for the genus I have been able to find. No Ceylon specimen on a coccid has yet been found.

Another species, *S. globuliferum*, Speg., is a well-known parasite of the Cinch-bug (*Blyssus leucopteris*). Inoculating experiments with it have been conducted in the United States of America.†

The genus Sporotrichum is closely related to Botrytis.

Genus *Verticillium*, Nees.

An example of this genus on a coccid was found for the first time some years ago in North Italy, and named *V. heterocladium*, by Penzig.‡ It was growing on *Lecanium hesperidum* on orange leaves, covering the scales with a white mould. This fungus according to Guégnen's account§ appears to be widely spread; it has been obtained both in Africa and the Antilles.

---

* Guégnen, *loc. cit.*, p. 251.

† Forbes, Illinois Agric. Exp. Station, No. 38, 1895; Garman, Amer. Monthly Micro. Journ. XXIII.

‡ Saccardo, S. F., vol. IV., 1886, p. 151.

§ Guegnen, *loc. cit.*, p. 252.

A mould referable to this genus was found by the author in the Royal Botanic Gardens, Peradeniya, Ceylon, on the scale, *Asterolecanium miliaris*, which was infesting the leaves of a bamboo bush. A curious point about the position of the fungus was its restriction to those scales fixed to the lower side of the leaves, while those on the upper surface were attacked by a species of Nectria already described (see p. 24).

The Verticillium covered the scale with a gray mycelium, which extended as well some distance around over the leaf surface. The scale together with the fungus could easily be detached with a needle from the leaf and mounted on a slide for examination. Through the microscope numerous conidiophores could be seen standing erect from the mycelium. Each is composed of a stalk bearing at the top a single whorl of 5–9 short pointed branches, sterigmata, bearing solitary conidia (fig. 55). The stalk measured 38–44 × 3μ, the sterigma 8–11μ in length, and the conidium 4 × 1·4μ. The latter is slightly curved, in fact sausage-shaped.

Thus the Ceylon specimen has an unbranched conidiophore with one whorl of sterigmata, whereas the genus is usually characterized by possessing several superposed or alternate whorls of sterigmata. *V. heterocladum*, already alluded to, has a compound conidiophore with verticillate branches ; so the Ceylon specimen is quite different from it.

Hyphomycetes-Dematiaceæ.

(?) Genus *Peziotrichum*, Sacc.

A totally distinct and new scale fungus was found by Mr. Green on *Chionaspis aspidistræ* on the leaf of a small pot palm at Peradeniya, October, 1899. More of this fungus has since been obtained by him on *Aonidia*, sp., on Memecylon leaf, Elephant Pass, Ceylon. It is a conidial form and was briefly referred to in the paper[*] read before the British

---

[*] Parkin, *loc. cit.*

Association in 1900, as belonging to the Dematiaceæ, probably near the genus Campsotrichum. On closer examination it agrees better with the neighbouring genus Peziotrichum founded by Saccardo in 1893,* to receive a fungus collected in Australia on twigs and thorns of *Bursaria spinosa*. It differs in having spherical instead of cylindrical conidia, and so agrees with Botryotrichum in this respect.

The Ceylon fungus appears to the naked eye as a minute tuft of brown or black bristles standing up around the scale, subtended by a small amount of brown mould covering and surrounding the scale (figs. 56 and 57). A microscopic examination reveals the following structures. From below the scale proceed horizontal hyphæ ramifying a little way over the leaf surface. These produce at frequent intervals very short side branches, each bearing a large apical spherical conidium (figs. 60 and 61). The upright sterile bristles are attached to the rest of the fungus close to the margin of the scale. In fact the external visible part of the fungus consists: (1) of a creeping mat of septate hyphæ covering and surrounding the scale, and bearing on short lateral processes single conidia; and (2) of sterile stouter septate hyphæ cohering together to some extent in bundles and standing erect around the periphery of the scale. The whole fungus, with the exception of the hyaline tips of the bristles, is brown throughout, including the conidia. The spherical conidium, 16μ in diameter, has a yellow-brown wall and contents which stain deeply with iodine, suggesting the presence of glycogen.

The main conidial hyphæ have a thickness of 4–5μ, and the bristle ones of 8–10μ near the base. These latter taper somewhat towards the apex, are regularly septated and have a colourless slightly swollen apical segment (figs. 58 and 59): total length 0·8–1 mm. They cling together as a rule in bundles of 12 or so, the lower parts are often separate, but the upper parts are closely coherent. Special sterile hyphæ

---

* Saccardo, Hedwigia, 1893, p. 58, and Syll. Fung. XI., 1895, p. 614.

(bristles) are common to several genera of this group (Amerosporæ) of the Dematiaceæ.

This Ceylon fungus differs in two small particulars from Saccardo's genus Peziotrichum. The conidia in colour are brown and not hyaline : in shape are spherical rather than cylindrical or rod-like. In fact, owing to its spherical conidia it approaches the next genus Botryotrichum.

As to the ascus-form of this fungus, no clue has yet been obtained.

HYPHOMYCETES-TUBERCULARIACEÆ.

Genus *Fusarium*, Sink.

(See Nectria, pp. 21 and 25)

Genus *Microcera*, Desm.

This conidial genus as already pointed out (p. 12) was established by Desmaziéres in 1848 for a red fungus, *M. coccophila*, he found attacking scale-insects on tree-stems in France. Tulasne, in 1865, described the ascus-stage of this fungus, and named it *Sphærostilbe coccophila* (see p. 27). The fungus has been shown in the past to be widely spread in Europe and N. America on coccids belonging to the Diaspidineæ.

Forms referable to Microcera have been found on several occasions in Ceylon in the year 1898 and subsequently. Specimens have also been received by the author through Mr. Green from West Africa, Mauritius, and the West Indies. Species considered distinct have been described for Australia and Tasmania. Thus Microcera is probably widely distributed on scale-insects throughout tropical and temperate regions.

In most cases only the conidial fructification (Microcera) has been seen. Perithecia (Sphærostilbe) appear to be commonly developed in the United States of America.* In the Ceylon examples and in others examined by the author they have never been found. Thus the ascus-stage

---

* Rolfs, Gossard, Forbes, *loc. cit.*

does not appear so readily as in the case of *Nectria coccidophthora.*

The forms of Microcera so far found on scale-insects have not all been referred to the original species, *M. coccophila.* Saccardo* gives the characters of six species, two of which, *M. coccophila* and *M. rectispora*, are described as situated on coccids. *M. rectispora* was collected in Queensland on the orange, and named so by Cook and Massee.

Recently McAlpine† has diagnosed two new species, *M. tasmaniensis* and *M. mytilaspis*, from examples discovered in Tasmania and Victoria respectively. The former was found by Lea in 1901 on *Aspidiotus*, sp., on Eucalyptus bark ; it differs from *M. coccophila* in colour, and in its conidia being only 3-septate. The latter was on *Mytilaspis*, sp., on *Hymenanthera dentata ;* it is bigger and has multiseptate conidia.

Ceylon Specimens of Microcera.

The fungus first appears from below the scale at several points as small red protuberances. These enlarge and join to form a thick coral red stroma around, and to some extent over the scale. As a rule the stroma does not cover the whole exterior surface of the scale, the central part being left bare. The conidial fructifications (sporodochia) arise from slight depressions in the peripheral part of the stroma; they often radiate outwards in star-fashion. Each in its young state is enveloped in a loose sheath of whitish parallel fibres (hyphæ). On maturity the fibres of the sheath break away from one another at the top, and the bright red apex of the sporodochium shows itself. The broken sheath persists, partially covering the conical or cushion-shaped sporodochium. The individual hyphæ of the sheath have a thickness of 4μ, and are joined to one another here and there by very short lateral ladder-like connections, as in the closely adherent sheath of Fusarium, already described under Nectria.

---

* Saccardo, S.F., vol. X., p. 731.

† McAlpine, Journ. Agric. Victoria ; XI., part 7, 1904.

The conidia are of the Fusarium type (fig. 66). The number of their septa were observed to vary from 3 to 9. On the whole they are somewhat more curved than the conidia of *Nectria coccidophthora*. The hyphæ bearing them are filiform and only branch at the base.

The Ceylon forms so far collected may be divided into three types; whether of specific value, it is difficult to say.

(*a*) On *Aspidiotus aurantii* and *Mytilaspis citricola* (fig. 62).

Stroma not conspicuously developed; sporodochia arranged in stellate fashion around the scale, as many as eight, cushion-shaped or conical, projecting outwards horizontally or slightly inclined upwards; its sheath may extend for 600μ, while the conidial part only projects 370μ, breadth varies from 337–525μ (fig. 63). Conidia, average size 103·8 × 4·6μ with several septa.

(*b*) On *Aonidia bullata* and *A. crenulata* (fig. 64).

Stroma well developed, broad border 133–160μ wide; sporodochium only one (or at most two) to a scale, springing from the posterior end of the insect as a horizontal or obliquely inclined conical structure with its bright pink tip usually just visible amid the jagged fringe of the sheath, measuring 150–300 × 180μ (fig. 65). Conidium 80–88 × 5–6·5μ.

The position of the sporodochium is probably accounted for by the structure of the insect. In the genus Aonidia the scale is closed below, so the anal and genital apertures would afford the easiest exit for the fungus.

(*c*) On *Aspidiotus camelliæ* (?) on the bark of a jungle tree.

Stroma conspicuous; sporodochia columnar or somewhat club-shaped, projecting vertically upwards around the scale, measuring 600 × 180μ. The sheath, white or buff in colour; conidia, usual curved septate type 80 × 8μ.

On one piece of bark around some of the scales pink perithecia of the Nectria or Sphærostilbe type were situated, probably the ascus-stage of this Microcera. However the proof of the two fungi being in connection was not clearly established by this material.

Forms of Microcera from other Countries examined by the Author.

1. On *Fiorinia fioriniæ*, lower surface of leaves of Camellia, Mauritius.
2. On *Aspidiotus articulatus*, Coffee leaf, West Coast, Africa.
3. On *Ischnaspis filiformis* and *Aspidiotus articulatus*, Coffee plant, Grenada, West Indies.

The above three appear identical with one another and also with the Ceylon type (*a*), which may be considered to be typical *M. coccophila*.

The septa of their conidia varied from 4–7. The conidium itself measured 70–99 × $3{\cdot}8\mu$. The sporodochia 500 × 350μ.

Guégnen remarks in a note[*] at the end of the section devoted to Fusarium, that Microcera in his opinion should be united to Fusarium, as the diagnosis originally given for it by Desmazières in 1818 is not distinctive enough. On referring to Desmazières' paper[†] I see that he lays stress on the sheath (velum) as a prominent feature. This structure has not been specially commented upon by later systematists. In "Die Pflanzenfamilien"[‡] the difference between the two genera is vague. Microcera is said to possess conical or cushion-shaped sporodochia, while Fusarium has cushion or irregular shaped ones. Massee,[§] in the British Fungus Flora, says Microcera is closely allied to Fusarium, but is distinguished by its small horn-like sporodochium. Both these authorities ignore the characters of the sheath. It is the presence of this white loose sheath,

---

[*] Guégnen, *loc. cit.*, p. 263.

[†] Desmazières, *loc. cit.*

[‡] Teil 1, Abtheil I., 1900, p. 508.

[§] Massee, *loc. cit.*, vol. III., p. 486.

which at first completely envelopes the conidial head and then partially breaks away, that distinguishes at a glance Microcera from the conidial stage (Fusarium) of the scale Nectriæ already described. The sporodochium of these latter has been shown to be surrounded by a sheath of sterile fibres, which, however, cling persistently to the mass of parallel conidiophores within, and cannot be readily detached as a separate covering. Such a sheath is only evident on microscopical examination, whereas that of Microcera is clearly visible to the unaided eye. Provisionally I should be inclined to keep the two genera apart on account of this difference in the external covering of the sporodochium ; Microcera, for example, to be characterized by having its sporodochium surrounded by a loose separate conspicuous sheath, and Fusarium by possessing a closely adherent inconspicuous one.

Brown sterile Fungus associated with Aschersonia.

Webber in his account of *Aschersonia aleyrodis* refers to another kind of fungus growth* on the mealy wing (*Aleurodes citri*). Since it never has been seen to produce any kind of fructification, he names it for convenience in his paper the "brown mealy wing fungus." He says it attacks the insect in any stage of development, and is more effective in destroying it than the Aschersonia ; to quote a sentence, "In the grove where the fungus was first discovered, its spread was so rapid during the past summer that the mealy wing was almost eradicated." It forms hard smooth flat circular brown pustules, 0·5-2 mm. in diameter, over the insects. From such stromata a silvery white mycelium spreads in all directions over the leaf surface, even as far as 13 mm. By this means other scales on the same leaf are readily infected.

Pustules resembling these have been found on three occasions in Ceylon on species of Aleurodes.

---

* Webber, *loc. cit.*, pp. 27-30.

1. On leaves of *Memecylon capitellatum* (fig. 33*b*), the same material as possessed the Aschersonia (p. 37).

The two fungi were irregularly distributed on the scales on the lower surface of the leaves throughout the bush. Some leaves possessed both kinds of stromata, while others might only have one sort.

2. On the lower surface of leaves of *Jasminum Sambac.*

In this case no Aschersonia, only brown pustules were present on the material received. The pustules are similar to the ones described by Webber, being rich brown in colour with a white membranous border from which hyphæ radiate out to some extent over the leaf surface.

3. On the lower surface of the leaf of *Calophyllum Walkeri.*

The brown pustules were not proved to be on scale-insects, but the supposition is likely.

Intermingled with the brightly coloured Aschersonia stromata on the leaf of *Flemingia strobilifera* (p. 37) were other brown ones. Many of these latter were evidently old or arrested Aschersonia stromata, as sections of them revealed closed pycnidia. Others again were flatter, more nearly resembling Webber's brown fungus, thus suggesting the possibility of all these sterile pustules being really connected with Aschersonia. The two fungi often appear in association on the same scale and even on the same leaf. Webber mentions that *A. aleyrodis* was present on those orange bushes containing also the "brown mealy wing fungus." In the Ceylon specimen on Memecylon the two were intimately associated. Atmospheric conditions such as dryness may so influence the development of the Aschersonia as to induce it to assume a sterile resting form. This, when conditions are again favourable, might send out infecting hyphæ over the leaf surface. Webber's account of how this brown fungus develops and spreads hardly favours such a view. However, its close association with Aschersonia is a point to be kept in mind. By cultures perhaps this sterile form might be induced to form some fructification, and so a clue to its nature and relationship might be obtained.

III.—GENERAL REMARKS.

Distribution.—Fungi parasitic, or at least subsisting on scale-insects, appear to be widely spread. They seem especially common in the tropics. As this paper shows, in the course of a few years many forms have been brought to light in Ceylon. Java has already produced several kinds. Specimens have also been received from various parts of Africa. Their occurrence has been noted in the West Indies. Maxwell-Lefroy,[*] in his treatise on the Scale-Insects of the West Indies, says that fungus diseases are occasionally responsible for a great mortality among coccids. He refers to several noticed by him, which have as yet received no investigation.

In temperate regions they also occur, but not so abundantly. Several forms have been found and used for infection experiments in the United States of America. Their presence in Australia has also been recognized, as well as in New Zealand. Maskell,[†] in his account of New Zealand scale-insects, writes that "the too rapid increase of coccids is checked by fungoid growths which permeate the whole body of the insect and soon kill it." The genera he noticed to be attacked are Ctenochiton, Lecanium, and probably Eriochelton. From his figures and short description the fungi suggest examples of Aschersonia. It is interesting to note that the specimens were observed on the natural vegetation of the forests.

In Europe the only scale-fungus which has been shown to be common is Microcera. In fact, for the British Isles they have hardly been recorded. Newstead, in his work on "The Coccidæ of the British Isles,"[‡] in a short section devoted

---

[*] Maxwell-Lefroy, West Indian Bulletin, vol. III., 1902, p. 314.

[†] Maskell, An account of New Zealand Scale-Insects, 1887, p. 22.

[‡] Newstead, vol. I., 1901, p. 12.

to micro-fungi says, " In this country micro-fungi are only occasionally destructive to coccids, and so far as my experience goes only infest those species found on plants under glass." Again, " I have not met with a single instance of an outdoor coccid in this country being attacked by a fungoid disease. But future research may prove they are not immune from such attacks."

As a rule these fungi cause epidemic diseases amongst the scale-insects they attack, few scales on a plant or group of plants escaping. They appear spasmodically when the conditions are favourable and rapidly spread over the coccids infesting any particular plant or crop. In Java and Ceylon the green-bug (*Lecanium viride*) has been noticed to be affected in epidemic fashion by Cephalosporium over large tracts of coffee. In Florida *Aschersonia aleyrodis* has been observed by Webber to spread rapidly over the mealy wing (*Aleurodes citri*) on the orange. Microcera can also cause epidemics amongst the San José Scale (*Aspidiotus perniciosus*). A remarkable example quite recently brought to notice occurred in the island of Martinique. The cocoanut palms were suffering severely from an attack of a coccid, closely allied to the S. José Scale. A fungous disease suddenly appeared and spread with such rapidity amongst the scales as practically to save these trees from probable destruction.

Considering how few scales escape, and how difficult it is sometimes to find a single unaffected insect on a leaf possessing the fungus, it is quite possible that many fungi described by systematists in the past, as growing on the surfaces of leaves and stems, might have had scale-insects a their true hosts. For example, it is probable that the genus Aschersonia at first considered a leaf-fungus is really in the main or wholly entomogenous. In the recognized coccidophagous forms the scale is so enveloped by the stroma of the fungus, that its remains can only be seen with the aid of sections and a microscope. As already pointed out Aschersonia is probably the conidial stage of Hypocrella;

consequently this genus also may be largely or wholly entomogenous.

Again, the entomogenous nature of some of these micro-fungi can readily be overlooked owing to certain scale-insects fixing themselves below the outer bark of stems and thus becoming invisible. A fungus growing on them consequently looks as if it was coming straight from the tissues of the plant. This is the case with *Chionaspis biclavis.* The coccid conceals itself beneath the dead external layers of the cortex, incorporating particles of the bark into its scale. The specimen of Nectria on this insect found in Ceylon exemplifies this point.

Systematic Position.

All the different forms of fungi so far discovered on scale-insects may be ranked as Ascomycetes, though the ascus-stage of many grouped under the Fungi-imperfecti is as yet unknown; but by analogy it is legitimate to consider them conidial fructifications of various Ascomycetes.

It is remarkable that no member of the simpler Phycomycetes has so far been discovered parasitic on coccids, considering that one of its divisions, the Entomophthorineæ, is almost wholly entomogenous, containing the well-known genus Empusa, so destructive to house-flies, plant-lice, &c.

The Ascomycetes already found on coccids belong almost entirely to the Hypocreales, a family of Pyrenomycetes. This is an interesting fact, for the Hypocreales contain the familiar and largely entomogenous genus Cordyceps, chiefly parasitic on caterpillars. Representatives of eight or nine genera of the Hypocreales have been found on scale-insects. In addition to these a species of Melanospora is known to be entomogenous. It would not then be surprising to find the habit still more widely spread amongst this group.

Of the other two Ascomycetous genera mentioned in the systematic part of this paper, Myriangium is doubtfully parasitic and Apiosporium (Capnodium) is little known at present.

The majority of the Fungi-imperfecti found on scale-insects are in all probability conidial stages of the Hypocreales.

It is to be noted that certain of these fungi appear to be restricted to definite genera or tribes of coccids.

Nectria (with the exception of the form on Asterolecanium) and Microcera (Sphærostilbe ?) are confined to the Diaspidineæ. The Nectria has already been met with on species of four genera and Microcera on those of five belonging to this subfamily.

Specimens of Aschersonia resembling Webber's *A. aleyrodis* have been found in nearly all cases parasitic on Aleurodes, spp. Another form appears restricted to species to Lecanium.

Cephalosporium has as yet only been examined on species of Lecanium, though Mr. Green has a recollection of observing such a fungus some years ago on Asterolecanium, which in spite of its name belongs to quite a different family.

To sum up, fungi have been found up to the present time on about ten distinct genera and on thirty species at least of Coccidæ and Aleurodidæ.

Judging from the epidemic character many of these fungi assume, there is little doubt that they are real parasites and cause the death of the various scale-insects upon which they have been found growing. In those instances where successful inoculating experiments have been carried out, any doubt is removed. Although we feel justified in recognizing the majority of forms described as parasites, yet their parasitism is not perhaps of a very specialized kind. As Webber points out for *Aschersonia aleyrodis*, they may be obligate parasites in the early stage of development, and then continue their growth for some time after the death of the insect, absorbing almost the entire body, thus becoming facultative saprophytes.

Cultural and Infection Experiments.

Such of the fungi as have been used for experiment are easily cultivated on artificial media, showing that they have not become so specialized as to need their own particular insect as food. The spores of several kinds tried by the author germinated readily in water.

Rolfs has succeeded in cultivating Sphærostilbe (Microcera) on bread, agar, gelatin, &c. He finds slightly acid bread a very useful material.

Zimmermann has shown that the Java Cephalosporium grows readily on agar substratum, provided with various nutrients. By this means crops of conidia can be obtained.

Guégnen found he could cultivate Acrostalagmus on a variety of substances.

The ease whereby these fungi can apparently be artificially cultivated is a point in their favour for their possible use as checks to scale-insects.

Infection experiments have not so far been extensively tried, but such as have been attempted have often been failures, except those with Microcera in the United States.

As regards the *Aschersonia aleyrodis* of Florida, Webber reports that orange trees infested with mealy wing, but possessing no fungus upon them, have been sprayed with a mixture of conidia and water on several occasions with no result. Another method attempted was to hang orange branches containing Aschersonia pustules over trees possessing healthy mealy wing larvæ. In this way it was thought that the conidia would be washed down by the rain and infect the insects. Only in one out of several trials did the Aschersonia make its appearance. Hence he goes on to say that the most satisfactory way of introducing the Aschersonia into orange groves is to transplant into them small trees containing the fungus, allowing the foliage to intermingle freely. Several experiments of this kind have given satisfactory results with the Aschersonia as well as with the "brown mealy wing fungus."

Zimmermann records in a footnote to his pamphlet (*loc. cit.*) a case of successful infection of the green-bug (*Lecanium viride*) on the Java coffee by an artificial culture of Cephalosporium. The conidia were apparently applied to the bugs with a damp brush.

Green has tried inoculating *Lecanium psidii* with an artificial culture of the Aschersonia found growing on it without success. In a letter he writes, "All endeavours to communicate the disease by these means to healthy individuals completely failed. I tried it under different conditions, but with equally negative results."

Attempts made by the author at Peradeniya to infect scales of *Lecanium viride* with Cephalosporium were also failures. The conidia were painted over the scales with a damp brush, but no development of the fungus upon them was shown after the lapse of several days.

Guégnen has tried inoculating coccids with the Acrostalagmus discovered by him without success, but it is not clear from his account as to whether the insect upon which he experimented was the same as the one upon which he found the fungus growing naturally.

The conditions for successful inoculation are, therefore, somewhat obscure. Possibly the fungus-spore has to exist previously on the area of the leaf upon which the coccid fixes itself. It then germinates beneath the young scale, penetrating the soft parts. Spraying with decoctions may not succeed owing to the germinating spores merely alighting on the hard external shell of the coccid where, unable to penetrate, they dry up, and die, before they can produce sufficient hyphæ to effect an entrance below the scale. It has been pointed out that many of these spores germinate readily in water, and of course once sprouted easily die if the conditions for growth are unfavourable.

Careful investigation is required to ascertain how the germinating tube of the spore first gains access to the interior of the scale-insect, as well as to follow out the early development of the fungus in the host. Perhaps these fungi chiefly attack the immature coccid larvæ, which at first are sheltered by the old mother scale, and then escaping lead a brief free existence before fixing themselves permanently to the plant. The insect may possibly pick up the fungus spore during its short active state.

Natural Means of Dispersal.

Fungus spores are most commonly carried by the wind. For many of these coccidophagous fungi, this can hardly be the case. The conidia of Nectria (Fusarium), Microcera, Cephalosporium, and others, are held together by soluble mucilage, so in these cases rain and dew must act as distributors to some extent, though owing to scale-insects being usually attached to the lower side of leaves, the fungi upon them are not so readily wetted by rain, nor can their spores be so easily carried by it from one leaf to another.

Considering the rapid spread some of these fungi have been observed to make in orange groves and coffee plantations affected by scale pests, they must have some quick means of distributing their conidia. Webber, in dwelling upon this point, suggests ants as a means, especially since such insects are in the habit of visiting those coccids which excrete honey dew. Ants are exceedingly common in the tropics. He also suggests that they may be attracted too by the brightly coloured conidial masses of the Aschersonia. Of course this idea about ants could not well apply to coccids of the sub-family Diaspidineæ which do not excrete honey dew, and are therefore not visited by them.

In Ascomycetes, as a rule, the conidia serve the purpose of increasing the fungus in the area in which it has established itself; they are produced in great abundance, germinate quickly, and soon lose their vitality. The ascospores serve rather to start new colonies elsewhere; they only appear towards the end of the life of the fungus and retain their vitality for a long time. This may also be the case with the coccidophagous fungi, such as Nectria which produces both kinds of fructifications. Hence the ascus stage is only to be expected in old material. In fact sometimes they may not be formed till the leaf has fallen.

Economic Value.

As regards the economic importance of these fungi, they have only as yet been used with success in the United States. Webber considers Aschersonia and its associate the sterile brown fungus as most useful in checking and even eradicating the mealy-wing (*Aleurodes citri*), and so indirectly the sooty mould of the orange. Rolfs, Forbes, and Gossard have shown that *Microcera coccophila* can be employed as a permanent check to the harmful San José Scale. In fact under certain circumstances the fungus is considered to be quite capable of controlling this pest without the aid of artificial insecticides. The conditions favourable for its growth are, as one might expect, moisture and warmth. For these reasons Ceylon should be especially suitable for experimental work with these natural enemies of scale-insects.

Perhaps a little caution should be exercised before making use too freely of these fungi, till their peculiarities are thoroughly known. Some species of Nectria are noted "wound" parasites on trees. The cacao-canker of Ceylon, recently studied by Carruthers, is due to a Nectria. It would be interesting to experiment and see if the scale Nectria of Ceylon could act as a "wound" parasite. Will its conidia germinate and cause disease when placed in a wounded region of a plant, especially such a one as is frequented by the particular coccid? It is hardly likely, but perhaps advisable to try, before recommending such a fungus as a remedy for certain scale pests.

Considering the importance "biological" species have assumed in the case of Rusts (Uredineæ) and Mildews (Erysipheæ), it would be instructive to see if anything of the kind exists amongst these scale-fungi. For example, will the Cephalosporium of *Lecanium viride* readily infect *Lecanium nigrum*, and *vice versâ;* or are these Cephalosporia physiologically distinct, though morphologically identical ? Some such distinction has been shown for species of Empusa on flies.*

IV.—SUMMARY.

1. Fungi growing upon scale-insects appear to be widely spread. They are especially common in the tropics, but less so in temperate regions. A great number have been found in Ceylon.

2. They often attack the insects in epidemic fashion This has been chiefly observed in the case of Aschersonia, Cephalosporium, and Microcera.

3. There seems no doubt of the parasitism of most of the forms, or at least that they are the direct cause of the insect's death. The parasitism is perhaps not of a very specialized kind. Some have been observed in America to check and even to eradicate such destructive pests as the San José Scale (*Aspidiotus perniciosus*) and the mealy wing (*Aleurodes citri.*)

4. The commonest genera are Nectria, Aschersonia, Cephalosporium, and Microcera : at least, as far as Ceylon is concerned.

5. Attention is called to the probability that certain fungi described in the past as growing upon the surface of leaves were really parasitic on scales. This is very likely the case for Aschersonia.

6. The ascus-forms nearly all belong to the Pyrenomycetes-Hypocreales, a group containing the well known entomogenous genus Cordyceps. Representatives of eight or nine genera have so far been found on coccids. Thus the entomogenous habit seems a common feature of the Hypocreales.

7. The remaining two Ascomycetes, Myriangium and Apiosporium, are of less importance. The former is

---

* Guègnen. *loc. cit.*, pp. 17 and 50.

doubtfully parasitic and the identity of the latter is uncertain. They are black fungi and one of them is known to follow "honey dew."

8. The forms placed amongst the Fungi imperfecti are probably in the main conidial stages of the Hypocrealess. Microcera is known to belong to Sphærostilbe, and Aschersonia to Hypocrella.

9. Some of these fungi appear to be restricted to definite kinds of scale-insects. Nectria and Microcera are confined to the sub-family Diaspidinæ; Cephalosporium to species of Lecanium; one type of Aschersonia to the Aleurodidæ (*Aleurodes* spp.); and another to Lecanium.

10. So far fungi have been found on ten distinct genera, and thirty species at least of Coccidæ and Aleurodidæ.

11. The interesting genus Torrubiella has only been found on spiders and coccids. It has not been so frequently met with in Ceylon as some of the others, *e.g.* Nectria.

12. Several of these fungi that have been tried grow well on various artificial media.

13. Inoculating experiments attempted by the application of watery decoctions of spores to healthy scales have not met with the success expected. The conditions favouring infection are evidently somewhat peculiar and require thorough investigation.

14. The conidia of many of these fungi are probably distributed by rain and ants, and not by wind.

15. The economic importance of these fungi must be kept in view. Some of them have been successfully employed in the United States against noted scale-pests, rendering ordinary insecticides unnecessary. As moisture and warmth naturally favour their growth, Ceylon should be a suitable country for testing their efficacy as a remedy for scale-attacks.

In conclusion, my thanks are due especially to Mr. E. E. Green for much assistance in many ways, and also to Mr. T. Petch for some useful criticism.

Cambridge, November, 1905.

Postscript.—A new conidial form from Natal.

While this paper was in preparation for the press, the writer received from the Government Entomologist of Natal a fine specimen of a coccid-fungus distinct from any hitherto examined. It is a conidial form attacking scales of *Mytilaspis citricola* on the stem of a Citrus (?), and was found in Zululand in November, 1905. A cursory examination has revealed the following features. Standing up around the scale are a few whitish bodies, resembling somewhat in general appearance the sporodochia of *Nectria coccidophthora.* Each consists of a short stout brown stalk, surmounted by a broad sub-conical white or cream-coloured head. An average sized one gave the following measurements :—

Stalk, length 0·5 mm., breadth 0·42 mm.

Head, height 0·33 mm., width 0·68 mm.

The stalk is stroma-like in texture, its component parts not separating in water. The head, on the other hand, swells in water liberating conidia. In fact, it consists solely of a mass of a conidia without any sheath or admixture of sterile hyphæ ; neither are there any separate fertile hyphæ bearing the conidia. These, in fact, sit upon the broad top of the stalk. They are borne in pairs—occasionally in threes—on the tips of hyphæ which barely project above the general level of the stalk-top. Thus the conidia may be regarded as sessile, the conidiophore being almost suppressed.

The conidia are long and straight, multiseptate with their free ends tapering. The longest measure about $150\mu \times 8\mu$, and have as many as 17–20 septa.

The fungus does not seem to fall readily into any of the recognized genera of the Fungi-imperfecti. It seems to have points of agreement with the conidial fructification of *Ophionectria coccicola* found in Java and described by Zimmermann (see p. 27).*

December 26, 1905.

---

* Zimmermann, Centralb. f. Bakt., Abth. II., Bd., VII., 1901, p. 372.

V.—Table of Species with their Hosts, &c.

Fungus.	Insect.	Plant.	Country.	Collector and Date.	Reference.*
ASCOMYCETES.					
Pyrenomycetes-Hypocreales.					
Torrubiella rubra, Pat. and Lagerh. ...	Unnamed ...	Melastoma and Solanum, leaf l.s. ...	Ecuador ...	—	14
Torrubiella luteorostrata, Zimm.	do. ...	Jungle tree, leaf ...	Java ...	—	21
Torrubiella, sp. ...	Aleurodes, sp. ... do. ...	Tetranthera, leaf l.s. Jungle tree, leaf l.s. ...	Pundalu-oya. Ceylon ... Pussella, Ceylon	Green, 1899 ... Macmillan, 1899	P
Do. sp. ...	Aspidiotus destructor, Sign. ...	do. ...	Pundalu-oya. Ceylon ...	Green, 1899 ...	P
Nectria aurantiicola, B. and Br.	Unnamed ...	Citrus aurantium, stem	Ceylon ...	—	1
Nectria coccorum, Speg. ...	do. ...	Bay tree, fallen leaves	Brazil ...	—	16*b*
Do. coccogena, Speg. ...	do. ...	Eugenia, sp. leaf ...	do. ...	—	16*c*
Nectria coccidophthora, Zimm. (Conidial stage = Fusarium) ...	Mytilaspis, sp. ... Parlatoria, sp. ...	Coffea arabica ... Citrus, sp. ...	Buitenzorg, Java ...	—	21

---

* These numbers refer to the bibliography.

V.—Table of Species with their Hosts, &c.—*contd.*

Fungus.	Insect.	Plant.	Country.	Collector and Date.	Reference.
ASCOMYCETES—*contd.*					
Pyrenomycetes-Hypocreales—contd.					
...	Aspidiotus aurantii Mask. ...	Citrus, sp., stem ; Rosa, sp. stem ...	R. B. G., Peradeniya, Pundalu-oya, Ceylon	Green and Parkin, 1898	P
— ...	Aspidiotus camelliæ, Sign. ...	Osbeckia, sp. stem ...	Pundalu-oya, Ceylon ...	Green. 1898	
— ...	Aspidiotus cydoniæ, Comst. ...	Citrus decumana, stem	do ...	do. 1898	
...	Aspidiotus phyllanthi. Green ...	Phyllanthus myrtifolius. stem ...	R. B. G., Peradeniya, Ceylon	do. 1900	
..	Chionaspis biclavis, Comst. ...	Tea and Tabernæmontana, stem ...	R. B. G., Peradeniya, and Pundalu-oya, Ceylon	Green and Parkin, 1898	

—	Mytilaspis lasianthi, Green	Codiæum variegatum, leaf	R. B. G., Peradeniya, Ceylon	Parkin, 1898	P
Nectria, sp.	Asterolecanium miliaris, Boisd.	A bamboo, leaf u.s.	R. B. G., Peradeniya, Ceylon	do. 1898	
Lisea Parlatoriæ, Zimm.	Parlatoria zizyphi	Citrus, leaf	Java	—	21
(?) Calonectria, sp.	Mytilaspis citricola, Pack.	Orange, leaf	Avisawella, Ceylon	Green, 1898	P
(?) Do.	Chionaspis vitis, Green	Loranthus, sp., leaf	Horton Plains, Ceylon	do. 1900	
Ophionectria coccicola (Ell. and Ev.) Berl. and Vogl.	Unnamed	Citrus, leaf	Java	—	21
Sphærostilbe coccophila Tulasne (see Microcera coccophila)	—	—	—	—	—
Broomella Ichnaspidis, Zimm.	Ichnaspis filiformis	Coffea liberica and Elæis, sp., leaf	Java	Raciborski	21
Broomella Ichnaspidis, var major	One of the Diaspidinæ	Pierardia, sp., leaf	—	—	—
Hypocrella Raciborskii, Zimm.	Unnamed	Citrus, sp., leaf	do.	do.	21
(?) Hypocrella, sp.	Lecanium expansum, Green	Schumacheria alnifolia, leaf u.s.	Maskeliya, Ceylon	Green, 1898	P

V.—Table of Species with their Hosts, &c.—*contd.*

Fungus.	Insect.	Plant.	Country.	Collector and Date.	Reference.
ASCOMYCETES—*contd.*					
Pyrenomycetes-Hypocreales—contd.					
(?) Hypocrella, sp. ...	Lecanium hemisphæricum, var coffeæ, Wlk.	Gelonium lanceolatum, leaf l s. ...	Pundalu-oya, Ceylon ...	Green, 1898 ...	P
(?) Do. ...	Chionaspis vitis, Green	Loranthus, sp., leaf	Horton Plains, Ceylon ...	do. 1900 ...	
(?) Drussiella, sp. ...	Aclerda distorta ...	Arundinaria, sp., stem ..	Pundalu-oya, Ceylon ...	do. 1899 ...	
Pyrenomycetes-Perisporiales.					
(?) Apiosporium (Capnodium), sp. ...	Aspidiotus perniciosus	—	—	—	2
Plectascineæ.					
Myriangium Duriæi, Mont. and Berk. ...	Unnamed ..	Coffea liberica and Elæis, sp., leaf ...	Java ...	—	21

Myriangium Duriæi, Mont. and Berk. ...	Aspidiotus camelliæ, Sign. ...	Osbeckia, sp. stem ...	Pundalu-oya, Ceylon ...	Green, 1898	P
—	Chionaspis biclavis, Comst. ..	Tabernæmontana, sp. stem ...	R. B. G., Peradeniya, Ceylon	do.	
—	Mytilaspis citricola, Pack. and M. pallida, Green ...	Codiæum variegatum, leaf ...	do. ...	Parkin, 1899	
FUNGI IMPERFECTI.					
Sphæropsidales-Nectrioidaceæ.					
Aschersonia aleyrodis, Webber ...	Aleurodes citri, R. & H.	Citrus, spp., leaf ...	Florida, U. S. A.	Webber, 1893 ...	18 and 19
Aschersonia turbinata, Berk (?) ...	Ceroplastes floridensis, Comst. ...	Citrus, spp. and Celtis occidentalis, leaf ...	do. ...	do. ...	19
Aschersonia, sp. ...	Lecanium hesperidum, L.	do. ...	do. ...	do. 1895 ...	19
Aschersonia aleyrodis, Webber (?) ...	Aleurodes, sp. ...	Andropogon muricatus, leaf, l.s. ...	Pundalu-oya, Ceylon ...	Green, 1898	P
—	Do. ...	Ochlandra, sp. leaf, l.s.	Pussella, Ceylon	Macmillan, 1899	
—	Do. ...	Memecylon capitellatum, leaf l.s. ...	R. B. G., Peradeniya. Ceylon	Parkin, 1899	

V.—Table of Species with their Hosts, &c.—*contd.*

Fungus.	Insect.	Plant.	Country.	Collector and Date.	Reference.
FUNGI IMPERFECTI—*contd.*					
Sphæropsidales—Nectrioidaceæ—contd.					
–	Aleurodes, sp. ...	Flemingia strobilifera, leaf l.s. ...	R. B. G., Peradeniya. Ceylon	Green, 1900	P
—	Do. ...	Diospyros Toposia, leaf l.s.	Balangoda, Ceylon ...	do. 1901	
—	Do. ...	Hedyotis verticillaris, leaf l.s. ...	Hakgala. Ceylon	do. 1901	
—	Do. ...	Filicium decipiens, leaf l.s. ...	R. B. G., Peradeniya. Ceylon	do. 1901	
Aschersonia aleyrodis, Webber (?) ...	Lecanium, sp. ...	Coffea liberica, leaf ...	Sumatra ...	1898 (examined)	P
Aschersonia, sp. ...	Lecanium psidii, Green	Myristica moschata, stem and leaf ...	R. B. G., Peradeniya. Ceylon	Green, 1899 ...	—
Do. ...	Lecanium hemisphæricum, var coffeæ, Wlk.	Tea, stem, and leaf ...	Upper Assam ...	1899 from Green	P
Do. ...	Lecanium, sp. ...	Tea plant ...	Kurseong and Darjeeling, India ...	1900 and do.	—

Aschersonia, sp.	Aleurodes, sp.	Eugenia revoluta, leaf l.s.	Horton Plains, Ceylon	Parkin, 1899	P
Aschersonia sclerotioides, P. Henn.	Lecanium sp.	Castilloa elastica	Java	Zimmermann	9
Hyphomycetes-Mucedinaceæ.					
Cephalosporium Lecanii, Zimm.	Lecanium viride, Green	Coffea liberica and C. arabica, leaf and stem	Java	Zimmermann, 1897	20
—	Do.	C. arabica, leaf and stem and Citrus decumana	Pundalu-oya, Ceylon	Green, 1898	P
—		Atalantia Zeylanica, leaf	Kandy, Ceylon	Parkin, 1898	
—	Lecanium nigrum, Nietn.	Hibiscus rosa-sinensis, stem	Pundalu-oya and Kandy, Ceylon	Green and Parkin, 1898	
—	Do.	Anona cherimolia, stem	Pundalu-oya, Ceylon	Green, 1899	
	Lecanium hemisphæricum, Targ.	Tea plant	Ramboda, Ceylon	do. 1901	
	Lecanium hemisphæricum, var. coffeæ, Wlk.	Jussiæa suffruticosa, stem	Pundalu-oya, Ceylon	do. 1898	
Hyalopus Yvonis, Dop.	Aspidiotus perniciosus, var.	Cocos nucifera	Martinique	— 1904	4

Fungus	Insect.	Plant.	Country.	Collector and Date.	Reference.
FUNGI IMPERFECTI—*contd.*					
Hyphomycetes-Mucedinaceæ—contd.					
Acrostalagmus coccidicola, Guéguen	Unnamed	Mikania (?)	Paris (green house) France	Guégnen, 1900	8
Sporotrichum Lecanii, Peck.	Lecanium, sp.	—	N. America	Peck	8
Verticillium heterocladum, Penzig.	Lecanium hesperidum	Citrus limonum	N. Italy	Penzig	16*a*
Verticillium, sp.	Asterolecanium miliaris, Boisd.	A bamboo, leaf l.s.	R. B. G., Peradeniya, Ceylon	Parkin, 1898	P
Hyphomycetes-Dematiaceæ.					
(?) Peziotrichum, sp. (Botryotrichum)	Chionaspis aspidistræ, Sign.	Palm, leaf	do.	Green, 1899	P
Do.	Aonidia, sp.	Memecylon, sp. leaf	Elephant Pass, Ceylon	do. 1901	
Hyphomycetes-Tuberculariaceæ.					
Fusarium (see Nectria).					
Microcera coccophila, Desm.	Aspidiotus, spp., &c.	Salix, Fraxinus, Alnus, &c., stem	France, Italy, Austria, Britain, Belgium	Desmazieres, 1848, and several observers since	3 and 17
[Sphærostilbe coccophila]					

—	Aspidiotus perniciosus and A. articulatus, Morgan	Citrus, sp.	U. S. A.	—	5 and 15
—	Aspidiotus coccineus and others	Citrus aurantium	Australia	Bailey and Maiden	11
—	Aspidiotus aurantii, Mask. and Mytilaspis citricola, Pack.	Citrus, sp., stem and leaf	R. B. G., Peradeniya, Ceylon	Parkin, 1898	P
—	Mytilaspis pallida, Green	Codiæum variegatum, leaf	do.	do.	
—	Do. lasianthi	Croton, leaf	do.	Green, 1900	
Microcera, sp.	Aonidia bullata, Green	Nothopegia Colebrookiana, leaf u.s.	Pundalu-oya, Ceylon	do. 1899	
	Do. crenulata	Memecylon umbellatum, leaf	R. B. G., Peradeniya, Ceylon	do. 1899	
Do. sp.	Aspidiotus camelliæ, Sign. (?)	Jungle tree, stem	Pundalu-oya, Ceylon	do. 1899	
Do. coccophila	Aspidiotus articulatus, Morgan	Coffee leaf	W. Africa	1899 examined	
—	Aspidiotus articulatus and Ischnaspis filiformis	do.	Grenada, W. Indies	Punch, from Newstead, 1898	P
—	Fiorinia fioriniæ, Targ.	Camellia, leaf l.s.	Mauritius	From Green, 1899	—

Fungus.	Insect.	Plant.	Country.	Collector and Date.	Reference.
FUNGI IMPERFECTI—*contd.*					
Hyphomycetes-Tuberculariaceæ—contd.					
Microcera rectispora, Cooke and Mass. ...	Unnamed ...	Citrus aurantium ...	Brisbane, Australia ...	—	16*e*
Microcera tasmaniensis, McAlpine ...	Aspidiotus, sp. ...	Eucalyptus ...	Tasmania ...	Lea, 1901	11
Microcera mytilaspis McAlpine ...	Mytilaspis, sp. ...	Hymenanthera dentata	Victoria, Australia ...	McAlpine	
Sterile Forms.					
"Brown mealy wing fungus" ...	Aleurodes citri R. and H.	Orange leaves ...	Florida, U.S.A....	Webber, 1896 ...	19
Do. ...	Do. sp. ...	Memecylon capitellatum, leaf l.s. ...	R. B. G., Peradeniya, Ceylon	Parkin, 1899	P
Do. ...	Do. sp. ...	Jasminum Sambac, leaf l.s. ...	Yatiyantota, Ceylon ...	Green, 1900	
Do. ...	Uncertain ...	Calophyllum Walkeri...	Horton Plains, Ceylon ...	Parkin, 1899	

VI.—BIBLIOGRAPHY.

(The fungus to which each paper particularly refers is placed in brackets.)

1.—Berkeley and Broome: "Fungi of Ceylon," Journ. Linn. Soc., XIV., 1875, p. 117. (Nectria.)

2.—Britton: "San José Scale, Natural Enemies in Connecticut," U.S.A. Exp. Station Conn. Report Entom., Part II., 1902. (Capnodium.)

3.—Desmazières: "Plantes Cryptogames Nouvelles," Ann. des Sc. Nat. 3rd ser., 1848, p. 359. (Microcera.)

4.—Dop: "Sur un nouveau Champignon, parasite des Coccides ou genre *Aspidiotus*." Bull. Scient. de la France et Belgique, XXXIX., 1905, p. 135. (Hyalopus.)

5.—Forbes: "Recent work on the San José Scale in Illinois." Illinois Agric. Exp. Station, Bull. 56, 1899. (Microcera.)

6.—Fuller: First Report of Government Entomologist. Dep. Agriculture, Natal, 1901, p. 99. (Sphærostilbe.)

7.—Gossard: "White Fly," Florida Exp. Station. Bull. No. 67, 1903. (Aschersonia, Sphærostilbe, and Brown sterile fungus), also "Two Peach Scales," Bull. 61. (Sphærostilbe.)

8.—Guégnen: "Les Champignons parasites de l'homme et des animaux." Paris, 1904, 8vo., 317 pp. (General account, Acrostalagmus.)

9.—Hennings: "Fungi Javanici Novi a cl. Prof. Zimmermann." Hedwigia, XLI., 1902, p. 140. (Aschersonia, 5 n. spp., one on a coccid.)

10.—Hennings: "Die Gattung Aschersonia Mont." Festschrift für P. Ascherson, 1904, pp. 68–73.

11.—McAlpine: "Two new fungi parasitic on Scale-Insects," Journ. Agric. Victoria, XI., Part 7, May, 1904. (Microcera.)

12.—Maskell: "An Account of New Zealand Scale-Insects," p. 22.

13.—Parkin: "Fungi found in Ceylon growing upon Scale-Insects (Coccidæ and Aleurodidæ)." Report British Assoc. Bradford, 1900, p. 932.

14.—Patouillard and Lagerheim : "Sur Champignons de l'Equateur," Bull. de la Soc. Mycol. de France, vol. IX., 1893, p. 154. (Torrubiella.)

15.—Rolfs : "A Fungus Disease of the San José Scale," Florida Agric. Exp. Station, Bull. 41, 1897. (Sphærostilbe.)

16.—Saccardo : Sylloge Fungorum. (*a*) Vol. IV., 1886, 151 p. (Verticillium) ; (*b*) Additamenta to vols. I.–IV., 1886, p. 203 (Nectria) ; (*c*) Vol. IX., 1891, p. 154 (Nectria) ; (*d*) Vol. IX., 1891, p. 996 (Ophionectria) ; (*e*) Vol. X., 1892 p. 731 (Microcera).

17.—Tulasne : Carpologia, vol. III., 1865, p. 105. (Sphærostilbe.)

18.—Webber : "Preliminary notice of a Fungus Parasite on *Aleyrodes citri*," Jour. of Mycol., vol. VII., p. 363. (Aschersonia.)

19.—Webber : "Sooty Mould of the Orange and its Treatment," U. S. A. Depart. Agric., Div. Veg. Physiol. and Pathol., 1897, No. 13. (Aschersonia and "brown mealy wing fungus.")

20.—Zimmermann : "Over eene Schimmel epidemie der Grœne Luizen," Voorloopig Rapport, 1898, Buitenzorg, Java (Cephalosporium.)

21.—Zimmermann : "Einige javanische, auf Coccidæ parasitierende Ascomyceten." Centralb. f. Bakt. Abth. II., Bd. VII., No. 24, 1901, pp. 872–876 (several genera of the Hypocreales).

Note on 11.—Saccardo, S. F., vol. *xviii.*, lists these two fungi as *M. tasmanica* and *M. mytilaspidis*, respectively.

EXPLANATION OF PLATES.

(The figures all illustrate Ceylon specimens.)

PLATE I.

Torrubiella.

Fig. 1.—*Species* 1 : Piece of leaf of Tetranthera with large brown stroma on the white mycelial fringe of which are borne deep pink perithecia *p* ; also a small stroma without perithecia with central part of scale *s* (*Aleurodes*, sp.), visible. × 5.

Fig. 2.—Perithecium, × 20. *Fig.* 3, Ascus, × 320. *Fig.* 4, Ascospore, × 320.

Fig. 5.—*Species* 2 : Piece of leaf of a jungle tree with *s*, scales (*Aspidiotus destructor*) without fungus and *p*, perithecia with coherent bases. × 5.

Nectria.

Fig. 6.—Piece of Citrus stem with scales of *Aspidiotus aurantii* attacked by fungus in conidial stage; *s*, scale without and *sf*, one with fungus. Natural size.

Fig. 7.—Detached scale of fig. 6 showing 7 sporodochia (conidial heads) around it. × 10.

Fig. 8.—Detached scale of *Chionaspis biclavis* showing fungus in ascus-stage. *p*, perithecia ; *sp*, remains of a sporodochium. × 10.

Fig. 9.—Four sporodochia in the dry state, showing various lengths of stalk, *st* ; *h*, glutinous heads of conidia ; *p*, young perithecia. × 20.

Fig. 10.—A sporodochium expanded by water which liberates the conidia ; *p*, young perithecia. × 20 (semi-diagrammatic).

Fig. 11.—Conidia, × 320. *Fig.* 12, Conidiophore; *c*, young conidium, × 320.

Fig. 13.—Sheath-hyphæ of sporodochium, showing cross-pieces *cp*. × 320.

Fig. 14.—Perithecium, × 20. *Fig.* 15, Ascus, × 320. *Fig.* 16, Ascospore. × 550.

PLATE II.

Fig. 17.—Nectria on scales of *Asterolecanium miliaris* on piece of bamboo leaf; *s*, scale without fungus; *sc*, scale with fungus on conidial stage; *sa*, in ascus stage. × 2.

Fig. 18.—Single scale of fig. 17 with sporodochia, *sp*, and two contiguous scales with perithecia, *p*. × 10.

Fig. 19.—Ascospores of Nectria of fig. 17. × 550.

Calonectria.

Fig. 20.—Ascus, × 320. *Fig.* 21, Ascospores with 4 septa. × 550.

Fig. 22.—Ascospore of another specimen—larger and with 5 septa. × 550.

Hypocrella.

Fig. 23.—Stromata covering scales of *Lecanium expansum* on leaf of *Schumacheria alnifolia*. Dark dots represent opening of perithecia. Natural size.

Fig. 24.—Section through two perithecia showing faintly the filiform asci. × 40.

Myriangium.

Fig. 25.—Scales of *Aspidiotus camelliæ* on Osbeckia stem. The dark bodies (perithecia) around the scales represent the fungus. × 5.

Fig. 26.—Ascus, × 320. *Fig,* 27, Ascospore, × 550.

Aschersonia, a.

Fig. 28.—Piece of leaf of a grass (*Andropogon muricatus*) with black scales (Aleurodes) attacked by Aschersonia. *s*, scales without fungus; *sp.*, scales partially covered with fungus; remainder *st*, scales completely covered with stromata, the dark dots representing the openings of the pycnidia. Natural size.

Fig. 29.—Detached stroma, being the largest one in fig. 28, *h*, hypothallus; *p*, openings of pycnidia. × 5.

Fig. 30.—Conidia. × 550.

Fig. 31.—Piece of bamboo (Ochlandra) leaf with black Aleurodes attacked by Aschersonia. *s*, scales without fungus; *st*, stromata covering or partially covering scales, minute dark dots representing openings of pycnidia. Natural size.

Fig. 32.—Detached stroma from fig. 21, side view. *p*, openings of pycnidia. × 5.

Fig. 33.—Leaf of *Memecylon capitellatum* (underside) with pale Aleurodes attacked by Aschersonia and "brown mealy wing fungus": *b*, pustules of latter; *s*, scales without fungus; *st*, scales covered with stromata of Aschersonia, showing hypothallus and openings of pycnidia. Natural size.

PLATE III.

Fig. 34.—Vertical section of stroma of fig. 33; *p*, pycnidia; *h*, hypothallus; *s*, remains of scale. × 10.

Fig. 35.—Section of stroma of fig. 33, showing *c*, conidial bearer with conidia and *p*, sterile hyphæ (paraphyses). × 100 (semi-diagrammatic).

Aschersonia, b.

Fig. 36.—Twig of *Myristica moschata*, showing numerous large stromata covering scales of *Lecanium psidii*. *s*, scales without fungus. Natural size.

Fig. 37.—Vertical section of a stroma; *p*, pycnidia, *s*, remains of scale. × 10. *Fig.* 38, conidia. × 550.

Aschersonia, c.

Fig. 39.—Leaf of *Eugenia revoluta*. *s*, scale (Aleurodes) without fungus; *st*, stromata over scales with 2 or 3 pycnidia each; *sp.*, scales partially covered with fungus. Natural size.

Fig. 40.—Uppermost stroma of fig. 39, showing openings to the two large pycnidia, and *h*, hypothallus. × 5.

Fig. 41.—Vertical section of fig. 40; *p*, pycnidia; *s*, remains of scale. × 5.

Fig. 42.—Conidia. × 550.

Black Aschersonia (?)

Fig. 43.—Stroma (side view), *μ*, upper part bearing surface conidia; *p*, openings to pycnidia; *b*, thickened basal border. × 5. *n*, natural size of stroma.

Fig. 44.—Vertical section of fig. 43; *p*, pycnidia; *c*, conidia-bearing superficial hymenium; *s*, remains of scale. × 5.

Fig. 45.—Conidia. × 550.

Fig. 46.—Vertical section of another stroma showing *p*, perithecia. × 5.

Fig. 47.—Perithecium of fig. 46 enlarged, showing faintly the filiform asci. × 40. *Fig* 48. Sporule from ascus. × 550.

Cephalosporium.

Fig. 49.—Piece of leaf of *Aphelandra tetragona* with scales of *Lecanium viride* affected by fungus which is represented by the light areas around the scales. *s*, scales without fungus. Natural size.

Fig. 50.—Piece of stem of *Anona cherimolia* with scale of *Lecanium nigrum* affected by the fungus, which is represented by the white part around and upon the scale. Natural size.

PLATE IV.

Fig. 51.—This shows the development of the Cephalosporium from below the scale—only a segment is drawn. *s*, portion of scale ; *c*, conidiophores. × 60.

Fig. 52.—Branched conidiophores of Cephalosporium. × 320.

Fig. 53.—Single conidiophore in dry state. *c*, globular head of mucilage in which the conidia are embedded. × 550.

Fig. 54.—Single conidiophore after treatment with acetic acid. The conidia *c*, are now visible. × 550.

Verticillium.

Fig. 55.—Conidiophore. *c*, conidium. × 550.

Peziotrichum (*Botryotrichum*) ?

Fig. 56.—Scales of Aonidia affected by fungus on piece of leaf of Memecylon. *s*, scales without fungus. × 3.

Fig. 57.—Detached scale with fungus. *b*, sterile bristles ; *m*, conidial mycelium. × 10.

Fig. 58.—One of bristle-hyphæ showing swollen hyaline tip. × 100.

Fig. 59.—Part of bristle-hypha more magnified. × 320.

Fig. 60.—Portion of conidial mycelium. *c*, conidia. × 320.

Fig. 61.—Conidium. × 550.

Microcera.

Fig. 62.—Piece of leaf containing scales of Aspidiotus affected with the fungus. *s*, scale without fungus. Natural size.

Fig. 63.—Detached scale of *Aspidiotus aurantii* viewed from above with 8 sporodochia radiating from margin; *sh*, sheath of sporodochium; *c*, conidial head inside. × 20.

Fig. 64.—Piece of leaf of *Nothopegia Colebrookiana* with three scales; *sf*, *Aonidia bullata* affected by a Microcera; and two scales, *s*, without fungus. Natural size.

Fig. 65.—Detached scale from fig. 64. Fungus forms a red stroma *st*, upon peripheral part of the scale. From the posterior extremity projects a single sporodochium; *sh*, its sheath, and *c*, the conical conidial head. × 20.

Fig. 66.—Conidia. × 320.

Studies in the Organization of a Botanical Department.

BY

J. C. WILLIS.

I.—*THE NAMING OF THE PLANTS.*

THE problem of getting the correct names to the plants, and of keeping them accurately when got, is one always before the Director of a Botanical establishment. Merely labelling the trees correctly is not enough, for the labels may be misplaced or stolen, or still more often may be transposed by the coolies when cutting the grass. In a garden like Peradeniya, containing many thousands of species, and still more in such a place as Kew, this problem becomes of very serious importance. If a plant be not correctly named, it were almost better that it should not be in the garden at all.

After much thinking over the question, and discussing it with the heads of several large botanical gardens in Europe and America, I have devised the plan described in the following pages, which has now been in operation at Peradeniya for some time, and which seems both simple and satisfactory. Any one thinking of adopting it should write to Peradeniya for copies of the form used, so that forms of the same size may be employed, a matter not without convenience in exchanging plants, and for other purposes.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. III., Part. I., March, 1906.]

The American "vertical file," so convenient for filing papers on any conceivable subject, is employed. This consists of drawers of standard and uniform size, arranged in cases of four one above another. Each group of four drawers forms a unit, and when it is full another unit is simply placed beside it, and so on to any extent.

In the drawers stand, with their edges upwards, folded sheets of paper (size folded 13½ in. by 8½ in.) consecutively numbered from No. 1 upwards. These are arranged in groups of ten, each ten in a similar brown paper cover, which is numbered outside on its top edge 1–10, 1,051–1,060, or whatever it may be, so that it is quite easy to turn over the whole contents of the drawer, and remove any one paper without disturbing the rest. This is the outstanding advantage of the vertical file.

Each sheet of paper has thus four sides, which are reproduced in miniature at the end of this paper. On these pages spaces are left for the outstanding facts most likely to be noted about the plants, and any further notes on anatomy, ecology, or morphology, for which no space is provided, can be simply written on loose sheets of paper and dropped inside the filed sheet.

On the first page about half the space is left for the name of the plant. The name under which the plant goes when collected, or the name under which it was received from elsewhere, should be put at the top, with a note of its origin, and the rest of the space is for the observations of people who may have worked with the plant. Thus a sheet may bear the legend :—

Ardisia humilis Vahl. (Trimen)
No ; I think it is a new species.—J. C. W.
Ardisia Willisii Mez ! C. Mez.

When the name is finally settled, the custom at Peradeniya is to provide the plant with a metal label—one of the new pattern with the name embossed or cast upon it, so that even though the paint may get rubbed off, the name can still be made out. These labels at Peradeniya are only put out to plants with well-ascertained names, so that the presence of a metal label is in general a guarantee that the plant is correctly named.

After the space for the name follow spaces for the Natural Order, the Distribution, the Garden (there are several gardens in Ceylon), and the exact position in the garden (in case of the loss of the label). Then follows space for the Source and History, *e.g.*—

Received from Messrs. Sander & Co., March, 1894.
Planted out June, 1895.

On the two centre pages are spaces for notes on the germination, the growth, the leaf-fall, flowering, fruiting, &c.

On the fourth page is room for miscellaneous notes, *e.g.*, on attacks of disease, adaptability to climate and soil, trial in other districts, distribution of seeds (*i.e.*, by officers of the Department), reports on the product, timber yield, and other points.

Every member of the staff of the department is supposed to carry a notebook with detachable leaves, in which he can note down, giving at the top of the page the number of the plant, anything that he may notice about it that is of general interest. These notes are subsequently detached, and put inside the sheets to which they refer, and the office clerks at intervals go over them, and copy them on to the sheets or attach them to the sheets. Every note must be signed by its author, to enable workers at later dates to know what value is to be attached to it.

So much for the registration of information. The next question is the application of this system to the actual plants in the garden. Every plant has a number, and this number once used is *never* used again, even though the plant to which it is attached should die or be otherwise disposed of. Every new plant has a fresh number. The numbers are embossed on little tickets of zinc about two inches square, so that they cannot be rubbed out, and these tickets are nailed to the trees, always on the south side, and at 5 feet from the ground (to prevent interference by children). In the case of shrubs they are wired to the branches on the south side. In the case of herbaceous plants, the plants are grown in beds, each of which has a number attached to it, and care is taken to see that the plants in beds side by side do not intermingle. At the same time that the number is affixed in the open, the same number is written against the plant or bed in the large map of the garden kept at the office, so that the number cannot be lost.

The numbers in the files have therefore no necessary relation to one another, While No. 1 may be Dendrobium Maccarthiæ, No. 2 may be Vitis Linnæi, No. 3 Dipterocarpus zeylanicus, and so on. An index of names is kept, and the numbers are entered on it, *e.g.*, Dipterocarpus zeylanicus, Nos. 3, 1,815, 10,162.

When the numbers become considerable, and the naming fairly complete, a further index, giving the numbers in order, and the name after each, should be compiled for the use of scientific visitors to the garden, so that they may take it round with them, and get the correct name for each plant, without having to depend too much on the labelling.

By this means, any isolated fact about any single plant in the gardens, takes its place in a system of collected information where it is readily available. If nothing is recorded about the plants no harm is done, and the index still works, while every fact recorded and filed is a gain. And it is becoming more and more recognized that in the tropics at any rate plants have considerable individual equations, so that, *e.g.*, the date of leaf fall recorded for one plant of a given species may be quite different from that recorded for another plant of the same species. It is almost needless to point out the value of such a filing system, not only to the regular workers in a garden but also to the scientific visitor who may come for a short time to work there.

ROYAL BOTANIC GARDENS, CEYLON: INDEX.

Authors to sign and date all notes.
Insert extra sheets in middle or at end
of forms as required.

No.

Name:

N. O.

Distribution:

Garden and Position:

Source and History:

LIFE-HISTORY NOTES.

Pollination-methods, insect
Ecological, Anatomical, or
entered on loose sheets and

Germination :

Growth :

Leaf-fall :

In young leaf :

LIFE–HISTORY NOTES.

visitors, and all other General Morphological notes to be enclosed. }

First Flowering :

In Flower :

In Ripe Fruit :

Death :

Specimen kept :

MISCELLANEOUS NOTES.

[Attacks of Disease, Adaptability to Climate, Soil, &c., Trial in other Districts, Distribution of Seed, Yield of Crop Reports on Product, Timber-yield and Value, and other miscellaneous information.]

REVIEWS.*

Revisions of Ceylon Natural Orders.

[A. Engler : Das Pflauzenreich. Leipzig, 1900 (in progress.)]

§ 1. *Musaceæ*, by K. Schumann. The only Ceylon species of Musa is referred, as in Trimen's Flora, to *M. paradisiaca*, L., but to subspecies 4, *troglodytarum*, L., Bak. Trimen, however remarks that he has seen nothing here with an erect inflorescence.

§ 2. *Typhaceæ*, by P. Graebner. The only Ceylon species, *Typha javanica*, Schnizl., is, as hinted by Hooker, placed as a subspecies under *T. angustifolia*, L.

§ 3. *Pandanaceæ*, by O. Warburg. *Freycinetia Walkeri*, Solms, *F. pycnophylla*, Solms, and *Pandanus zeylanicus*, Solms, are retained. The other species of Pandanus given for Ceylon by Trimen (*odoratissimus* L. f. and *foetidus* (var) Roxb., the latter given as *P. affinis*, S. Kurz) are not mentioned as occurring in Ceylon. The whole account appears to have been made up at Buitenzorg and Berlin, and ignores the contents of the Peradeniya and Kew herbaria.

§ 4. *Monimiaceæ*, by J. Perkins and E. Gilg. *Hortonia ovalifolia*, Wight, given as a variety of *H. floribunda* by Trimen, is raised to specific rank, as well as *H. angustifolia*, Trim., and *H. floribunda*, Wight.

§ 5. *Rafflesiaceæ* and *Hydnoraceæ*, by H. Graf zu Solms-Laubach. None in Ceylon.

§ 6. *Symplocaceæ*, by A. Brand. The genus Symplocos, placed in Styraceæ by Trimen, is here given a separate family. To deal with the species in Trimen's order : (1) *S. spicata*, Roxb., is made to include (5) *S. versicolor*, Clarke ; (2) *S. obtusa*, Wall, is said not to occur in Ceylon, and the plant thus described (C. P. 626, Gardner, 538, in Hb. Brussels, Walker, in Hb. Berlin) is described as a new species, *S. furcata*, Brand. The variety β. *major*, Thw., is described as a new species, *S. major*, Brand. The var. γ *obovata*, Thw., was not seen, but is suspected of being a new species, and the var. δ., *cucullata*, Thw., is made into a new species, *S. cucullata*, Brand ; (3) *S. læta*, Thw., and (4) *S. bractealis*, Thw., are maintained ; (5) *S. versicolor*, Clarke, is sunk in *S. spicata* ; (6)

---

* The articles which appear under this head are written primarily for the Ceylon constituency of this journal, and deal chiefly with advances in Science which are of immediate local interest.

S. acuta, Thw.: (7) *S. cuneata*, Thw., and (8) *S. hispidula*, Thw., are maintained; (9) part of *S. jucunda*, Thw. (C. P. 3,454) is made into a new species, *S. diversifolia*, Brand, the remainder (C. P. 2,435) being retained under the old name; (10) *S. angustata*, Clarke, and (11) *S. latiflora* Clarke are retained; (12) *S. elegans*, Thw. (C.P. 23) is divided, part being retained under the old name, part described as a new species, *S. amabilis*, Brand; (13) *S. minor*, Clarke is retained, but the var *β. glabrescens*, Thw., is made into a new species, *S. glabrescens*, Brand; (14) *S. hebantha*, Thw.; (15) *S. cordifolia*, Thw., and (16) *S. apicalis*, Thw., are retained, but the variety *β. glabrifolia*, Thw., of the latter is raised to specific rank as *S. glabrifolia* (Thw.,) Brand; (17) *S. marginalis*, Thw., and (18) *S. coronata*, Thw., are retained, while (19) *S. pauciflora*, Wight, is put back into *S. pendula*, Wight. And another new species, *S. Walkeri*, Brand., is described from material collected by Walker under the name *S. pulchra*.

§ 7. *Naiadaceæ*, by A. B. Rendle. Naias is the only genus left in this family. *N. major*. All., of Trimen's Flora is placed as var. *v. muricata* (Del). A. Br. ex K. Sch. under N. *marina*. The other species, *N. graminea*, Del., and *N. minor*, All., are not mentioned for Ceylon.

§ 8. *Aceraceæ*, by F. Pax. None in Ceylon.

§ 9. *Myrsinaceæ*, by C. Mez. The one Ceylon species of Mæsa, *M. indica*, A. DC. is merged in *M. Perrottetiana*, A. DC. *Ægiceras majus*, Gaertn. is merged in *A. corniculatum*, (L.) Blanco *Ardisia Missionis*, Wall. is retained. *A. humilis*, Vahl. is divided into *A. Willisii*, Mez., n. sp. (Gardner, 516; Hügel, 3,681; Thwaites, C.P. 2,829, Willis), *A. Wightiana*, Wall. (Thwaites, Wight ap. Wallich, 2,230), and *A. humilis*, Vahl., including in the latter *A elliptica*, Thunb. *A. Gardneri*, Clarke, is retained, and *A. zeylanica*, Clarke, given by Trimen as a variety of it, is again given specific rank. *A. Moonii*, Clarke, is retained. *A. pauciflora*, Heyne, has the new species, *A. polylepis*, Mez. (Gardner, 519; Thwaites, C. P. 15 p.p.) split off from it. *A. solanacea*, Roxb., given by Trimen as not wild, is also given for Ceylon. *Embelia Ribes*, Burm. is retained. *E. robusta*, Roxb., is transferred to *E. tsjeriam-cottam* (Roem. et Schult.) A.DC. the former species being confined to Bengal. *E. viridiflora*, Scheff., is *E. viridiflora*, Clarke (non Scheff.), and is described as *E. basaal* (Roem et. Schult. A.DC. *Myrsine capitellata*, Wall., is Thwaites (non Wall.) and is transferred to Rapanea, where it forms the species, *R. Thwaitesii*, Mez., n. sp.; (Gardner, 513, 514, 515., Thwaites, C. P. 623; Warburg, 1,081), *R. zeylanica*, Mez., n. sp. (Thwaites, C. P. 285, 1806, and in Hb. Hance, 688; Walker, 234); *R. robusta*, Mez., n. sp., (Thwaites, C. P. 623, p.p.) *R. exigua*, Mez., n. sp. (top of Adam's Peak, Thwaites, C. P. 2,598 ; and *R. rubens*, Mez., n. sp. (Thwaites C. P. 3,009).

§ 10. *Tropacolaceæ.* None in Ceylon.

J. C. W.

(To be continued at intervals.)

Apogamy in Elatostema.

(M. Treub. L' Apogamie de l' Elatostema acuminatum.
Brongn., Ann. Jard. Buit., 2. V., p. 141.)

THIS species occurs, though it is very rare, in the lower montane zone, in Dolosbage. The embryo-sac developes 4 or 6 nuclei,and the tissue above it becomes sclerenchymatous, and then one of the nuclei in the sac developes into an embryo without fertilization.

J. C. W.

Ant-inhabited Plants in Ceylon.

(E. Morteos : Sopra due piante formicarie, *Humboldtia laurifolia*,
L. e. *Triplaris americuna*, Vahl. Malpighia, vol.
XVIII., 1904, pp. 504–511, pl. X., XI.)

Humboldtia laurifolia Vahl (not L.), the Gal-karanda of the Sinhalese, is common in most low-country forests, and is a graceful little tree with spreading branches and pendulous young foliage. The young branches have curiously swollen internodes with perforations near the top, inhabited by ants.

J. C. W.

NOTES.

Mould growing in solution of Cupric Sulphate.

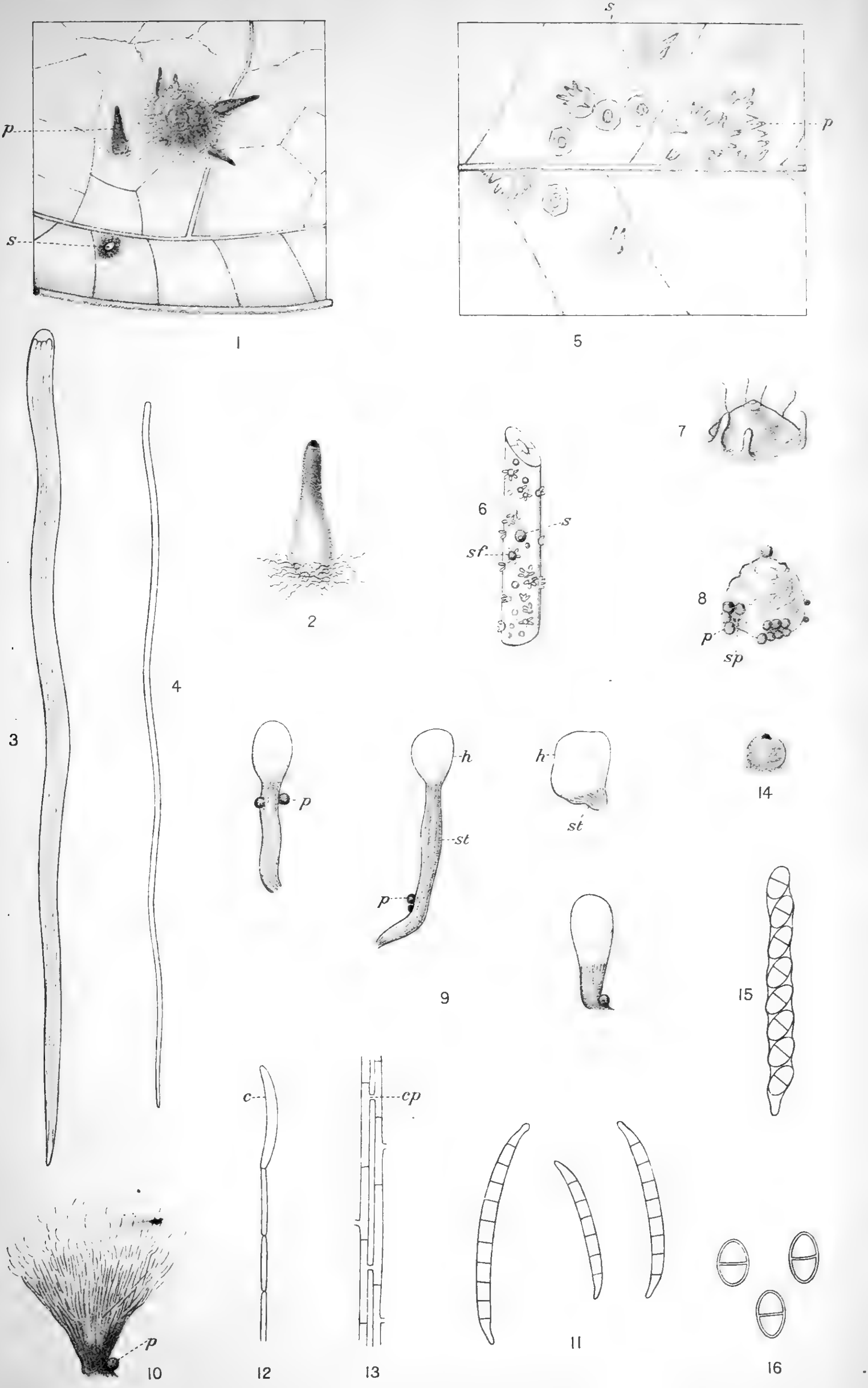
In his monograph of *Penicillium glaucum,* Brefeld remarks (p.3) that this mould can withstand the injurious effect of copper sulphate. An instance of this has recently been furnished at Peradeniya. The Government Entomologist, Mr. E. E. Green, desiring to protect his specimens from the ravages of moulds, tried the plan of brushing copper sulphate solution over his setting boards, but the experiment was brought to an abrupt conclusion by the discovery of large and flourishing colonies of *Penicillium glaucum* in the liquid employed. In a few days, the sides of the jar below the surface of the liquid were covered with hemispherical tufts of hyphæ from three to five millimeters in diameter; other tufts resting at the bottom attained a length of three centimetres, while others of various sizes floated on the surface.

Each tuft contained a few wing scales or hairs which had been transferred by the brush from the setting board to the solution. The hyphæ forming the tufts were 2–4 μ diameter, and apparently normal. The conidiophores were 50–70 μ high, 2·5μ diameter, *unbranched,* bearing sterigmata 6–8μ long and 2μ diameter, and spores 3–4 μ diameter. Only one branched conidiophore was observed: this was 70 μ high, and bore one side branch half way up. This reduction of the conidiophore to an unbranched, erect, hypha, bearing one group of sterigmata, appears to be the only departure from the normal development.

No spores were found on the submerged tufts; those became brown when exposed to the air through the removal of part of the liquid for analyses. Germinating spores were observed on the surface, usually in contact with an insect scale, and the growth of these continued in a hanging drop when copper sulphate was crystallizing out at the edge.

The solution contained 8·56 per cent. of copper sulphate ($Cu SO_4 5H_2O$). "Normal" Bordeaux mixture, which is considered the most efficacious fungicide, contains 1·6 per cent. copper sulphate.

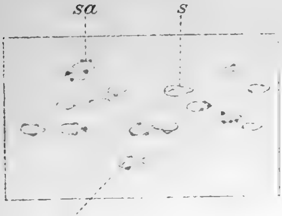
T. PETCH.



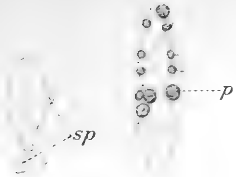
J. Parkin del.

E. Wilson, Cambridge.

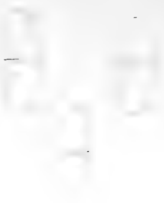
FUNGI PARASITIC ON SCALE-INSECTS.



17



18



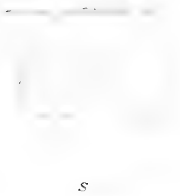
19

20

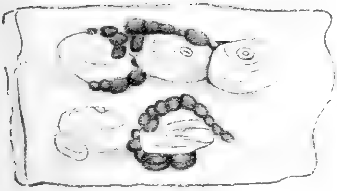
21

22

23



24



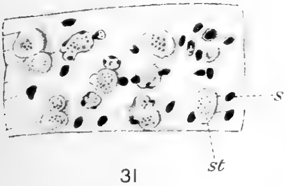
25

26

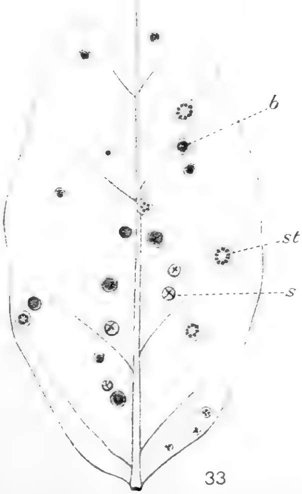
27

28

30

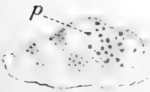


31



33

29

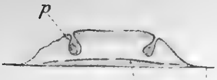


32

J. Parkin del.

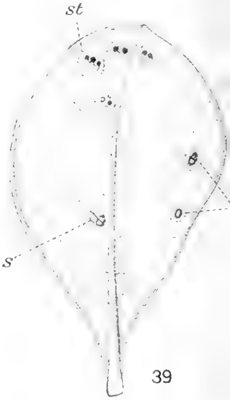
E. Wilson, Cambridge.

FUNGI PARASITIC ON SCALE INSECTS.

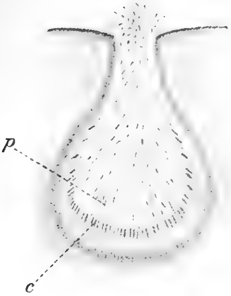


34

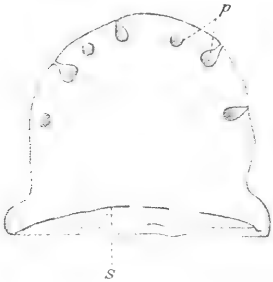
36



39



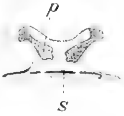
35



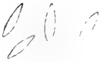
37

40

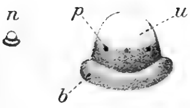
42



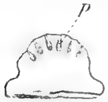
41



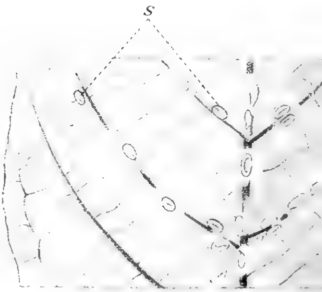
38



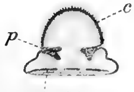
43



46



49



44

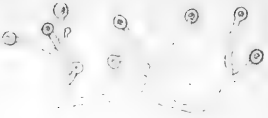
47

45

48

50

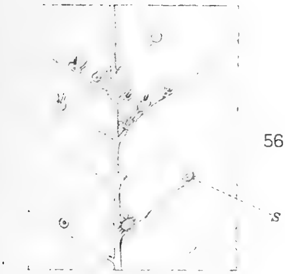
51



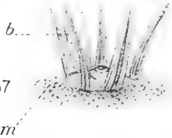
52

53

54

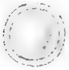


56

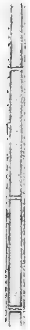


57

55

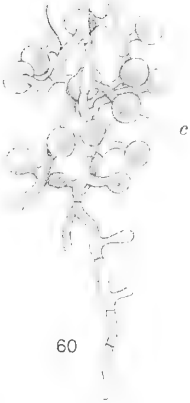


61

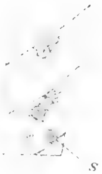


59

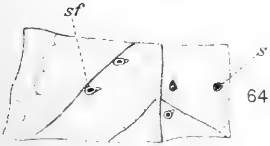
58



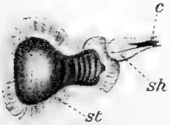
60



62

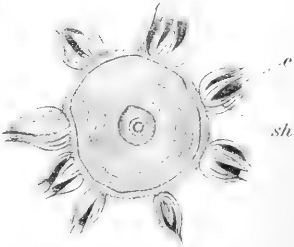


64



65

66



63

J. Parkin del. E. Wilson, Cambridge.

NOTICE.

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

Willis : a Revision of the Podostemaceæ of India and Ceylon, 70 pages	Re. 1·50 or 2*s.* 0*d.*
Willis : Studies in the Morphology and Ecology of the Podostemaceæ of Ceylon and India, 200 pages with 33 plates	Rs. 7·50 or 10*s.* 0*d.*
Wright : The Genus Diospyros in Ceylon : its Morphology, Anatomy, and Taxonomy, 185 pages with 20 plates	Rs. 6 or 8*s.* 0*d.*
Lock : On the Growth of Giant Bamboos, with special reference to the relations between conditions of Moisture and the Rate of Growth, 56 pages with 3 plates ...	Re. 1·50 or 2*s.* 0*d.*

NOTICE.

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

Willis : a Revision of the Podostemaceæ of India and Ceylon, 70 pages	Re. 1·50 or 2*s*. 0*d*.
Willis : Studies in the Morphology and Ecology of the Podostemaceæ of Ceylon and India, 200 pages with 33 plates	Rs. 7·50 or 10*s*. 0*d*.
Wright : The Genus Diospyros in Ceylon : its Morphology, Anatomy, and Taxonomy, 185 pages with 20 plates	Rs. 6 or 8*s*. 0*d*.
Lock : On the Growth of Giant Bamboos, with special reference to the relations between conditions of Moisture and the Rate of Growth, 56 pages with 3 plates	Re. 1·50 or 2*s*. 0*d*.

CEYLON PUBLICATIONS.

FOR SALE AT THE GOVERNMENT RECORD OFFICE, COLOMBO.

Oriental Literature.

	Rs.	c.
The Mahawansa :—		
Original Pali Text, Part I.	7	50
Do. Part II.	7	50
Sinhalese Translation, Part I.	5	0
Do. Part II.	5	0
Wijesinha's English Translation of Part II., with Turnour's Translation of Part I.	7	50
The Mahawansa Tika, with original Pali, bound in stiff covers	7	50
Do. do. unbound	6	50
Saddharmalankaraya (Sinhalese)	2	0
Extracts from the Pujawaliya (English)	1	0
Do. do. (Sinhalese)	0	75
Nitinighanduwa, English	1	0
Do. Sinhalese	1	0
Moggallana Panchika Pradipa (Pali)	1	0
Abhidhanappadipika, a Dictionary of the Pali Language	3	0
The Tesawalamai	0	50
Lapidarium Zeylanicum	31	50
Dravidian Comparative Grammar	13	0
Glossary of Native Words occurring in Official Documents (third edition)	0	30
Catalogue of Pali, Sinhalese, and Sanskrit Manuscripts in Temple Libraries	0	50
Alwis's Descriptive Catalogue of Sanskrit, Pali, and Sinhalese Works	5	0
Mugdhabodha Wyakarana (Sanskrit)	5	0
Mukhamatta Dipani (Pali)	5	0
Kawsilumina (Sinhalese)	1	50
Pybus's Mission to Kandy	0	50
Papers on the Custom of Polyandry as practised in Ceylon	0	15
The Rajavaliya: or, a Historical Narrative of Sinhalese Kings (in English and in Sinhalese) each	0	75

Archæology.

	Rs.	c.
Dr. Müller's Report on Inscriptions of Ceylon :—		
Text	5	0
Plates	5	0
Architectural Remains of Anuradhapura (with plates), by J. G. Smither, F.R.I.B.A. :—		
In boards	40	0
In cloth	60	0
Return of Architectural and Archæological Remains and other Antiquities in Ceylon	1	20
Reports on the Archæological Survey of Ceylon :—		
Kegalla District	6	0
Anuradhapura (I.)	0	50
Do. (II.)	1	0
Do. (III.)	1	65
Do. (IV.)	1	0
Do. (V.)	2	20
Do. (VI.)	2	0
Do. (VII.)	4	0

Natural History.

	Rs.	c.
Report on Brown Scale (or Bug) on Coffee	1	0
The Green-Scale Bug in connection with the Cultivation of Coffee.—Observations by Mr. E. Ernest Green (illustrated)	1	0
The Flora of Ceylon, by Dr. Trimen :— Parts III., IV., and V. (with plates) each	20	0
Lepidoptera of Ceylon, in 13 Parts, with coloured plates each Part	14	50
The Kitul Palm and its Uses, by T. B. Pohath-Kehelpannala	0	15
Report on the Ceylon Pearl Fisheries	1	35

District Manuals.

	Rs.	c.
Mannar, by W. J. S. Boake	1	0
Uva, by H. White	2	50
Nuwara Eliya, by C. J. R. Le Mesurier	5	0
Vanni Districts, by J. P. Lewis	5	0
North-Central Province, by R. W. Ievers	2	50

	Rs.	c.
Ceylon Civil List	1	0
Ceylon Blue Book	10	0
Administration Reports (annual volumes)	10	0
Sessional Papers (annual volumes)	10	0

◆

TO BE OBTAINED OF H. W. CAVE & Co., COLOMBO.

	Rs.	c.
The Ruined Cities of Ceylon. Demy 8vo. Illustrated with collotypes	9	0
Golden Tips: A description of Ceylon and its great Tea Industry. 214 illustrations from photographs by the Author. Demy 8vo.	10	0
Kandy and Peradeniya: an illustrated description, with 33 full-page photogravures. Demy 4to., Roxburgh binding	18	0
Nuwara Eliya and Adam's Peak: an illustrated description of the Highlands of Ceylon, with 34 full-page photogravures. Demy 4to., Roxburgh binding	18	0

◆

PUBLISHED AT THE "CEYLON OBSERVER" OFFICE.

	Rs.	c.
Skeen's Guide to Colombo (with maps and illustrated) Re. 1·50 and	1	75
Do. to Kandy (do.)	1	0
Burrows' Guide to Kandy and Nuwara Eliya	1	50
Do. to the Buried Cities	2	0

DOUBLE NUMBER.

Vol. III., Pt. II. NOVEMBER, 1906. Price Rs. 7·50. 10s. 0d.

ANNALS

OF THE

ROYAL BOTANIC GARDENS, PERADENIYA.

EDITED BY

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

DIRECTOR.

CONTENTS.

Colombo:

H. C. COTTLE, GOVERNMENT PRINTER, CEYLON.

London:

DULAU & CO., 37, SOHO SQUARE, W.

[*All rights of Reproduction and Translation reserved.*]

ANNALS OF THE ROYAL BOTANIC GARDENS, PERADENIYA.

NOTICE TO SUBSCRIBERS.

THE subscription rate is, for regular residents in Ceylon, Rs. 2·50 per annum, post free, payable in advance to the DIRECTOR, Royal Botanic Gardens, Peradeniya; for residents in other countries, Rs. 6 per annum, post free, payable in advance to the above, or eight shillings, payable to Messrs. DULAU & CO., 37, Soho Square, London, W.

The "Annals" will appear at irregular intervals, as matter is ready for publication, probably averaging 250 pages per annum, and when a volume of convenient size has been formed the Title Page and Contents will be issued. Individual Numbers or Papers may be purchased from the DIRECTOR, Royal Botanic Gardens, Peradeniya, or from Messrs. DULAU & CO., at prices marked upon them (considerably exceeding the subscription rate).

The "Circular" of the Royal Botanic Gardens, containing more popularly written articles on planting, agricultural, and botanical topics, may be received with the Annals by adding cents 50 to the Ceylon residents', and Re. 1·50, or 2*s*., to the foreign residents' subscription.

NOTICE TO CONTRIBUTORS.

All contributions should be addressed to the DIRECTOR, Royal Botanic Gardens, Peradeniya, Ceylon. They must be clearly written on one side of the paper only (Papers in French or German must be typewritten), and the figures must be ready for reproduction, and planned so as to properly fill a plate.

Each contributor is entitled to receive gratis fifty separate copies of his Paper, and may, by giving notice when returning proofs, purchase others at the rate, approximately, of two cents per page (including covers, if required), and 20 cents per full-page plate, for each copy, provided not less than 10 be taken.

Studies in Plant Breeding in the Tropics.

BY

R. H. LOCK.

(Fellow and late Frank Smart Student of Gonville and Caius College, Cambridge.)

III.—EXPERIMENTS WITH MAIZE.

LIBRARY
NEW YORK
BOTANICAL
GARDEN

CONTENTS.

Note.—This paper was completed in October, 1905, and the author has had no opportunity of revising it in the light of the numerous important results which have since appeared.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. III., Part II., November, 1906.]

INTRODUCTION.

THE present description of experiments with Indian corn (*Zea Mays*, L.) brings to a conclusion the account of a series of experiments in cross breeding carried out at Peradeniya during the years 1902-04. The results are for the most part concerned with the foundations of the new Mendelian science, rather than with any fresh developments; and statistics of considerable extent and uniformity are here brought forward as a contribution towards the firmer establishment of the original simple law, which describes the segregation of discontinuous characters during the formation of the germ cells in heterozygote plants.

It is to be regretted that difficulties are still found to stand in the way of our arriving at unanimity as to the use of the term Mendel's law.* De Vries, in his latest utterance upon the subject, employs the law of Mendel as a term to describe the proportion in which the different types appear in F_2 from a monohybrid, which he expresses in the form :— 1 A : 2 H : 1 L. (A active, H hybrid, L latent.)

Others again include the idea of dominance in their application of the phrase Mendel's law, and the expression is often used without definition. It seems necessary, therefore, to repeat that in the present series of papers the term "Mendel's law" is invariably used in the sense in which Correns first enunciated it, namely, as applying to the fact that in the germ cells of a heterozygote, the parental allelomorphs become segregated in all possible combinations in equal numbers. It must once more be insisted that, in cases of discontinuous inheritance, the only examples where this rule has so far been proved not to be followed are those in which correlation or coupling between different allelomorphs is found to occur—if we leave out of account the little understood cases of supposed blended inheritance.

---

* *Cf.* Annals II., 305. Also Karl Pearson in Nature, vol. 70, p. 627.

ACCOUNT OF CORRENS' EXPERIMENTS ON "XENIA."

Any one who sets about describing experiments in the cross breeding of Indian corn must of necessity begin with a reference to the admirable work of Correns described in his monograph in Bibliotheka Botanika, 1901. Correns has there analysed the behaviour on crossing of a large number of characters, especially those characters of the grain which may be affected as the immediate result of the cross, owing to so called "xenia,"* resulting from the double fertilization which takes place in maize. The following brief summary may serve to call to mind a few of the more important details of Correns's work. His more general conclusions have already been shortly referred to.

Correns found that characters belonging to the following categories followed Mendel's law on crossing; *i.e.*, were *schizogonous* :—

1. Colour of the pericarp. (Not fully proved.)
2. Colour of the endosperm. (Yellow, or non-yellow—*i.e.*, "white.")
3. Colour of the aleurone layer. (Blue, or non-blue—*i.e.*, "white.")
4. Chemical nature of the endosperm. (Starchy, or sugary.)
5. Shape of the aleurone cells. (Long or short.)

The following pairs of characters on the other hand are stated by Correns to be *homoogonous*; *i.e.*, the cross-bred plants produce gametes bearing these characters unsegregated :—

1. Shape of grain. (Round or pointed.)
2. Size of grains.
3. Relative weight of embryo and endosperm.

---

* The term xenia would probably be better confined to cases of direct action by the embryo upon the maternal tissues, but since there is no good term which can be used to denote the phenomena in maize, I have retained the word "xenia," placing it between inverted commas to indicate its special application.

In relation to the above it is suggestive that all the categories which exhibit "xenia" were found to be schizogonous. Those which did not do so were either plant characters (including fruit characters) or such a character of the seed as indentation, which behaves as if it were a fruit character, showing complete correlation (if it may be so expressed) with the plant which bears it. *

The behaviour of such characters as these, whether Mendelian or otherwise, is clearly less easy to determine than in the case of seed characters; and so far as the published records go there does not seem to be sufficient evidence to support a definite statement that these characters are really homoogonous.

Correns seems to have shown quite clearly that "xenia" grains invariably yield hybrid plants, which are heterozygotes in respect of the characters concerned in the act of "xenia." From this it follows that the ovum and the combined polar nuclei on the one hand, and the two generative nuclei of the same pollen tube on the other, bear always the same allelomorph.

The power of manifestation of an allelomorph in the heterozygote (or its valency or degree of dominance) was found to vary according to the individual plant and germ cell, and also to differ in different races. This was especially the case with the allelomorphs blue—non-blue in relation to the aleurone layer, since heterozygote grains of the same composition (white × blue) might be either pure white, pure blue, or intermediate in colour. In the reverse case (blue × white) blue appeared to be always fully dominant in first crosses in the few cases examined, but it is not known whether this is universally the case. The degree of dominance of blue was usually found to be

---

* This is the practical effect whatever the true explanation may be. Correns explains the phenomena by reference to the fact that in the formation of the endosperm two polar nuclei are combined with only one generative nucleus from the pollen tube; and he supposes that this can in some cases cause such a predominance of the female character as entirely to swamp the factor introduced from the pollen parent.

lessened after the process of segregation had taken place, as compared with that of the same character in a pure race.

It will not be necessary to follow Correns through the whole of his account of the details of "xenia" in the case of various characters. Suffice it to say that, so far as my experience goes, that account is remarkably accurate, and that I have found no case of disagreement in my own experiments. Thus, so far as "xenia" itself is concerned, it will only be necessary to describe a few cases in which races were examined which Correns did not make use of, and these will afford differences only of detail.

Correns's results were uncomplicated by cases of coupling, no such effect being observed in any of the characters mentioned above.

Various cases were observed where a cross of the form A × a differed in appearance from one of the form a × A, such cases being also confined to characters of the endosperm. These again are explained by reference to the greater quantity of heritable substance presumably introduced on the female side of the transaction.

In a later paper Correns records a curious apparent exception to Mendel's law in the case of a cross between a blue sugar corn and a non-blue pop corn. Here the heterozygote on self-pollination yielded only 15·61 per cent. of sugary grains among a total of nearly 9,000. On pollination with the recessive parent, however, there appeared nearly 50 per cent. of sugar grains, so that the segregation of at least the female germ cells was of the normal character. Correns suggests that in this case the combinations A × A, A × a, a × A, a × a, do not all take place with equal facility, owing to competition among the pollen cells or to some other cause.

CULTIVATION OF MAIZE IN CEYLON.

At the elevation of Peradeniya not only the native strain commonly cultivated, but also several American sorts which were specially introduced for the purpose of crossing with the above, made very good growth at almost any time of year, and ripened their fruit after between four and five months from the time of sowing. Some of the smaller American kinds, especially sugar and pop corns, were less suited to the climate and yielded scarcely any crop.

The growth and strength of maize plants appeared to depend to a quite remarkable extent upon the amount of nutriment available. This may best be illustrated by describing an experiment which failed in its proper object owing to this very propensity. The experiment in question was designed for the purpose of showing whether nutrition had any effect upon the development and intensity of the blue pigment appearing in the aleurone layer of certain cross-bred plants. For this purpose an acre of ground was divided longitudinally into a series of narrow plots intended for separate treatment with chemical fertilizers, whilst the seed was sown in such a manner that each row ran right across the series of plots and included grains of one kind only.

The central part of the land in question consisted of an old rice field which turned out to have become almost completely exhausted so far as grain crops were concerned. At the ends, the field rose towards higher ground where trees had been growing.

At the centre of the field, plants, to which artificial non-nitrogenous manures were applied after sowing, produced a few male flowers but usually no female inflorescence, and their average height was about 4 feet. At the ends of these plots similar plants treated with the same fertilizers grew to an average height of 6 feet and produced a few poor cobs. The only good cobs were produced on a strip of ground running from end to end of the plot which had been treated six months earlier with a heavy dressing of cattle manure, and from which a scanty crop of sugar corn had already been taken. Here the plants reached a height of from 7–9 feet, a height which I am accustomed to regard as normal for the particular varieties used under generous cultivation.

METHODS EMPLOYED.

The plants were grown as a rule in rows 3 feet apart, the distance between individual grains sown being 1 foot in the case of the larger varieties, and rather less in that of the smaller.

In the first instance a number of direct pollinations were effected between particular parent plants, the method being to enclose the stigmas from the time of their first appearance in a bag of parchment paper, the male inflorescences being treated in the same way, and then to transfer the whole mass of male flowers to the bag enclosing the stigmas of the plant to be pollinated. Even by this method it is not possible to be certain that foreign pollen is completely excluded, and the result of some of the first experiments with the blue character led me to suppose the method to be much less accurate than was really the case.

Afterwards the following method was adopted. The grains of the recessive strain which was to be used as the pollen parent were sown in alternate rows upon an isolated plot of ground of considerable size, and in the remaining rows were planted the various forms which it was desired to test by crossing with the recessive. The tassels of the seed parents were removed previous to the opening of the staminal flowers, and pollination was left to the agency of the wind.

This method is open to certain objections, the most serious of which lies in the fact that the individual pollinating parent is not known in any particular case, so that possible individual differences between the members of the recessive strain used are quite uncontrolled. Even for a broadly statistical result it is necessary that a very uniform strain should be used as the source of pollen, and the point must be tested by examining the cobs produced by every plant of the pollinating form. If a single wrong seed escape notice in the sowing, the plant arising from it may wrongly pollinate all its neighbours. Great care must further be exercised in removing all the staminal flowers of the seed parents before any pollen escapes from them; and some are very liable to be overlooked on a large plot of tall plants, especially when, as sometimes happens, staminal flowers are produced on a seed-bearing spike.

In the following experiments there was now and then evidence of stray pollen grains having escaped owing to the latter cause, but never in sufficient numbers to vitiate a statistical result.

DESCRIPTION OF STRAINS USED IN THE EXPERIMENTS.

1.—(W. D.) "*Boone County*" white dent corn. Loose grains of this variety were obtained from Mr. Webber of the U. S. Dept. of Agriculture, Washington. A figure of a perfect cob of this strain appears in Webber and Bessy's pamphlet (74), 1889, in which there is also given a picture of the type from which it was derived by selection. The cobs of the first generation grown at Peradeniya—sown December, 1902, in comparatively poor soil—resembled the latter type, but were smaller and less perfect. None were covered to the top with grains as in the improved "Boone County" type. By dint of careful selection and heavy manuring of the plants at my disposal I was able in four generations to obtain a large percentage of perfect cobs of the improved type. The shape of the grains meanwhile remained perfectly constant, being flat, elongated, and much indented at the apex, and they were always pure white.

This result is interesting in more than one way. In the first place it very clearly illustrates the fact that races produced by selection owe their continued existence to the continuance of the process under the proper conditions. And in the second it entirely discredits the idea quoted by Darwin from Metzger, that corn transferred to new conditions reverts to the type prevalent in the new country.

What is clearly the true explanation of Metzger's phenomena, namely, the effect of crossing with the local form, has been clearly pointed out by de Vries, and Vernon's recent use of these supposed facts as a proof of the inheritance of acquired characters is inadmissible.

This type of corn is very much more indented than Correns's "Leucodon," which is properly a half-dent form.

2.—(Y. D.) "*Rileya favourite*," yellow dent corn, from Webber. Deep yellow in colour and even more indented than the W. D. It gave a poorer crop than the latter, and was only grown for two generations.

3.—(W. S.) "*Moor's Concord*" white sugar corn, from Webber. A form corresponding to the "Dulcis" of Correns, and yielding typical hyaline, much wrinkled, sugary grains without pigment. Only very small plants and poor cobs were obtained.

4.—(G. W. S.) Giant white sugar corn obtained from a seedsman in Philadelphia. Similar to the above in essential characters, but the grains were less hyaline and occasionally a few of them showed some approach to starchiness. This strain yielded much larger plants and finer cobs than the last mentioned.

5.—(B. S.) "*Black Mexican*" sugar corn, from Webber. This corresponds to the "Cœruleodulcis" of Correns. The cells of the aleurone layer contain a deep purple pigment which makes the grains appear almost black. In other respects this form closely resembles W. S. In the Ceylon climate it fared even worse than that variety.

6.—(W. P.) White pop corn from Philadelphia. Very hard round grains of a hyaline nature, without pigment; cobs and grains very small.

7.—(Y. P.) Yellow pop corn from Philadelphia. Resembled the above, but the endosperm was of a clear bright yellow colour.

Besides the above, some strains of pointed pop corn, as well as the very large starchy variety known as Cuzco, were tried, but failed to produce fruit.

8.—The strain commonly grown by natives in Ceylon was of the flint type and exhibited the colours white, blue, yellow, and red in various combinations, appearing to include a mixture of the "Alba," "Cyanea," "Gilva," and "Rubra" forms of Correns. The original specimens were obtained from Mr. A. J. Kellow of Albion, Nuwara Eliya.

THE CHARACTERS CONSIDERED.

A.—COLOUR OF GRAINS.

1. *White* indicates the absence or non-development of other colours. Such grains are seldom pure white, and in particular sugary grains of this class have a glassy grayish appearance.

2. *Yellow.*—This colour appears in chromatophores within the cells of the endosperm, including those of the aleurone layer.

3. *Blue, black, or purple.*—These pigments occur in a soluble form, and are confined to the cells of the aleurone layer. In cross-bred grains the colour is very liable to vary in shade and intensity in different grains of the same cob and in different parts of the same grain. No definite distinction was drawn between the different shades included in this group, but the terms blue or black are used according as either appeared more suitable in any particular case.

4. *Red.*—This colour is confined to the pericarp—a maternal structure. The pigment is situated in the cells and to some extent also in the cell walls of the pericarp.

In the case of cross-bred cobs it is thus possible for white, yellow, and blue grains to occur mixed together in the same cob, and further the same grain may contain both the blue and the yellow pigments. On the other hand, the red pigment appears either in all the grains of a particular plant or not in any of them, since it belongs in fact to a different generation from the endosperm and embryo enclosed in that particular pericarp.

B.—SHAPE OF GRAINS.

1. *Roundness* as opposed to *wrinkledness.*—The difference between these two characters depends upon the chemical nature of the endosperm. In the wrinkled grains the chemical changes which take place in the reserve materials during

ripening apparently undergo a check prior to the formation of starch, and the final product is of a sugary as opposed to a starchy character. The grain on drying shrinks considerably so that its surface is thrown into folds, and this fact affords a visible external distinction by which the two types of grain may be separated. It must be remembered, however, that the fundamental distinction is a chemical one. In crosses where the starchy (round) parent shows a very hard hyaline endosperm, grains may occasionally be seen in F_2, which are intermediate between the typical round and wrinkled kinds. In such cases there is no evidence that the chemical difference does not still hold good, and the grains can always be distinguished with certainty if their offspring are examined.

2. *Indentation* as opposed to *roundness.*—Plants bearing the former character produce elongated grains, the skins of which are folded inwards at the extremity instead of being convex. This difference appears to depend partly upon what Correns calls the physical nature of the endosperm, but partly also upon the characteristic shape assumed by the pericarp—for the characters behave as if they belong to the parent plants and not to individual grains. With regard to the former point, the indented type of grain contains a larger proportion of the loose floury inner endosperm as compared with the amount of the hyaline substance which occupies the more external region. According to my observations, however, the relative amount of loose material seem to increase with the size of the grain as we pass from the small "pop corns," which are almost entirely hyaline, to the large Cuzco, which is almost entirely starchy, and even upon the same plant it may be observed that the larger lower grains of a cob are more floury than the smaller upper ones.

The above were the only characters with which it was found possible to deal on a large scale. Such characters as size, whether of grain, cob, or plant, were too indefinite or required too much time for their full determination to allow of their use on the large statistical scale proposed.

THE EXPERIMENTS.

I.—CROSSES BETWEEN DEFINITE RACES.

According to the modern method, the use of which is now well established, these crosses will be dealt with under the heads of the separate pairs of characters concerned. Simple pairs of characters will be treated first, the behaviour of more than one pair being considered later.

A.—SINGLE PAIRS OF CHARACTERS (MONOHYBRID CROSSES).

1.—STARCH CORN CROSSED WITH SUGAR CORN.

In the case of crosses of this kind, Correns and de Vries have shown that there is dominance of the starchy (round) character over the sugary (wrinkled), and that these characters segregate in a regular manner at the formation of the germ cells. The evidence which follows shows that Mendel's law of segregation in equal numbers is usually fulfilled with great exactness.

F 1.

The immediate result of Crossing (visible as "xenia").

(*a*) **Sugar Corn × Starch Corn.***—

The following cases were observed :—

Experiment 1.—*Black Mexican* × *White Dent.*
,, 2.—*Black Mexican* × *Flint corn.*†
,, 3.—*Black Mexican* × *Yellow Dent.*
,, 4.—*Moore's Concord* × *White Dent.*
,, 5.—*Moore's Concord* × *Flint corn.*†
,, 6.—*Moore's Concord* × *Yellow Dent.*

In all these cases the result was practically identical. The grains produced took on a smooth rounded form, and the consistency became mealy or floury to a degree nearly resembling that of flint corn, no matter whether the pollinating parent was flint or dent. It seems clear that the particular degree of

---

* Here and elsewhere the seed parent stands first, the pollen parent second.

† The flint corn was a mixed strain so far as colour is concerned, but there is no reason for supposing that it was impure in respect of the flint (smooth, round, starch) character.

mealiness produced in such a case (the physical as opposed to the chemical nature of the endosperm) is something which belongs to the sugary seed parent. It depends, that is to say, on a maternal character hitherto "latent." Subsequent generations will illustrate this point more clearly.

(*b*) **Starch Corn × Sugar Corn.—**

Experiment 7.—*White Dent* × *Black Mexican.*
,, 8.—*Yellow Dent* × *Black Mexican.*
,, 9.—*Yellow flint* × *Black Mexican.*
,, 10.—*White Dent* × *Giant white sugar corn.*
,, 11.—*Yellow pop* × *G. W. S.*
,, 12.—*White pop* × *G. W. S.*

There was no change in the shape or consistency of the resulting grains in any of the above cases; in both respects these grains resembled uncrossed grains of their proper varieties.

F 2.

1.—The result of mutual Pollination between Plants grown from the Grains produced in F 1.

Expt. 13.—*White Dent* × *Black Mexican.*

TABLE 1.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
1	290	92	382	76·1	23·9
2	309	100	409	75·7	24·3
3	379	135	514	73·7	26·3
4	333	131	464	71·8	28·2
5	272	98	370	73·5	26·5
6	337	95	432	78·1	21·9
7	300	97	397	75·5	24·5
8	320	125	447	71·5	28·5
9	253	78	331	76·4	23·6
10	288	87	375	77·0	23·0
11	308	117	425	72·4	27·6
12	292	97	389	75·1	24·9
13	277	91	368	75·2	24·8
14	243	72	315	77·0	23·0
15	290	98	388	74·7	25·3
16	286	97	383	74·6	25·4
17	232	60	292	79·4	20·6
18	299	93	392	76·2	23·8
Total	5,310	1,765	7,075	75·06	24·94

Expectation : 75 *starchy* ; 25 *sugary.*

On any particular plant the starchy grains were all of the same shape, except that the smaller grains at the apex were rather more rounded than the larger grains towards the middle of the cob. From plant to plant there was some variation in the shape of the grains, but all the starchy grains were intermediate between the flint and dent types. The sugary grains on the other hand were all closely similar in appearance, and resembled the grains of B. S. almost exactly in shape and consistency.

Expt. 14.—*Yellow flint* × *Black Mexican* (plants from F_1 grains mutually pollinated).

TABLE 2.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
1	405	144	549	73·8	26·2
2	470	139	609	77·1	22·9
3	378	120	498	75·9	24·1
4	294	103	397	75·0	25·0
5	226	65	291	77·6	22·4
6	399	103	502	79·5	20·5
7	344	115	459	74·9	25·1
8	322	101	423	76·1	23·9
9	163	47	210	77·6	22·4
10	329	89	418	78·7	21·3
11	231	73	304	75·9	24·1
12	367	123	470	78·1	21·9
13	162	59	221	73·3	26·7
14	275	79	354	77·7	22·3
15	228	73	301	75·7	24·3
16	264	67	331	79·7	20·3
17	299	82	381	78·5	21·5
18	366	118	484	73·7	26·3
19	353	104	457	77·2	22·8
20	174	64	238	73·4	26·6
21	290	90	380	76·3	23·7
22	279	73	352	79·3	20·7
Total	6,618	2,031	8,649	76·54	23·46

Expectation : 75 *starchy* ; 25 *sugary.*

As in the previous case there was never the least cause for hesitation in deciding from its external appearance whether a grain belonged to the starchy or to the sugary category. The starchy grains showed no alteration in shape or consistency from those born by the parental type. The sugary grains differed a little in shape owing to the fact that the cobs, each taken as a whole, showed some dominance of the shape characteristic of the flint variety.

2.—The result of crossing F1 Plants with a Dominant Form.

Expt. 15 :—(*Yellow dent* × *White dent*) × (*White dent* × *Black Mexican*).

Thirteen cobs bearing altogether 5,431 grains were examined. All the grains were of a fully indented type and showed no trace of the sugary parent.

Expt. 16.—(*White dent* × *Black Mexican*) × *White dent.*

Nine cobs bearing 2,992 grains were examined. All the grains were alike, being starchy and intermediate between the flint and dent types.

Expt. 17.—(*Yellow flint* × *Black Mexican*) × *White flint.*

Nine cobs with 2,412 grains were examined. All the grains were found to be of the full flint type.

3.—The result of crossing F1 Plants with a Recessive Form.

Expt. 18.— (*Yellow pop corn* × *G.W.S.*) × *G.W.S.*

TABLE 3.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent Sugary.
1	260	217	477	54·6	45·4
2	209	204	413	50·7	49·3
3	167	198	365	45·7	54·3
4	196	230	426	46·0	54·0
5	206	201	407	50·3	49·7
6	151	133	284	53·1	46·9
7	171	165	336	50·8	49·2
8	239	209	448	53·3	46·7
9	234	224	458	51·1	48·9
10	185	165	350	52·9	47·1
Total	2,018	1,946	3,964	51·0	49·0

Expectation : 50 starchy ; 50 sugary.

Starchy and sugary grains were again very easily distinguishable.

The grains were intermediate in size between those of the (larger) sugary parent and those of the original pop corn. The consistency of the starchy grains was less hyaline than that characterizing the pop corn, being intermediate between that of the latter and that of a typical flint grain.

Expt. 19.—Table 4 shows the result of the same cross as the last in the case of the offspring of a particular grain of the original sample of yellow pop corn (P) which by the behaviour of its offspring in F1 was shown to have arisen by crossing with a white starchy strain of some kind. (See also Expt. 32.) As far as the characters now under consideration are concerned its behaviour is normal.

TABLE 4.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
1	265	233	498	53·2	46·8
2	275	247	522	52·7	47·3
3	206	207	413	49·9	50·1
4	233	282	515	45·2	54·8
5	227	239	466	48·7	51·3
6	195	201	396	49·2	50·8
7	210	162	372	56·4	43·6
8	150	162	312	48·1	51·9
9	217	203	420	51·6	48·4
10	157	164	321	48·9	51·1
11	170	165	335	50·8	49·2
12	233	257	490	47·6	52·4
13	137	165	302	45·4	54·6
14	222	207	429	51·7	48·3
15	120	112	232	51·7	48·3
16	177	183	360	49·1	50·9
17	230	194	424	54·3	45·7
18	131	103	234	56·0	44·0
19	144	116	260	55·4	44·6
20	82	56	138	59·4	40·6
21	256	245	501	51·1	48·9
22	230	219	449	51·2	48·8

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
23	280	290	570	49·1	50·9
24	189	195	384	49·2	50·8
25	244	264	508	48·1	51·9
26	184	177	361	50·9	49·1
27	303	232	535	56·6	43·4
28	200	163	363	55·1	44·9
29	223	209	432	51·6	48·4
30	242	224	466	51·9	48·1
31	244	262	506	48·2	51·8
32	231	218	449	51·4	48·6
33	273	274	547	49·9	50·1
Total	6,903	6,627	13,530	51·0	49·0

Expectation : 50 starchy ; 50 sugary.

There is here an evident slight bias towards an excess of starchy grains above the expected number. It is possible that this is partly due to pollination having taken place in a few cases from the plants of a neighbouring plot in which starch corn was grown, though it was believed that the latter had ceased to give off pollen before the present plants were ready to receive it.

Expt. 20.—(White pop corn × G.W.S.) × G. W. S.

This was the only case in which there was found to be a difficulty in distinguishing the two classes of grain. The great majority of grains were either smooth or obviously wrinkled, but a smaller number were only slightly rough on the surface and constituted a group intermediate between the other two. The result indicated in Table 5 was obtained by counting as sugary all those grains which showed any trace of roughness, a proceeding which was found to be justified by the evidence of a further generation. The supposed starchy grains are still distinctly in excess, and it seems possible that a few of the quite smooth grains are also really sugary in nature.

TABLE 5.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
1	219	217	436	50·2	49·8
2	130	140	270	48·2	51·8
3	203	168	371	54·7	45·3
4	164	142	306	53·6	46·4
5	211	196	407	51·9	48·1
6	186	119	305	60·0	40·0
7	95	106	201	47·3	52·7
8	136	134	270	50·4	49·6
9	98	89	187	52·3	47·7
10	134	156	290	46·2	53·8
11	111	109	220	50·5	49·5
12	116	99	215	54·0	46·0
13	166	132	298	55·7	44·3
14	156	162	318	49·1	50·9
Total	2,125	1,970	4,095	51·9	48·1

Expectation: 50 starchy ; 50 sugary.

Expt. 21.—(*White flint* × *G.W.S.*) × *G.W.S.*

TABLE 6.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
1	246	261	507	48·5	51·5
2	218	259	477	45·8	54·2
3	322	320	642	50·1	49·9
4	317	311	628	50·4	49·6
5	207	242	449	46·1	53·9
6	269	235	504	53·3	46·7
7	158	181	339	46·6	53·4
8	231	234	465	49·6	50·4
9	196	220	416	47·1	52·9
10	303	300	603	50·2	49·8
11	303	299	602	50·3	49·7
12	267	257	524	51·0	49·0
13	264	214	478	55·2	44·8
14	319	313	632	50·5	49·5
Total	3,620	3,646	7,266	49·5	50·5

Expectation : 50 starchy : 50 sugary.

Here although a few of the sugary grains showed traces of starchiness, as is also the case in the parent form G. W. S., there was no difficulty in distinguishing these from the true starchy type which made up nearly 50 per cent. of the total.

F 3.

Offspring of Plant No. 1, *Table* 5:—(*a*) smooth, (*b*) fully wrinkled, and (*c*) slightly rough grains were sown. After removal of the male flowers the plants were freely exposed to the pollen of G. W. S.

(*a*) *Expt.* 22.—Twenty plants were examined. In every case the cobs showed approximately equal numbers of starchy and sugary grains. The three largest gave the following numbers:—

TABLE 7.

Plant.	Starchy.	Sugary.	Total.	Per cent. Starchy.	Per cent. Sugary.
1	217	216	433	50·2	49·8
2	159	177	336	47·3	52·7
3	188	198	386	48·7	51·3
Total	564	591	1,155	48·8	51·2

Expectation: 50 starchy; 50 sugary.

All the grains counted as sugary were well wrinkled.

(*b*) *Expt.* 23.—Twenty plants produced only sugary grains, over 6,000 in number.

(*c*) *Expt.* 24.—Out of a total of 19 plants, 18 produced sugary grains only, the remaining plant yielded 148 st., 140 su., or 51·4 per cent. of the former.

F 4.

In this generation a large number of recessive grains were grown—the offspring of plants described in several of the above experiments, and in particular of experiments 22, 23, 24. Such recessive grains yielded without exception recessive offspring.

2.—YELLOW VARIETIES CROSSED WITH WHITE VARIETIES.

Here the colour of the heterozygote grains was usually more or less intermediate between the parental colours. In only a few cases did the yellow colour appear to be fully dominant. It will however be convenient in practice always to call the white or non-yellow character "recessive," and this procedure is justified by the fact that it was always possible to distinguish the recessive (so defined) from the heterozygote form.

F 1.

The immediate result of crossing.

(*a*) White × Yellow.

Expt. 25—*White dent* × *Yellow dent.*—

The starchy apical part of the "xenia" grains resulting from this cross remained nearly pure white whilst the lower part took on a pale yellow tint, the colour varying slightly in different grains.

(*b*) Yellow × White.

Expt. 26.—*Yellow dent* × *White dent.*—

In these grains the colour of the apical part became changed from strong yellow to very pale yellow, whilst the lower part remained deep yellow and showed scarcely any alteration. The grains as a whole were thus very much yellower than those which resulted from the reciprocal cross.

Expt. 27.—*Yellow pop corn* × *G. W. S.*—

The cross-bred grains showed no change in colour as compared with those of the yellow parent, yellow being in this case dominant. (The reciprocal cross was not made.) As an exception, one plant out of many raised yielded nearly equal numbers of white and of yellow grains; namely, 132 W and 141 Y. The conclusion to be drawn from this is that the particular flower of the parental strain, which gave rise to the grain from which this plant sprung, must have been accidentally fertilized with pollen from a smooth white variety. The unknown parent must have been starchy because all the grains of the plant under consideration were starchy, although the pollen parent was sugary.

F 2.

The result of crossing F 1 Plants with the "Recessive."

Expt. 28.—(*White dent* × *Yellow dent*) × *White dent.*—

TABLE 8.

	Yellow.	White.	Total.	Per cent. Yellow.	Per cent. White.
1	276	280	556	49·6	50·4
2	200	165	365	54·8	45·2
3	213	179	392	54·3	45·7
4	144	159	303	47·5	52·5
5	237	215	452	52·5	47·5
Total	1,070	998	2,068	51·74	48·26

Expectation : 50 yellow ; 50 white.

Expt. 29.—(*Yellow dent* × *White dent*) × *White dent.*—

TABLE 9.

	Yellow.	White.	Total.	Per cent. Yellow.	Per cent. White.
1	365	279	644	56·7	43·3
2	281	367	648	43·4	56·6
3	257	254	511	50·3	49·7
4	222	293	515	43·1	56·9
5	229	227	456	50·4	49·6
Total	1,354	1,420	2,774	48·8	51·2

Expectation : 50 yellow ; 50 white.

Expts. 28 and 29.—In both these cases the resulting "yellow" grains closely resembled those which were obtained from the first cross—white × yellow—in F_1. The colour was rather more variable, and perhaps on the whole slightly darker, but was much nearer to that mentioned than to the result of the reciprocal cross in F_1.

Expt. 30.—(*Yellow dent* × *White dent*) × (*White dent* × *Black Mexican*).

A considerable number of the grains produced had a black or blackish aleurone layer (see Expt. 40) and in these the colour of the underlying endosperm was usually not distinguishable. The following table includes only those grains which showed no black pigment in the aleurone layer.

TABLE 10.

	Yellow.	White.	Total.	Per cent. Yellow.	Per cent. White.
1	116	149	265	43·8	56·2
2	171	163	334	51·2	48·8
3	136	134	270	50·4	49·6
4	135	117	252	53·6	46·4
5	79	103	182	43·4	56·6
6	93	109	202	48·6	51·4
7	132	121	253	52·2	47·8
8	174	122	296	58·8	41·2
9	90	105	195	46·2	53·8
Total	1,126	1,123	2,249	50·07	49·93

Expectation : 50 yellow : 50 white.

Expt. 31.—(Yellow pop corn × G. W. S.) × G. W. S.—

TABLE 11.

	Yellow.	White.	Total.	Per cent. Yellow.	Per cent. White.
1	234	243	477	49·1	50·9
2	212	201	413	51·3	48·7
3	170	195	365	46·6	53·4
4	208	218	426	48·9	51·1
5	191	216	407	46·9	53·1
6	137	147	284	48·3	51·7
7	177	159	336	52·7	47·3
8	226	222	448	50·5	49·5
9	225	233	458	49·1	50·9
10	173	177	350	49·5	50·5
Total	1,953	2,011	3,964	49·3	50·7

Expectation : 50 yellow ; 50 white.

Half of the above grains were starchy and half sugary (see Table 4). As in the case of peas, the colour of the wrinkled grains was a less intense yellow than that of the smooth ones. The latter were a good deal paler than those of the previous generation, so that the successive introduction of white has some diluting effect,* but there was still no difficulty in distinguishing either kind from those grains from which the yellow pigment was wanting.

---

* The increased size of the grains, as compared with the pigmented parent, may account for part of this effect.

Expt. 32.—The offspring of yellow grains from the exceptional cob recorded above as having shown equality of yellow and white grains in F_1—also pollinated again from G. W. S.—were in no way distinguishable from the specimens last described. The following numbers were obtained :—

TABLE 12.

	Yellow.	White.	Total.	Per cent. Yellow.	Per cent. White.
1	250	248	498	50·3	49·7
2	268	254	522	51·3	48·7
3	210	203	413	50·8	49·2
4	275	240	515	53·4	46·6
5	225	241	466	48·3	51·7
6	195	201	396	49·2	50·8
7	189	183	372	50·8	49·2
8	145	167	312	46·5	53·5
9	212	208	420	50·5	49·5
10	173	148	321	54·0	46·0
11	173	162	335	51·7	48·3
12	236	254	490	48·2	51·8
13	151	151	302	50·0	50·0
14	208	221	429	48·5	51·5
15	119	113	232	51·3	48·7
16	157	203	360	43·6	56·4
17	208	216	424	49·1	50·9
18	129	105	234	55·2	44·8
19	128	132	260	49·2	50·8
20	63	75	138	45·6	54·4
Total	3,714	3,725	7,459	49·7	50·3

Expectation : 50 *yellow ;* 50 *white.*

3.—BLACK ALEURONE LAYER CROSSED WITH WHITE.

(*a*). *Black* × *White.*

Expt. 33. *Black Mexican* × *Moore's Concord.*

The grains so produced were all of a blue black tint, and were not perceptibly paler in colour than those of the pure black strain.

(*b*). *White* × *Black.*

Expt. 34.—*Moore's Concord* × *Black Mexican.*

The resulting grains were either black, intermediate, or pure white, and a considerable number of the intermediate grains were mottled. The proportionate numbers in which the different types appeared was not determined, but the number of pure white grains was considerably less than the whole number of black and blackish grains taken together.

Expt. 35.—*White dent* × *Black Mexican.*

The result was similar to the last, but the proportion of pure white grains which resulted was nearly 50 per cent.

Expt. 36.—*Yellow dent* × *Black Mexican.*

Five brightly mottled yellow and black grains were obtained as the result of accidental pollination.

Expt. 37.—*Yellow flint* × *Black Mexican.*

Nearly equal numbers of yellow grains and of grains slightly mottled with pale bluish black were obtained.

F 2.

1.—The result of mutual Pollination between Plants arising from the Grains of F 1.

Expt. 38.—*Offspring of the cross Moore's Concord* × *Black Mexican.*

TABLE 13.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	220	162	382	57·9	42·1
2	236	173	409	57·8	42·2
3	282	232	514	55·8	44·2
4	262	202	464	56·6	43·4
5	201	159	370	57·0	43·0
6	258	174	432	59·7	40·3
7	214	183	397	53·9	46·1
8	260	187	447	58·1	41·9
9	190	141	331	57·4	42·6
10	201	174	375	53·6	46·4
11	243	182	425	57·1	42·9
12	214	175	389	55·0	45·0
13	220	148	368	59·8	40·2
14	191	124	315	60·4	39·6
15	210	178	388	54·1	45·9
16	233	150	383	60·8	39·2
17	175	117	292	59·9	40·1
18	230	162	392	58·7	41·3
Total	4,052	3,023	7,075	57·27	42·73

A considerable proportion of the grains included under the heading " Black " in the above table were mottled in appearance, showing darker spots on a paler ground. These, as well as the uniformly coloured grains, ranged from deep black to very pale slate colour, the majority being dark. In later generations the mottling almost entirely disappeared, and the grains recorded as black or blue were also of a more uniformly dark shade of colour. It was found impossible to draw any sharp distinction between the darker and paler grains, and an attempt to examine their progeny separately failed almost entirely owing to failure of the crop. A few of the mottled F_2 grains which were sown separately yielded in F_3—on pollination by G. W. S.—a mixture of blue and white grains among which the blues were now almost uniform in appearance.

It may be remarked that the ratio of blacks to whites was the same in the case of starchy grains as in that of sugary grains, the percentages derived from the total figures being as follows :—

Black starchy ..	.. 42·99
White starchy ..	.. 32·06
Black sugary ..	.. 14·27
White sugary ..	.. 10·67

And the proportionate number of mottled grains seemed to be nearly the same in either case.

2.—Heterozygotes crossed with Pollen from the Recessive Form.

Expt. 39.— (*White dent* × *Black Mexican*) × *White dent.*

TABLE 14.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1 ..	117 ..	232 ..	349 ..	33·5 ..	66·5
2 ..	168 ..	306 ..	474 ..	35·5 ..	64·5
3 ..	133 ..	269 ..	402 ..	33·1 ..	66·9
4 ..	121 ..	296 ..	417 ..	29·0 ..	71·0
5 ..	90 ..	217 ..	307 ..	29·3 ..	70·7
6 ..	104 ..	233 ..	337 ..	30·9 ..	69·1
7 ..	83 ..	166 ..	249 ..	32·1 ..	67·9
8 ..	81 ..	146 ..	227 ..	35·7 ..	64·3
9 ..	77 ..	153 ..	230 ..	33·5 ..	66·5
Total..	974	2,018	2,992	32·6	67·4

3.—A non-black form crossed with Pollen from the Heterozygotes.

Expt. 40.—(*Yellow dent* × *White dent*) × (*White dent* × *Black Mexican.*)

TABLE 15.

	Black.	White and Yellow.	Total.	Per cent. Black.	Per cent. White.
1	166	265	431	38·5	61·5
2	235	334	569	40·9	59·1
3	160	270	430	37·2	62·8
4	160	252	412	38·8	61·2
5	107	182	289	37·0	63·0
6	118	202	320	36·9	63·1
7	105	253	358	29·3	70·7
8	47	296	343	13·7	86·3
9	97	195	292	36·6	63·4
10	127	319	446	28·5	71·5
11	179	362	541	33·1	66·9
12	117	447	564	20·7	79·3
13	170	266	436	39·0	61·0
Total	1,788	3,643	5,431	32·9	67·1

The comparatively wide variation in the percentage of black grains on individual plants in the case of the last series (**3**) must depend upon differences in the seed parents which we have no means of checking.

Considering now the above results **1**, **2**, and **3** (*Expts.* 38, 39, and 40): in series **1**, if Mendel's law holds good, we must suppose that—in terms of percentages of the whole—25 white grains are of the nature w × w, and 25 black grains are of the nature b × b. Among the remaining 50 grains, which we suppose to be of the nature w × b or b × w, 32·27 were actually found to be black. This number agrees closely with these obtained in the case of series **2** and **3**. We must, therefore, suppose that in **1** also a nearly equal number of black grains arises from each of the reciprocal methods of fertilization w × b and b × w.*

---

* Correns explained a similar numerical result in the case of a self-fertilized heterozygote, by supposing that in this generation (as was known to be the case in F_1) b × w gave blue exclusively, whilst w × b gave such a percentage of blue as to make up the remaining number actually found. The results obtained in series 2 and 3 above seem to preclude such a possibility in the present instance.

F3

Grains of each form and colour from the three series described above were sown, and pollination was effected by growing plants of G. W. S. among them. Owing to the time of flowering of the latter variety having been miscalculated, only a few plants set any grains, and such as did so produced only a few grains per plant. In the cases described enough grains remained to indicate the nature of the plant in question.

We have already seen reason to suppose that heterozygote grains may be white as well as blue. We may now hope, by the examination of F_3, derived from white F_2 grains, to distinguish which of these white grains are pure homozygotes and which heterozygotes; since the latter may be expected to produce a certain number of black grains on again pollinating by white, whilst pure white grains so treated will produce only white. The following table sums up shortly the results obtained in this generation :—

TABLE 16.

F_2 Grains belonged to Series.	Colour of F_3 Grains.	Number of F_2 Plants, which produced Grains (F_3) of the characters stated below, when pollinated by White.			
		All White.	Black and White.	All Black.	Total.
1	White	16	15	—	31
	Black	—	22	2	24
2	White	21	8	—	29
	Black	—	17	—	17
3	White	19	8	—	27
	Black	—	54	—	54

Besides the information with regard to the offspring of white F_2 grains, the table shows that black grains always produced some black offspring. This indicates that the two germinal nuclei of any pollen grain always bear the same allelomorph, and so do the oosphere and combined polar nuclei of any female flower. Consequently segregation of the characters under consideration takes place prior to the separation of the two germinal nuclei in the pollen tube.

1.—Offspring of F2, Series 1.

Expt. 41.—*Offspring of white grains* (crossed with G. W. S.).

Out of 31 plants examined 16 produced white grains only, whilst 15 yielded both black and white grains, the expectation being that about 25 out of 43 plants (the offspring of 25 per cent. of the total number of F_2 grains) would yield white only. Of plants which yielded both black and white grains the following produced a sufficient number to allow of the proportion being determined.

TABLE 17.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	269	188	457	58·8	41·2
2	117	126	243	48·2	51·8
3	82	115	197	41·6	58·4
4	231	87	318	72·7	27·3
5	59	95	154	38·3	61·7
6	159	219	378	42·1	57·9
7	169	200	369	45·8	54·2
Total omitting No. 4	855	943	1,798	47·8	52·2

There seems to be no way of accounting for number 4 of table 17 except as the result of some kind of error.

Expt. 42.—*Offspring of black or blackish grains* (do.)

Among 24 plants 2 produced exclusively black grains (all sugary). The remaining 22 produced both black and white grains, the proportion being as follows in the case of ten of them. (The rest produced only a few grains each.)

TABLE 18.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	169	47	216	78·3	21·7
2	240	86	326	73·6	26·7
3	133	25	158	84·1	15·9
4	69	72	141	48·9	51·1
5	70	79	149	47·0	53·0
6	147	177	324	45·4	54·6
7	56	83	139	40·3	59·7
8	69	101	170	40·6	59·4
9	255	250	505	50·5	49·5
10	169	191	360	46·9	53·1
1-3	542	158	700	77·5	22·5
4-10	835	953	1,788	46·7	53·3

Thus, of determinable cobs, 7 showed 50 per cent. or less of black grains, whilst 5 (including the two with black grains only) showed a very much higher proportion. Among the F2 grains from which these plants were grown, 25 were expected to be homozygotes (b × b) and 32 to be heterozygotes. This is not far from the proportion 5 : 7 found between the two groups as distinguished above.

2.—Offspring of F2 Series 2. (White Dent × Black Mexican) × (White Dent × G. W. S.)

Expt. 43.—*Offspring of white grains.*

21 plants out of 29 produced white grains only, the remainder producing some black grains in addition. The expected proportion of homozygote grains among the whites in F2 was 50 out of 67. In the case of 4 plants the proportion of black and white grains was determinable.

TABLE 19.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	88	104	192	45·8	54·2
2	67	200	267	25·2	74·8
3	95	300	395	24·1	75·9
4	90	361	451	20·0	80·0

Expt. 44.—*Offspring of black grains.*

17 plants all showed a considerable proportion of black grains in addition to whites. The actual proportion was determined in seven cases.

TABLE 20.

	Black.	White	Total.	Per cent. Black.	Per cent. White.
1	208	233	441	47·1	52·9
2	112	106	218	51·4	48·6
3	93	94	187	49·7	50·3
4	112	108	220	50·9	49·1
5	88	78	166	53·0	47·0
6	112	157	269	41·6	48·4
7	90	93	183	49·2	50·8
Total	815	869	1,684	48·4	51·6

Considering the individual numbers obtained in Expts. 43 and 44, we notice that the proportion of blacks among the offspring of white grains is notably less than among the offspring of black grains. In the case of the latter the total number does not fall far short of 50 per cent., which is the proportion expected if black is regularly dominant. In the case of the offspring of whites, on the other hand, we must suppose dominance of black to fail altogether in a considerable proportion of cases.

3.—Offspring of F2, Series 3. (Yellow Dent × White Dent) × (White Dent × Black Mexican) × G. W. S.

Expt. 45.—*Offspring of white grains.*

8 plants out of 27 showed a certain proportion of black grains; the remainder bore only white grains. *Expectation* 17 *out of* 67.

Expt. 46.—*Offspring of black grains.*

54 plants all showed a certain proportion of black grains.

F4.

Pollination was again by G. W. S. throughout.

1. Offspring of one of the Plants with exclusively Black Grains described in Expt. 42.

Expt. 47.—32 plants were obtained, all of them showing approximately 50 per cent. of black grains, though in several of them only a few grains ripened. It would seem, therefore, that we have now arrived by selection at a strain in which the black character is practically always dominant.[*]

The four most prolific plants yielded the following grains:—

TABLE 21.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	152	199	351	43·3	56·7
2	134	116	250	53·6	46·4
3	104	97	201	51·7	48·3
4	78	70	148	52·7	47·3
5	102	101	203	50·2	49·8
Total	570	583	1,153	49·4	50·6

---

[*] *Cf.* McCracken in Journ. Exp. Zool. 1906.

2.—Offspring of Plant No. 1 of Table 18.

Expt. 48.—*White grains gave rise to* 32 plants, all of which produced both black and white grains (it was expected that all the plants would yield some black grains), but in every case the proportion of black grains could be seen at a glance to be less than 50 per cent. The four strongest plants gave the following results :—

TABLE 22.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	67	184	251	26·7	73·3
2	62	171	233	26·6	73·4
3	55	155	210	26·2	73·8
4	71	153	224	31·7	68·3

Expt. 49.—*Black grains* gave rise to 40 plants, all of which produced about 50 per cent. of black grains. 8 plants yielded cobs of a fair size.*

TABLE 23.

Plant.	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	212	186	398	53·3	46·7
2	156	153	309	50·5	49·5
3	168	167	335	50·2	49·8
4	185	171	356	52·0	48·0
5	154	179	333	46·2	53·8
6	155	171	326	47·6	52·4
7	173	176	349	49·6	50·4
8	124	140	264	47·0	53·0
Total	1,327	1,343	2,670	49·7	50·3

2a.—The offspring of Plant No. 2 of Table 18.

This gave a closely similar result.

Expt. 50.—*Offspring of white grains.*

30 plants all produced both black and white grains, the white being in a minority.

---

* It may be noted as a curious fact, but one which amounts probably only to a coincidence, that plants 1–4 of table 23 bore exclusively sugary grains, whilst plants 5–8 produced some 49 per cent. of starchy grains.

TABLE 24.

Plant.	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1 ..	177 ..	264 ..	441 ..	40·1 ..	59·9
2 ..	110 ..	290 ..	400 ..	27·5 ..	72·5
3 ..	120 ..	288 ..	408 ..	29·4 ..	70·6
4 ..	78 ..	185 ..	263 ..	29·6 ..	70·4
5 ..	77 ..	144 ..	221 ..	34·8 ..	65·2
Total..	562	1,171	1,733	32·4	67·6

Expt. 51.—*Offspring of black grains.*

30 plants were obtained showing an obviously larger percentage of black than in the previous case. The actual proportions were counted in the case of 10 plants.

TABLE 25.

	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1 ..	229 ..	198 ..	427 ..	53·6 ..	46·4
2 ..	230 ..	211 ..	441 ..	52·2 ..	47·8
3 ..	200 ..	190 ..	390 ..	51·3 ..	48·7
4 ..	209 ..	234 ..	443 ..	47·2 ..	52·8
5 ..	158 ..	190 ..	348 ..	45·4 ..	54·6
6 ..	116 ..	204 ..	320 ..	36·3 ..	63·7
7 ..	117 ..	127 ..	244 ..	48·6 ..	52·0
8 ..	90 ..	158 ..	248 ..	36·3 ..	63·7
9 ..	207 ..	179 ..	386 ..	53·6 ..	46·4
10 ..	74 ..	141 ..	215 ..	34·4 ..	65·6
Total	1,630	1,830	3,462	47·1	52·9
Excluding 6, 8, 10	1,350	1,327	2,677	50·5	49·5

We may consider the results of Expts. 48–51 together. They show that all the grains of the plants denoted as 1 and 2 in Table 18 were heterozygotes in respect of the pair blue-white, although in a minority of them the white character was dominant : thus the proof is afforded, which was hitherto wanting, that 5 out of 12 blue grains of Expt. 38 were homozygotes, in spite of the appearance of white grains among their offspring when crossed with a white strain (G. W. S.).

3.—Offspring of No. 1 of Table 20.

Expt. 52.—*White grains* gave rise to 43 plants, 42 of which produced white grains only, whilst one bore a few black grains in addition. This must be taken as showing that the bias shown in Table 20 towards a lower percentage of black grains than 50 per cent. is a real one and not simply fortuitous. In other words plants which show very nearly 50 per cent. of black grains may still be bearing a small number of grains in which dominance of black is wanting.

Expt. 53.—*Black grains* gave rise to 50 plants, bearing black and white grains—usually 50 per cent. of the former but in some cases fewer.

TABLE 26.

Plant.	Black.	White.	Total.	Per cent. Black.	Per cent. White.
1	161	226	387	41·7	58·3
2	189	164	353	53·6	46·4
3	171	154	325	52·6	47·4
4	135	156	291	46·4	53·6
5	260	266	526	49·4	50·6
6	222	317	539	41·2	58·8
7	208	185	393	53·0	47·0
8	142	223	365	38·9	61·1
9	125	120	245	51·0	49·0
10	152	150	302	50·3	49·7
11	129	260	389	33·2	66·8
12	152	154	306	49·7	50·3
Total	2,046	2,375	4,421	46·3	53·7
Excluding 6, 8, 11	1,553	1,575	3,128	49·7	50·3

DISCUSSION OF THE RESULTS OBTAINED WITH THE BLACK CHARACTER.

By the examination of F_3 and F_4 it was found that the result of crossing the heterozygote (black × white) with white was not always the same, but that one of two things might happen. In the one case dominance of black was complete, so that the ordinary Mendelian proportion—equality of black and white—was found. In the second case the proportion of black grains was less than 50 per cent. (usually about 30 per cent.—as was the case with the offspring of black grains in F_2), black being then recessive in the case of certain grains.

Most usually the behaviour of *black* heterozygote grains when crossed with a pure white strain was of the former kind ; whereas the offspring of *white* heterozygote grains, similarly pollinated, showed the reduced proportion of black grains, but this was by no means always the case.

In F_1, it will be remembered, full dominance of black was found as the result of the cross black × white, whereas, in the case of the reciprocal cross (white × black), white was sometimes dominant.

In F_2—from black F_1 grains (white × black)—the evidence showed that dominance of black failed in nearly the same number of cases, no matter whether the white strain was the pollen or the seed parent.

In later generations there occurred sometimes the one and sometimes the other kind of behaviour, although the part of pollen parent was now always taken by a pure white strain.

It did not appear that particular white strains as a whole behaved in a particular way. On the contrary, it seems as if the result can be better described as being due to a high degree of variability in the relative dominance or "Entfaltungsstarke" of the blue "Anlagen" in different individual grains, the degree of dominance being inherited to some extent.

The phenomenon may be compared to some of those which have been described by De Vries under the title of "ever-sporting varieties," and in particular the cases have this much in common, that the facts are derived from cultures to which somewhat wholesale methods of pollination have been applied. It is doubtful whether they can be discussed to advantage at any greater length until the experiments have been repeated using the more precise method of exact pollination between particular individuals.

A closely similar series of experiments, in which somewhat larger numbers of individuals were dealt with, will be found described in the second part of this paper.

4.—INDENTATION OF GRAINS.

It has already been pointed out that, when the indented type of corn was crossed with a smooth variety, the grains produced showed no change from the shape characteristic of the seed parent—there is no effect of such a kind as to be visible as "xenia." In later generations therefore this character can be treated as a plant character, all the grains on the same plant being alike, except that the grains near the apex of a cob are generally less indented than the lower ones.

F_1 from the cross smooth × indented shows a strictly intermediate character, the grains so produced being of the type known as half-dent.

In F_2, arising from the intercrossing of F_1 plants, a high degree of variability makes its appearance; and plants were obtained which closely approached the fully indented type as well as others in which the grains were almost completely smooth, but the great majority of plants were intermediate, showing every kind of blending between the two original types.

On crossing F_1 with the full-dent type, every gradation between the full-dent and the half-dent types were obtained in F_2.

Without making pollinations between individual plants it therefore appears impossible to decide whether Mendel's law is or is not followed in this case.

Biffen finds that in wheats the characters hard and soft endosperms (which may be compared with the flinty and indented characters respectively) on crossing show dominance of the hard type in F_1 (plants). and Mendelian segregation in F_2 (of plants—F_3 of grains). This perhaps renders it the more likely that there is segregation of the corresponding characters in maize also, although in the latter plant the phenomenon is masked by the intermediate form and variability of the hybrid type.

5.—HEIGHT OF PLANTS.

This is a character which it is almost impossible to deal with in exact terms owing to its very large dependence upon external conditions. Some of the strains which were made use of were uniformly much taller than others. In F_1 the height of the cross-breds between such strains was obviously intermediate. In a number of cases the cross was made between the F_1 plants and the shorter of the parental types. The offspring of this cross showed no such segregation into short and intermediate plants as was to be expected if Mendel's law held good. On the contrary, the plants produced were remarkably uniform in height and showed none of that variability which was shown, for instance, in the offspring of the cross indent × smooth. It appears therefore that the case must be regarded as one in which homoogonous development of the germ cell takes place.

B.—COMBINATIONS OF CHARACTERS.

In the majority of experiments described under A **1, 2, 3,** above, the plants obtained showed as a matter of fact more than one of the pairs of characters dealt with. In all such cases the evidence showed quite clearly that all the possible combinations of these characters occurred in equal numbers within the ordinary limits of error. The results were in fact strictly in accordance with Mendel's law, and were uncomplicated by the phenomena of coupling.

The following experiment will serve as an example of a case in which several distinct strains were combined, and in which all the following characters were kept under observation—sugary, round, and indented types of grain, and the colours blue, yellow, and white.

F1.

Expt. 54.—*Yellow dent* × *Black Mexican sugar corn.*

On a plant of Riley's Favourite growing close to plants of Black Mexican there were found 5 grains of a brightly mottled black and yellow colour amongst the normal yellow grains. These grains were clearly of the above parentage. It may be noted at once that in later generations none of the grains showed this mottled character, though the black pigment was of course present in many of them. This fact may be compared with the abundance of speckled grains in F_1 and F_2 from the cross White dent × Black sugar, and their absence from later generations of the same, as well as from all the individuals of the mongrel strain described later on, the latter being doubtless still further removed from the original cross from which we must suppose them to be descended.

The shape of these 5 grains was exactly like that of the surrounding grains of the same cob.

F2.

3 plants arose from the above grains and their flowers received pollen from flowers of white dent, with the following result :-

TABLE 27.

Plant.	Black.	White.	Yellow.	Total.	Per cent. Black.
1	75	84	56	215	35
2	94	32	31	157	60
3	92	31	38	161	57

All the grains were of a semi-dent form and showed no trace of the sugary character. The black grains were all of a deep and uniform colour. We must suppose that there was defective dominance of black in the case of No. 1, whilst there was full dominance of black in Nos. 2 and 3, in which case the expected number of grains would be 50 per cent.

F3.

Grains from No. 1 of Table 27 were sown and pollination was effected from plants of G. W. S. Only a few good plants were obtained. In the following table the plants (*a*) were derived from black grains, (*b*) from white. The results are in accordance with those already described for each pair of similar characters taken separately, except as regard the paucity of starchy grains on the (*b*) plants. Upon these a few grains were intermediate in appearance between typical dent and typical sugar grains : such grains were counted as sugary but possibly not quite all of them were really of this nature. Out of 85 supposed sugary grains grown in F_4 (pollination again from G. W. S.) only one yielded a cob bearing both starchy and sugary grains, whilst the remaining 84 gave nothing but sugary.

Among plants (*a*), a certain number of the yellow grains were distinctly paler than the others, and it appeared from an examination of the next generation that these belong more properly to the " white " than to the " yellow " group. The appearance of these grains causes the white group to grade into the yellow to some extent, and consequently the figures for white and yellow are not fully trustworthy.

TABLE 28.

		Starchy.			Sugary.			Per cent. Bl.	Per cent. St.	Total.
		W.	Y.	Bl.	W.	Y.	Bl.			
(*a*)	1	43	35	56	42	40	44	38·5	51·5	260
	2	79	64	88	62	73	93	39·4	50·3	459
	3	36	40	48	44	45	50	38·3	47·2	263
(*b*)	1	87	—	—	131	—	—	—	39·9	218
	2	143	—	—	169	—	—	—	45·8	312
	3	125		78	—	—	—	38·4	—	203
	4	71	—	23	100	—	26	21·2	42·7	220

F4.

Grains representing all the combinations of characters sown by (*a*) 1 of Table 28 were sown. Pollination was once more from G. W. S. With the single exception already mentioned (*e*. 7 of Table 30), the shape of the grains, whether sugary or half-dent (3 of the great-grand parents were of the indent form and 5 of the sugary), worked out quite simply according to Mendelian expectation.

The results as regards colour are indicated in the following table, in which Y denotes strong yellow, y very pale yellow.

TABLE 29.

Cob produced the following grains:—

Parent Grain.	W. only.	W. & y.	W. & Y., (& y).*	Bl. & W.	Bl.&W. & y.	Bl. & W.& Y. (& y).	Total.
W.	22	18	—	5	—	—	45
Y.	—	—	37	—	—	7	44
y.	—	7	—	—	1	—	8
Bl.	—	—	—	11	9	18	38

* (& y) = and y in some cases.

It will be clear from the above that the result as regards yellow and white may be considered to be Mendelian if the pale yellow grains are ranked with the " whites " instead of with the " yellows." A more or less similar state of things is now known to occur in several groups of plants, having been first recorded by Tschermak in the case of kidney beans. In the present case the observations are not sufficient to allow of a complete account of the phenomena. It is not clear, moreover, from which of the various parental strains this character took its origin.

The actual proportion of pale yellow grains was difficult to determine, but they made up approximately 10 per cent. of the total number in the cobs in which they occurred. In Table 30 the pale yellow grains were counted as far as possible with the whites, but they were probably not always truly distinguished from the full yellows, so that the recorded proportion of the latter to whites is only approximately accurate.

TABLE 30.

No.	Starchy.			Sugary.			Total.	Per cent. B.	Per cent Sug
	W.	Y.	B.	W.	Y.	B.			
(a) 1 ..	177	—	—	190	—	—	367	—	51·8
2 ..	161	—	—	151	—	—	312	—	48·4
3 ..	140	—	—	140	—	—	280	—	50·0
4 ..	145	—	—	160	—	—	305	—	52·4
5 ..	51	—	52	62	—	48	213	47·0	51·7
(b) 1 ..	150	—	119	154	—	82	505	39·8	46.7
2 ..	131	—	73	106	—	65	375	37·8	45·6
3 ..	36	40	73	38	41	96	324	52·2	54·9
4 ..	47	38	82	41	59	82	349	47·0	52·2
5 ..	31	41	49	22	24	41	208	43·2	41·8
6 ..	58	—	66	65	—	58	247	50·2	49·8
(c) 1 ..	70	69	—	65	63	—	267	—	47·9
2 ..	65	68	—	73	76	—	282	—	52·9
3 ..	72	64	—	65	62	—	263	—	48·3
4 ..	81	82	—	83	84	—	330	—	50·6
5 ..	71	75	—	79	79	—	302	—	51·7
6 ..	47	40	13	50	37	12	199	12·6	49·7
(d) 1 ..	—	—	—	267	—	180	447	40·3	100
2 ..	—	—	—	181	—	118	299	39·5	100
3 ..	—	—	—	60	64	162	286	56·6	100
4 ..	—	—	—	61	47	122	230	53·1	100
5 ..	—	—	—	92	78	137	307	44·6	100
6 ..	—	—	—	68	52	131	251	52·2	100
7 ..	—	—	—	77	65	141	283	49·8	100
8 ..	—	—	—	82	78	177	337	52·6	100
9 ..	—	—	—	210	—	158	368	42·9	100
(e) 1 ..	—	—	—	203	202	—	405	—	100
2 ..	—	—	—	117	130	—	247	—	100
3 ..	—	—	—	205	172	—	377	—	100
4 ..	—	—	—	141	156	—	297	—	100
5 ..	—	—	—	138	144	—	282	—	100
6 ..	—	—	—	172	150	—	322	—	100
7 ..	75	77	—	72	54	91	278	—	45·3
8 ..	—	—	—	87	75		253	36·9	100
(f) 1 ..	99	—	—	105	—	—	204	—	51·5

(a) denotes offspring of starchy white grains.
(b) do. do. do. black grains.
(c) do. do. do. yellow grains.
(d) do. do. sugary black grains.
(e) do. do. do. yellow grains.
(f) do. do. a starchy pale yellow grain.

II.—AN ANALYSIS OF THE METHOD OF INHERITANCE OF CERTAIN COLOUR CHARACTERS IN THE CASE OF A MONGREL STRAIN.

The material for the following experiments consisted of a few specimens of the common kind of corn grown locally—a flint variety in which the colours yellow, blue, red, and white were to be found mingled together in great confusion. Yellow, blue, and white grains were often seen on the same cob, whilst on certain plants all the grains showed the red pericarp character in addition.

As will presently appear, it was possible to show that the pair of characters yellow—white behave in a simple Mendelian way. The presence or absence of red in the pericarp behaves in a similar manner. The blue-non-blue was found to behave in essentially the same way as was the case with the definite crosses already described, but here again the mass methods of pollination employed were inadequate to elucidate the phenomena completely.

Among the cobs of unknown parentage first obtained, the grains (endosperms) of which were regarded as the parental generation (P), were the following :—

No. 1 bore the following grains: yellow 415, white 224, and blue 118, total 757; only the non-blue grains being distinguished into whites and yellows. The pericarp was transparent and colourless (white).

No. 5. Dark red pericarp. 10 grains near the base of the cob showed a blue colouration, whilst the remainder—some 500—were yellow or white, the colour of the endosperm being externally indistinguishable.

All the different kinds of grain mentioned, from both the above cobs, were sown in small patches which lay close together, and in the neighbourhood of plots sown with grains from other cobs. A large majority of all the grains sown was white, and all were of the same flint form. The intention was to make artificial pollinations, and a considerable number were actually carried out. But in spite of careful attention it was difficult to ensure the complete exclusion of foreign pollen and, in the absence of other information as to the behaviour of the blue character, such cases as the following seemed to show that the method employed was quite inadequate.

Expt. 55.—The stigmas of a plant arising from a blue grain of No. 1 were covered with a paper bag and fertilized with pollen from the male flowers of the same plant. The cob yielded 172 blue grains, 99 yellow, and 36 white. Among non-blue grains there were thus 73 per cent. of yellow and 27 per cent. of white grains, a proportion which approaches the Mendelian ratio 3 : 1. But the ratio of blue to non-blue grains was 56 : 44.

Expt. 56.—A plant from a blue grain of No. 5 yielded on self-pollination 268 blue grains and 182 non-blue, or 59·5 : 40·5

Subsequent observations showed that the error in these cases was probably small or even non-existent, but at the time no explanation was forthcoming.* For this reason, and also because the cobs so produced yielded as a rule only a small number of scattered grains, the remaining crosses made at this time were not noted very fully, and in subsequent generations a different method was adopted. This was the same as was used in all the later generations from the definite crosses previously described, namely, fertilization in mass of the emasculated cross-bred plants by the pollen of a white strain.

A.—SINGLE PAIRS OF CHARACTERS.

1.—YELLOW AND NON-YELLOW (WHITE).

White grains (P) from cob No. 1 produced plants which, on pollination principally among themselves, yielded 90 per cent. or more of white grains ; they also showed as a rule less than 10 per cent. of yellow grains and less than 5 per cent. of blue grains (F_1). These yellow and blue grains were doubtless cases of "xenia" produced by the pollens of surrounding plants

---

* The definite crosses already described, which throw light on these phenomena, were not carried out until a later date.

which bore the yellow and blue characters. Other plants again produced grains with a red pericarp, but these as well as the blue grains may be at present disregarded.

F2.

Expt. 57.—In order to test the point as to their origin, a number of the above yellow grains were sown in a plot where pollination was effected from plants produced from the white grains of the same cobs. These white grains proved to be true extracted recessives, since less than one per thousand of the whole number of grains produced by them were yellow or blue, and these are to be accounted for by accidental escape of pollen from the crossed plants grown on the same plot. Many of these white recessives were, however, impure in respect of the red pericarp character not visible as the immediate result of crossing, and consequently a considerable number of red coated cobs were produced by them. Some of the supposed white × yellow plants with which we are now dealing showed the same character. Of those in which the pericarp was white the following were counted:—

TABLE 31.

Plant.	White.	Yellow.	Blue.	Total.	Per cent. of Y.
1	202	286	—	488	58·6
2	223	217	—	440	49·3
3	256	216	1	472	45·7
4	222	201	—	423	47·6
5	280	244	—	524	46·6
6	222	207	—	429	48·2
7	211	249	6	460	54·2
8	173	166	3	339	49·0
9	193	177	—	370	47·7
Total	1,982	1,963	10	3,955	49·6

Expectation: 50 yellow: 50 white.

The intensity of colour in the yellow grains varied to some extent on different plants, but the grains on any given cob were very uniform in this respect. The two kinds—white and yellow—could be distinguished easily and rapidly.

In order to test the accuracy of the sampling, and at the same time to obtain a longer series of numbers, a further generation was raised.

F3.

78 white and 126 yellow grains (not specially selected) were taken for this purpose from cob No. 5, Table 31—a cob which showed a rather distinct deficiency of yellow grains (46·6 per cent). In this generation a pure white dent variety was used as the pollen parent, as it was desired at this stage to eliminate the red pericarp character.

Expt. 58.—From the *white grains* 59 plants produced fruit, 44 of these bore exclusively white grains. The remaining 15 cobs showed white grains with the following exceptions:—

TABLE 32.

1 cob showed 2 blue grains ..	2
6 cobs showed each 1 yellow grain ..	6
6 cobs showed each 2 yellow grains ..	12
1 cob showed 3 yellow grains ..	3
1 cob showed 6 yellow grains ..	6
Total yellow ..	27

All the plants on which these yellow grains appeared grew close together near one end of a row, and it seems clear that some pollen bearing the yellow character had escaped from a plant in the next row. The purity of the recessive form is thus well established in this generation.

Expt. 59.—With regard to the offspring of *yellow grains*, a single cob was gathered from each of 96 plants. One of these cobs showed 32 blue grains in addition to 253 yellow and 205 white, due doubtless to an accidental previous cross by blue not visible as "xenia."

The remaining cobs without exception showed yellow and white grains only, in the proportion of approximately 50 per cent. of each in every cob. The actual percentages are given in Table 33.

TABLE 33.

No.	Yellow.	White.	Total.	Per cent. of Y.
1	360	317	677	53·2
2	300	311	611	49·1
3	382	348	730	52·4
4	250	284	534	46·8
5	388	380	768	50·5
6	301	278	579	51·9
7	362	328	690	52·5
8	293	355	648	45·2
9	303	256	559	54·2
10	340	315	655	51·9
11	245	245	490	50·0
12	292	329	621	47·0
13	283	296	579	48·8
14	323	311	634	50·9
15	253	237	490	51·6
16	281	279	560	50·1
17	338	362	700	48·3
18	213	280	493	43·2
19	241	239	480	50·1
20	295	352	647	45·6
21	309	308	617	50·1
22	263	245	508	51·7
23	264	256	520	50·8
24	270	277	547	49·4
25	380	385	765	49·7
26	304	299	603	50·4
27	379	329	708	53·5
28	372	328	700	53·2
29	378	361	739	51·1
30	233	205	438	53·1
31	334	369	703	47·5
32	196	210	406	48·3
33	275	236	511	53·8
34	287	339	626	45·8
35	296	323	619	47·8
36	357	422	779	45·9
37	221	220	441	50·0
38	310	331	641	48·4
39	265	262	527	50·2
40	177	152	329	53·8
41	225	224	449	50·1
42	341	302	643	53·0
43	270	295	565	47·8
44	211	230	441	47·9
45	269	279	548	49·1
46	219	215	434	50·4
47	314	338	652	48·2
48	221	227	448	49·3

No.	Yellow.	White.	Total.	Per cent. of Y.
49	254	255	509	49·9
50	250	217	467	53·6
51	251	256	507	49·4
52	286	280	566	50·6
53	199	207	406	49·0
54	262	294	556	47·2
55	197	210	407	48·4
56	202	189	391	51·7
57	304	278	582	53·2
58	237	200	437	54·3
59	153	156	309	49·6
60	174	183	357	48·7
61	338	322	660	51·2
62	320	318	638	50·2
63	445	417	862	51·6
64	298	305	603	49·4
65	279	266	545	51·2
66	308	293	601	51·3
67	251	276	527	47·7
68	385	340	725	53·1
69	280	277	557	50·3
70	333	328	661	50·4
71	362	384	746	48·6
72	414	321	735	56·3
73	262	248	510	51·4
74	251	326	577	43·6
75	268	291	559	47·9
76	302	296	598	50·4
77	283	346	629	45·0
78	334	317	651	51·3
79	368	330	698	52·7
80	319	299	618	51·6
81	158	171	329	47·0
82	175	158	333	52·6
83	154	187	341	45·2
84	223	232	455	49·1
85	279	296	575	48·6
86	297	286	583	50·9
87	369	328	697	53·0
88	276	275	551	50·1
89	309	333	642	48·2
90	327	338	665	49·2
91	280	274	554	50·6
92	290	273	563	51·4
93	207	224	431	48·0
94	151	156	307	49·2
95	145	126	271	53·6

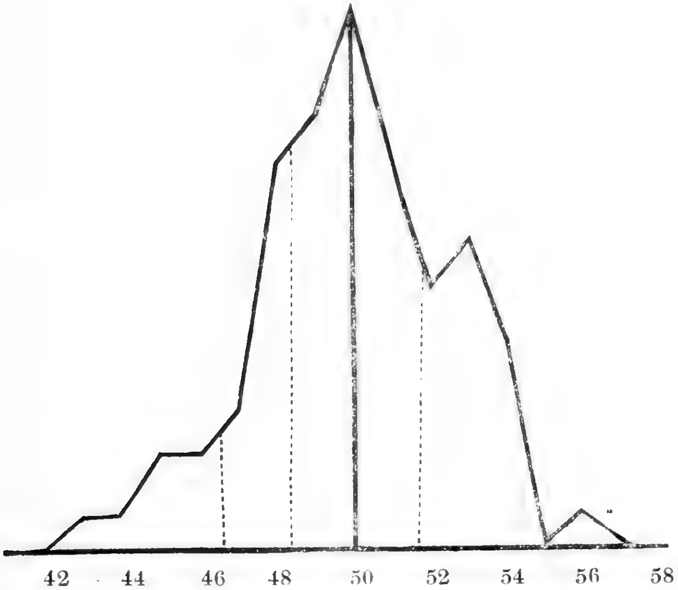
Total: y 26,792. w 26,751. Grand total 53,543.
Percentage of yellow 50·03. *Expectation* 50 + or — ·15.
Average number of grains per cob 564.

If we arrange the figures obtained in Table 33 in groups under the various percentages we get the following series of numbers :—

Per Cent.	43	44	45	46	47	48	49	50	51	52	53	54	55	56
No.	1	1	3	3	4·5	11·5	14	17·5	12·5	8·5	10	6·5	—	1

These numbers are plotted in the accompanying diagram, in which the different percentages are represented by equal distances along the base line, whilst the vertical distances represent the number of individuals which showed each percentage of yellow grains. :—

Fig. 1.



The above curve (or rather polygon) is somewhat irregular, for the number of "variants" (individual samples) included is small. Nevertheless it bears some resemblance to a normal curve of probability.

By Galton's method the probable error or "mid departure" of this polygon (the average distance from the mean of the vertical lines which together with the ordinate at the mean divide the area of the polygon into four equal parts) is 1·7.

Now, if all the samples contained the same number of individuals, and that number were the same as the average of all the actual samples, *i.e.*, 564, the theoretical probable error would be 1·33, this being the distance from the mean beyond which half the percentages may be expected to vary in the case of a series of samples containing 564 individuals each, taken at random from a mixture of two kinds of things in equal numbers.

The result actually obtained is so close to this that it appears likely that the actual samples do really represent random batches from a mixture of yellows and whites in equal numbers. And this again implies the literal truth of Mendel's law that an equal number of the germ cells of a heterozygote bears one or the other member of the pair of allelomorphs concerned—in this case yellow and white—clear evidence as to the nature of the germ cells being afforded by the process of crossing with the recessive form.

Turning once more to the diagram, it may be pointed out that the particular proportion of yellow and white grains (46·6 : 53·4) exhibited by the F_3 plant of which the offspring was examined, appears to have no influence upon the proportions shown by those offspring.

On growing extracted dominants on a small scale it was found that the homozygote (yellow × yellow) was of a distinctly deeper yellow colour than the average heterozygote form (yellow × white), which exhibited a blended character intermediate between the two parental types which had now been extracted.

F4.

Expt. 60.—One further generation was grown for the purpose of determining the proportion in which the male germ cells segregated. The pollen parents in this case were the offspring of yellow grains from several of the plants enumerated in Table 33. A few of the finest of these F4 plants (self-pollinated) produced the following numbers of yellow and white grains :—

TABLE 34.

No.	Yellow.	White.	Total.	Per cent. of Y.
1	508	172	680	74·7
2	667	221	888	75·1
3	461	164	625	73·8
4	532	156	688	77·3
5	486	167	653	74·4
6	503	169	672	74·8
7	536	174	710	75·5
8	519	179	688	74·0
9	616	184	800	77·0
10	754	231	985	76·5
11	474	147	621	76·4
12	453	186	639	70·9
13	590	189	779	75·7
14	656	213	869	75·5
15	610	222	832	73·5
16	405	165	570	71·0
17	621	214	835	74·4
18	783	295	1,078	72·6
19	393	112	505	77·8
20	679	257	936	72·6
21	425	146	571	74·4
22	488	176	664	73·4
23	639	209	848	75·3
24	556	204	760	73·2
25	455	158	613	74·2
26	544	186	730	74·5
27	399	140	539	74·0
28	609	200	809	75·3
29	545	205	750	72·7
30	686	240	926	74·1

The total proportion is 74·5 yellow : 25·5 white. *Expectation* 75 : 25. Plants Nos. 12 and 20 bore each one parti-coloured grain—yellow and white. These were counted as yellow. No. 26 produced 2 blue grains, doubtless due to accidental pollination.

About a third of the total number of yellow grains were distinctly darker in tint than the remaining two-thirds. To take a particular instance, out of 100 yellow grains taken at random from the total number on a particular cob, some thirty grains could be distinguished as being of a decidedly deeper yellow tint than sixty of the remainder. So that in not more than 10 per cent. of cases was it doubtful whether a particular yellow grain was a homozygote or a heterozygote.

Having obtained the proportion 3 yellow to 1 white as the result of mutual pollination between heterozygote plants, and knowing as we do that the female germ cells of similar plants carry the yellow and white characters in equal numbers, we may infer at once that these allelomorphs segregate in the male germ cells in the same proportion. As a further and conclusive piece of evidence, a white strain (indented) was subjected to pollination from the plants enumerated in Table 34, with the following result (*Expt.* 61) :—

TABLE 35.

	Yellow.	White.	Total.	Per cent. of Y.
1	240	232	472	50·8
2	294	339	633	46·5
3	307	305	612	50·2
4	216	253	469	46·1
5	305	316	621	49·1
6	284	299	583	48·6
7	223	201	424	52·6
8	302	320	622	48·6
9	329	348	677	48·6
10	223	233	456	48·9
Total	2,723	2,846	5,569	48·0

Expectation : 50 *per cent.*

There is once more a slight excess of white grains over the expected number, and it has to be noted that any accidental escape of pollen from these plants would tend in this direction.

2.—EXPERIMENTS IN WHICH THE BLUE CHARACTER WAS CONCERNED.

Expt. 62.—It has been already stated that F_1 derived from the white grains of cob No. 1 (P) produced 5 per cent. or less of blue grains. A number of these blue grains were grown upon the same plot as the F_2 from the corresponding yellow grains already described, the pollen parents being the extracted white recessives.

F2.

There resulted (F_2) 1 cob with red pericarp and 39 per cent. of blue grains, and 11 cobs (plants) with white pericarps and from 19·6 to 26·4 per cent. of blue grains. Details are given in the accompanying table (36) :—

TABLE 36.

	White.	Blue.	Total.	Per cent. White.	Per cent. Blue.
1	244	156	400	61·0	39·0
2	308	86	394	78·2	21·8
3	440	143	583	75·4	24·6
4	311	118	429	72·5	27·5
5	425	125	550	77·3	22·7
6	356	87	443	80·3	19·7
7	293	88	381	76·9	23·1
8	302	108	410	73·6	26·4
9	286	70	356	80·4	19·6
10	262	73	335	78·2	21·8
11	256	78	334	76·6	23·4
12	234	74	308	76·0	24·0
Total	3,717	1,206	4,923	75·5	24·5

At first sight this would perhaps seem to indicate that the female germ cells were produced in the proportion 3 white to 1 blue, but a reference to the evidence of the definite crosses described in the first part of the paper renders it more probable that we have here another case of irregularity in dominance and no exception to the ordinary course of Mendelian segregation. Another possible suggestion, that embryo and endosperm might in some cases bear opposite characters, is also shown to be inadmissible by the subsequent evidence, which shows that the offspring of blue grains always included some which bore the blue character.

If Mendel's law of segregation is simply followed in the present instance it is clear that some of the white grains must be heterozygotes, because 50 per cent. of the total number of grains must be of that nature, and 75 per cent. of the whole number are white.

The point can be tested by sowing the white grains and once more pollinating by white. From cob No. 12 of table 36, which contained just 76 per cent. of white grains, a number of both white and blue grains were sown separately, and pollination was effected from a white dent form.

If Mendel's law holds good we must expect 50 out of 76 of the white F_2 grains to be pure white homozygotes, whilst the remaining 26 will be heterozygotes in which white was dominant—making up 50 per cent. of the original total when added to 24, which is the number of grains already known to be heterozygotes from their external appearance.

F3.

Expt. 63.—The actual offspring of the white F_2 grains was as follows in F_3, 1 cob being gathered from each of 37 plants :—

23 cobs bore white grains exclusively.

4 cobs bore from 1 to 4 blue grains, the rest being white.

10 cobs bore from 1·7 to 5·7 per cent. of blue grains, *i.e.*, 12 or more in each cob.

Details regarding these last 14 cobs are given in Table 37 :—

TABLE 37.

	White.	Blue.	Total.	Per cent. Blue.
1	431	149	580	25·7
2	327	95	422	22·5
3	496	46	542	8·5
4	542	43	585	7·4
5	595	37	632	5·9
6	533	35	568	6·2
7	501	30	531	5·6
8	664	16	680	2·4
9	566	13	579	2·2
10	699	12	711	1·7
11	511	1	512	—
12	488	2	490	—
13	626	4	630	—
14	543	2	545	—
Total omitting 11 to 14	5,354	476	5,830	8·0

Here and in similar cases the average of the different percentages is of little moment, since the range in variation is far beyond the ordinary limits of error.

Assuming that the 4 cobs with 1 to 4 blue grains are cases of accidental "xenia," a supposition which is rendered probable by the fact that from 1 to 5 blue grains appeared in about 10 per cent. of cobs of the white dent in neighbouring rows, we get 73 per cent. or 55·5 out of 76 as the proportion of white F_2 grains which were homozygotes;* the expectation being 50 out of 76, as has been already pointed out.

The essential point to be noticed is that grains which were to all appearances white showed themselves, upon a study of the offspring, to have been of impure constitution: such a number of them however bred true as to indicate that Mendel's law of purity of the gametes still holds good in such a case. We therefore conclude that in this instance the heterozygote does not necessarily exhibit that character, namely blue, which might have been expected to be dominant, but may appear either blue or white. We may here refer back to Expt. 34, in which a similar circumstance was actually observed in the first generation of a cross (blue × white) between definite strains.

Expt. 64.—The plants arising from the blue grains of the same generation, and pollinated by the same white dent strain, produced a number of cobs—F_3—containing from 22 to 40 per cent. of blue grains, the remainder of the grains in each cob being white. Altogether 4,034 blue and 10,300 white, or 28·1 per cent. of blue.

---

* If on the other hand these plants represent the lowest terms of the series properly showing various numbers of blue grains, this proportion becomes 62 per cent. or 47 out of 76. The point could have been tested by growing a further generation on a very large scale, but in either case, in consideration of the small number of plants obtained, the agreement with Mendelian expectation is reasonably close.

TABLE 38.

No.	White.	Blue.	Total.	Per cent. Blue.
1	497	201	698	28·8
2	429	151	580	26·1
3	388	135	523	25·8
4	433	194	627	30·9
5	347	128	475	26·9
6	503	174	677	25·7
7	633	284	917	31·0
8	338	119	457	23·8
9	398	177	575	30·8
10	365	116	481	24·0
11	361	122	483	25·2
12	418	220	638	34·4
13	347	120	467	25·7
14	352	166	518	31·1
15	267	130	397	32·8
16	364	137	501	27·3
17	330	142	472	30·1
18	474	169	643	26·3
19	282	97	379	25·6
20	269	115	384	29·9
21	422	120	542	22·1
22	305	110	415	26·4
23	188	76	264	29·9
24	226	62	288	21·6
25	242	72	314	22·9
26	338	127	465	27·3
27	249	94	343	27·4
28	140	94	234	40·4
29	151	77	228	33·8
30	244	105	349	30·1

The general percentage of blue grains in F_2 was 24·6, and the slight increase in the number of blue grains appearing in F_3 may perhaps be associated with the different pollen parent employed—flint in F_2, dent in F_3.

F2.

Expt. 65.—A number of blue "xenia" grains of F_1, similar to those employed in Expt. 62, were sown together in an isolated spot and the plants allowed freely to pollinate one another. In this case the variations in the number of blue grains appearing on different plants is of smaller interest because the pollen of the whole number was mingled.

TABLE 39.

No.	White.	Blue.	Total.	Per cent. White.	Per cent. Blue.
1	206	232	438	47·0	53·0
2	207	252	459	45·0	55·0
3	206	221	427	48·2	51·8
4	187	217	404	46·3	53·7
5	157	193	350	44·9	55·1
6	98	90	188	52·8	47·2
Total	1,063	1,203	2,266	46·91	53·09

The particular cob chosen for further examination (No. 2) had 55 per cent. of blue grains. If blue had been dominant in every case we should have expected the proportion 75 per cent. of blue grains to 25 per cent. of white. Hence, as it is, only 25 out of 45 white grains should be pure recessive homozygotes.

F3.

On sowing the white grains and exposing the emasculated plants to the pollen of white dent, 36 plants out of 63 were found to bear either exclusively white grains (or in 7 cases 1 or 2 blue grains in addition to white), whilst 27 plants bore from 1 to 36 per cent. of blue grains. Thus 57 per cent. of the whites in F_2, or a proportion of 26 out of 45, were shown by an examination of their progeny to be pure recessives; that is, 26 per cent. of the total number of grains of F_2, which comes very near the Mendelian 25 per cent.

Table 40 shows the actual proportion of blue and white grains among the offspring of white grains in F3 :—

TABLE 40.

No.	White.	Blue.	Total.	Per cent. Blue.
1	235	135	370	36·5
2	292	152	444	34·2
3	378	187	565	33·0
4	451	185	636	29·1
5	282	96	378	25·4
6	169	57	226	25·2

No.	White.	Blue.	Total	Per cent. Blue.
7	386	106	492	21·5
8	503	120	623	19·3
9	504	90	594	15·1
10	466	81	547	14·8
11	311	47	358	13·1
12	542	69	611	11·3
13	576	65	641	10·1
14	528	58	586	9·9
15	233	25	258	9·7
16	538	52	590	8·8
17	364	33	397	8·3
18	452	39	491	8·0
19	399	33	432	7·6
20	672	47	719	6·5
21	453	27	480	5·6
22	670	35	705	5·1
23	296	16	312	5·1
24	584	23	607	3·4
25	529	8	537	1·5
26	541	4	545	·7
(27	27	13	40	32·5)

The above table shows a very wide range in the percentage number of grains in which the blue colour is dominant, but in no case does the number approach the possible maximum, namely 50 per cent.

Expt. 66.—We pass now to a consideration of the offspring of the blue grains of F_2. Out of every 55 blue grains in F_2 we expect 25 to be of the constitution blue × blue, and the remaining 30 to be heterozygotes, making up a total of 50 heterozygotes when added to the 20 white grains out of a total of 45 white, already shown to be of that nature.

The offspring of the blue grains pollinated by white dent were as follows in F_3.

73 plants were obtained, of which 10 bore blue grains exclusively, whilst the remainder produced both blue and white grains in varying proportions. These proportions were determined in the case of the 36 finest cobs—each from a separate plant—all the other cobs being more or less imperfect. The result of this determination is shown in Table 41.

TABLE 41.

No.	White.	Blue.	Total.	Per cent. Blue.
1	117	313	430	72·7
2	86	170	256	66·5
3	181	306	487	62·9
4	211	343	554	61·9
5	90	142	232	61·2
6	163	253	416	60·7
7	314	403	717	57·7
8	259	332	591	56·2
9	235	296	531	55·7
10	177	227	404	56·2
11	143	199	342	55·6
12	273	317	590	53·7
13	209	226	435	51·9
14	279	298	577	51·6
15	309	326	635	51·3
16	94	96	190	50·5
17	279	275	554	49·6
18	199	189	388	48·7
19	262	248	510	48·6
20	193	169	362	46·7
21	389	331	720	46·0
22	242	144	386	36·8
23	349	191	540	35·3
24	378	204	582	35·0
25	328	159	487	32·6
26	231	105	336	31·3
27	450	200	650	30·8
28	540	240	780	30·8
29	316	134	450	29·8
30	258	108	366	29·6
31	222	90	312	28·9
32	272	110	382	28·8
33	271	108	379	28·5
34	376	150	526	28·5
35	345	135	480	28·1
36	342	98	440	22·3

It will now be necessary to consider these results a little more in detail :—(1) The plants bearing blue grains only must have arisen from homozygote grains (blue × blue), in the offspring of which the dominance of blue has become so much strengthened as to be effective in the case of every grain. We should naturally expect to find a corresponding group of plants which have arisen from heterozygote grains. Referring to the table we find (2) a number of plants which produced about 50 per cent. of blue grains—Mendelian expectation for heterozygote plants in which blue is dominant. Those plants which lie first on the list, (3) showing percentages of blue well above 50 per cent. must be the produce of homozygote grains in which blue is not invariably dominant. And towards the end of the table percentages of from 22 to 37 indicate the produce of heterozygote grains of the corresponding kind (4) with dominance of blue in the case of certain grains only. The only difficulty which presents itself is that of definitely separating the second group of plants from the third; we may perhaps make an arbitrary division at the value 55 per cent.

The result may then be summed up in a table—42.

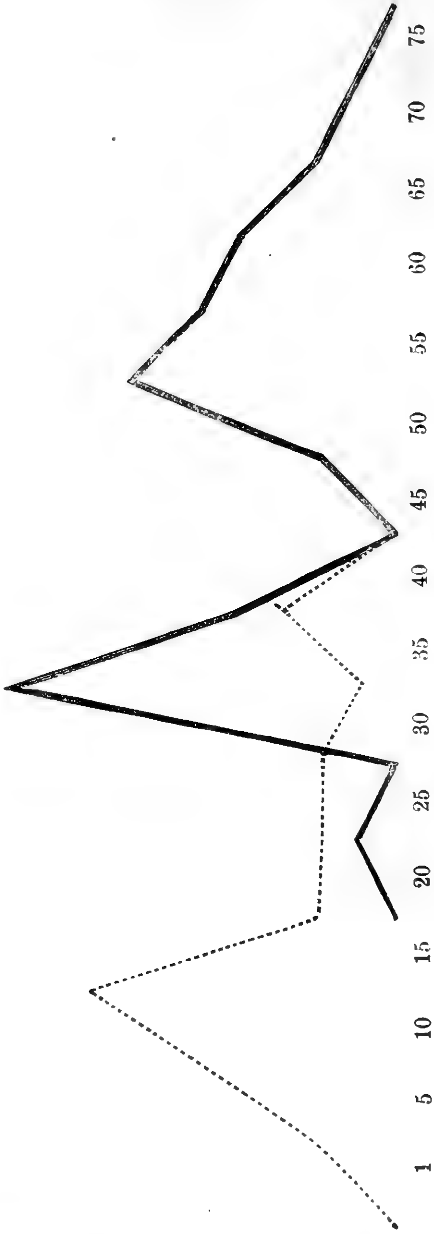
TABLE 42.

Percentage Number of F2 Grains.			Observed behaviour of offspring in F_3.
Blue :	7·5	22 (*expectation* 25)	.. Blue exclusively (1).
	14·5		.. Over 55 % blue (3).
	13·3	52 (*expectation* 50)	.. About 50 % blue (2).
	19·7		.. 22–37 % blue (4).
White :	19		.. 1–36 % blue.
	26	.. (*expectation* 25)	.. White exclusively.

From the arrangement of the figures in the above table it is clear that in spite of the great variability in the proportions in which the blue grains appear in F_3, the Mendelian ratio can still be clearly traced out for F_2; 22 : 52 : 26 being as near to 1 : 2 : 1 as could reasonably be expected considering the comparatively small number of plants which it was possible to examine.

In fig. 2 the black curve represents for the offspring of blue grains the number of individuals which showed different percentages of blue, those with 100 per cent. being omitted. The dotted curve gives the same information with regard to the offspring of white grains (Expt. 65), those which showed no blue grains being also omitted.

Fig. 2.



The figure clearly shows the discontinuity between the heterozygotes in which dominance has become regular and those in which this is not the case. It also indicates on the whole a wide distinction between the offspring of white and of blue heterozygotes. According to the present interpretation of the facts, the offspring of two kinds of individual grains are mingled in the group which lies just above 50 per cent., namely, of homozygotes in whose offspring dominance of blue sometimes fails, and of heterozygotes among whose offspring dominance is regular or nearly so. The distinction made between these two groups is admittedly more or less artificial.

F4.

Expt. 67.—In the next generation (F_4) the offspring of a plant of the above series (Expt. 66) which produced exclusively blue grains was examined. The plants in this case were grown in an isolated situation and allowed to undergo mutual pollination. This process unfortunately obscures the natural differences in the proportion of blue and white grains shown by individual plants, nevertheless it seems clear from a comparison with the preceding evidence that there was regular dominance of blue in the case of a majority of plants, whilst in the remainder blue was again recessive in the case of a certain proportion of the germ cells.

TABLE 43.

No.	White.	Blue.	Total.	Per cent. White.
1	190	245	435	43·7
2	216	344	560	38·6
3	175	283	458	38·2
4	249	436	685	37·4
5	252	439	691	36·5
6	211	378	589	35·8
7	207	383	590	35·1
8	169	328	497	34·0
9	211	419	630	33·5
10	242	481	723	33·4
11	199	401	600	33·1

No.	White.	Blue.	Total.	Per cent. White.
12	269	551	820	32·8
13	264	557	821	32·2
14	141	326	467	30·2
15	249	610	859	29·0
16	191	469	660	29·0
17	103	258	361	28·4
18	194	510	704	27·6
19	166	444	610	27·3
20	199	542	741	26·9
21	134	371	505	26·6
22	147	416	563	26·1
23	149	424	573	26·0
24	200	569	769	26·0
25	153	441	594	25·8
26	102	297	399	25·6
27	219	648	867	25·3
28	171	515	686	25·0
29	170	516	686	24·8
30	179	546	725	24·7
31	149	459	608	24·6
32	174	539	713	24·4
33	132	412	544	24·3
34	165	516	681	24·3
35	111	348	459	24·2
36	154	490	644	23·9
37	60	192	252	23·8
38	140	454	594	23·6
39	183	602	785	23·3
40	216	709	925	23·3
41	103	337	440	23·2
42	155	528	683	22·7
43	182	633	815	22·4
44	157	553	710	22·2
45	190	670	860	22·1
46	100	382	482	20·8
Total	8,092	20,971	29,063	27·9
Total excluding 1-13	5,238	15,726	20,964	25·0

The numbers given above appear to prove rather too much, since the effect of the pollen of Nos. 1–13 might be expected to have raised the percentage of white in the remaining plants to a value higher than 25 per cent. Thus plants No. 14–46 if mutually pollinated by themselves would have yielded on the average less than 25 per cent. of white grains. The difference would probably not be greater than the amount of possible error, in which case the interpretation given may still hold good. Moreover the separation of Nos. 1–13 from Nos. 14 onwards is again an arbitrary one.

Expt. 68.—The male germ cells of the above plants were also examined in bulk by the method of exposing a white strain to their pollen. The result is given in Table 44 :—

TABLE 44.

No.	White.	Blue.	Total.	Per cent. Blue
1	280	261	541	48·5
2	350	290	640	45·3
3	271	209	480	43·5
4	410	300	710	42·2
5	397	288	685	42·0
6	300	190	490	38·8
7	404	246	650	37·9
8	264	216	480	45·0
9	473	267	740	36·1
10	297	153	450	34·0
11	595	305	900	33·9
12	479	241	720	33·6
13	545	275	820	33·5
14	362	168	530	31·7
15	492	208	700	29·7
16	466	144	610	23·6
17	715	205	920	22·3
18	464	116	580	20·0
19	694	156	850	18·4
20	462	98	560	17·5
21	652	118	770	15·3
Total	9,372	4,454	13,826	33·7

The information obtained in this case is however only of a very general kind, since the variation in the percentage of blue grains shown by different plants doubtless depends chiefly upon differences in the "valency" of white in the various plants of the white dent strain used in this case as seed parent.

Similar results were obtained in plants of quite a different line of ancestry.

As was previously stated, cob No. 5 of generation P possessed a dark red pericarp, and 10 out of some 500 grains showed blue pigment in the aleuron layer. The offspring of one of these blue grains yielded on self-pollination 59·5 per cent. of blue grains—F_1. (Cp. Expt. 56.)

F2.

Expt. 69.—A number of these blue grains were sown and the plants arising from them received pollen from plants of white dent. Cobs bearing F_2 grains were gathered from 30 plants, and three of them had either exclusively blue grains (1 plant) or 1 or 2 white grains only (2 cobs). All three of these cobs showed the red pericarp colour. In the remaining cobs the proportion of blue grains varied considerably, being as follows in the case of 6 cobs which had white pericarps: 51, 46, 42, 24, 23, and 20 per cent. of blue. These figures give of course no idea of the statistical distribution of the percentages in F2, but they serve to indicate a general agreement in range with that shown in Expt. 66.

F3.

Expt. 70.—Grains from the cob with exclusively blue aleurone layers were next sown and the plants again pollinated from a further generation of white dent. The proportion of blue and white grains was counted in the case of one cob from each of 58 plants, and the percentage of blue grains was found to range from 54 to 26, the modal value being approximately 37 per cent.

Table 45 and fig. 3 (the black line) show, then, the effect of pollination by white upon grains of a similar origin to those in the case of which the effect of mutual pollination was shown in Table 43. The present case differs notably from the latter in the fact that only a very small proportion of the plants showed dominance of blue in all the heterozygote grains produced by them.

Fig. 3.

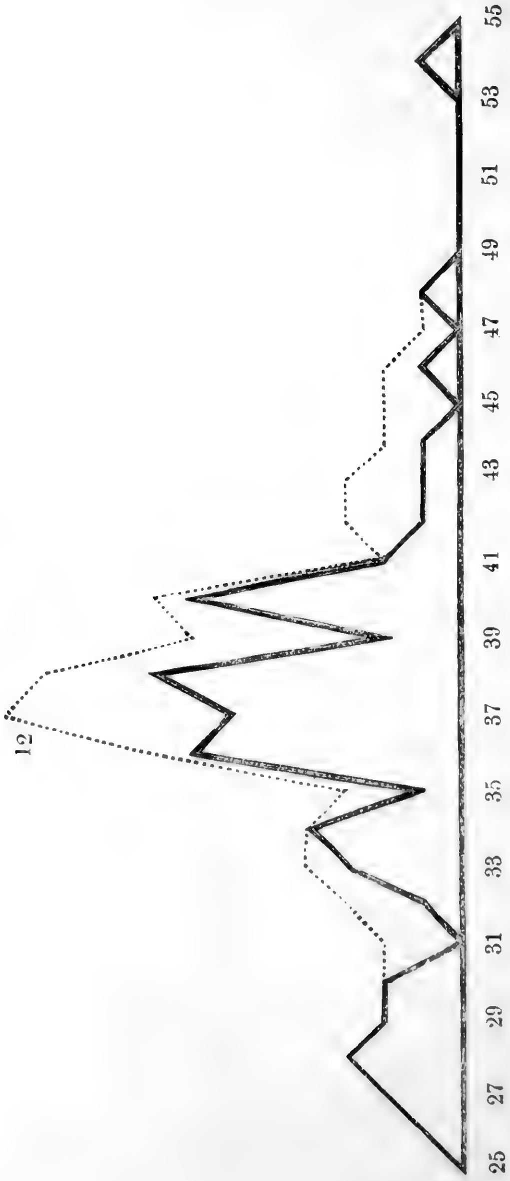


TABLE 45.

No.	White.	Blue.	Total.	Per cent. Blue.
1	326	384	710	54·1
2	441	399	840	47·6
3	242	205	447	45·8
4	472	365	837	43·6
5	478	321	799	40·2
6	530	353	883	40·0
7	241	166	407	40·0
8	434	288	722	39·9
9	422	279	701	39·8
10	420	278	698	39·6
11	447	289	736	39·3
12	522	332	854	38·9
13	503	309	812	38·0
14	449	272	721	37·8
15	469	284	753	37·7
16	428	259	687	37·7
17	576	342	918	37·3
18	531	315	846	37·2
19	393	231	624	37·0
20	491	281	772	36·4
21	494	280	774	36·2
22	469	259	728	35·6
23	464	256	720	35·6
24	483	252	735	34·3
25	414	256	670	33·7
26	543	273	816	33·4
27	421	181	602	29·6
28	636	261	897	29·1
29	611	232	843	27·6
30	653	229	882	25·9
31	652	407	1,059	44·4
32	386	286	672	42·6
33	387	280	667	41·9
34	398	275	673	40·9
35	147	101	248	40·7
36	347	229	576	39·9
37	427	259	686	38·3
38	322	195	517	37·7
39	498	295	793	37·7
40	538	324	862	37·6
41	318	191	509	37·4
42	442	245	687	36·7
43	506	292	798	36·6
44	490	277	767	36·1
45	587	330	917	36·0
46	481	270	751	36·0
47	600	319	919	35·1
48	499	253	752	33·6

No.	White.	Blue.	Total.	Per cent. Blue.
49	484	244	728	33·6
50	561	267	828	33·4
51	343	168	511	32·9
52	702	333	1,035	32·2
53	453	192	645	29·8
54	622	259	881	29·4
55	528	208	736	28·3
56	576	222	798	27·8
57	499	185	684	27·4
58	579	213	792	26·9

28 plants of this generation, Nos. 31–58 of Table 45, showed the red pericarp character and 33 the white; 3 of the latter produced only a small number of grains.

From that cob in F2 (see Expt. 69) which showed only 24 per cent. of blue grains (pericarp red) both white and blue grains were sown separately, pollination being once more effected from white dent.

Expt. 71.—From the *blue grains* (red pericarp) there were obtained 24 plants with white pericarps and 26 with red: the proportion of blue grains in all the former and 8 of the latter were counted, with the result shown in Table 46:—

TABLE 46.

No.	White.	Blue.	Total.	Per cent. Blue.
1	389	351	740	47·4
2	363	308	671	45·9
3	387	331	728	45·4
4	237	196	433	45·3
5	469	358	827	43·6
6	378	290	668	43·4
7	351	265	616	43·0
8	295	215	510	42·2
9	393	279	672	41·6
10	383	260	643	40·4
11	502	326	828	39·4
12	493	319	812	39·3
13	428	287	715	38·7
14	454	282	736	38·6
15	439	276	715	38·6
16	500	310	810	38·3
17	438	267	705	37·8
18	340	206	546	37·7

No.	White.	Blue.	Total.	Per cent. Blue.
19	487	292	779	37·4
20	485	290	775	37·4
21	580	359	939	37·3
22	414	244	658	37·1
23	485	283	768	36·9
24	465	271	736	36·8
25	367	207	574	36·1
26	451	245	696	35·2
27	522	278	800	34·7
28	459	227	686	33·1
29	533	253	786	32·2
30	361	167	528	31·6
31	582	264	846	31·2
32	553	247	800	30·9

The proportions of blue grains shown by these 32 plants are indicated in fig. 3 by the dotted curve, which is constructed from the whole number of percentages in Tables 45 and 46 combined, whilst the unbroken curve shows those from Table 45 only.

The range of variation and the modal value will be seen to be closely similar in the two cases, in spite of the fact that in the parent cob of one series of plants blue was dominant in every grain, whilst in the other only 24 out of a possible 50 grains showed dominance of blue. No explanation of this remarkable result presents itself.

Expt. 72.—*Non-blue grains* from the same F_2 cob (showing 24 per cent. of blue) gave rise to 34 plants. Of these, 20 showed no blue grains at all, and with these must be reckoned 3 which showed only 1 or 2 blue grains. The remaining 11 cobs bore from 5 to 37 per cent. of blue grains, again noticeably fewer than were born by the offspring of blue F_2 grains from the same cob and of the same supposed constitution, *i.e.*, heterozygotes of the nature blue × white.

23 out of 34 therefore of the non-blue grains of F_2 are shown by the behaviour of their offspring to have been pure homozygotes, whilst 11 were heterozygotes. That is to say the homozygotes made up 51·4 per cent. of the total number of grains on F2, whilst the expected number was 50 per cent.

18 of the above plants had red pericarps and 16 white.

Table 47 shows only the percentages of the two extreme specimens of the above series and of three intermediate specimens (chosen for their large size).

TABLE 47.

No.	White.	Blue.	Total.	Per cent. Blue.
1	361	275	736	37·4
2	481	199	680	29·3
3	273	111	384	29·0
4	560	140	700	20·0
5	748	41	789	5·2

Summary of Behaviour of Blue in Mongrel Crosses.

(1) The offspring of the cross (w × b) × w showed as a general rule less than 50 per cent. of blue grains. It is therefore inferred that the blue character is dominant only in the case of certain grains, namely, those in which the blue colour is visible, whilst white is assumed to be dominant in such a number of the white grains as will make up the expected number of 50 per cent. heterozygotes. The offspring of the white grains was found on examination to confirm this last assumption in every case.

(2) Another notable phenomenon was the sporadic appearance of dominance of blue in all those grains of a cob which were expected to bear the blue character, *i.e.*, in all the grains of a cob when these were of the nature (b × b) × w, or in 50 per cent. of grains of the nature (b × w) × w, so that in these cases, as an exception to the more general rule, the Mendelian laws of dominance and segregation were followed in the simplest manner possible.

In one experiment this appearance of regular dominance was found to be largely inherited, but in another scarcely at all.

The explanation of this sudden appearance of a regular Mendelian behaviour was not arrived at. Its elucidation would be a somewhat tedious process, but by no means an impossible one, provided that all the plants examined were fertilized by hand, so that both male and female parents could be known accurately, which was not the case in the above experiments.

It is especially to be remarked that such a process as was actually adopted, by which only the seed parent was capable of exact identification, is quite inadequate for the elucidation of anything beyond the very simplest of hereditary processes, such as are found for example in the cases of the yellow and white or red and white pairs of characters. The reason of this is that the supposed uniform strain used as a pollen parent may bear invisible but segregable characters, which, on meeting with certain characters in the strain under examination, may produce different results. Such phenomena are now known to occur in several species of plants, but were less clearly understood at the time when the present experiments were begun.

The present observations must therefore serve as a preliminary survey of phenomena, the complete elucidation of which remains as an interesting occasion for further research.

3.—RED CROSSED WITH WHITE.

The red colouration has been a source of trouble to many observers owing to its non-appearance as "xenia." In the experiments last described however (70–72) two successive generations were pollinated by a pure strain with exclusively white pericarps. We therefore have presumably plants of the form (red × white) red × white, and the expectation according to Mendel's law is an equality of plants with red and plants with white pericarps. The actual numbers have been already alluded to incidentally; adding them together we get—

$$\left.\begin{array}{l}\text{Red: } 28 + 26 + 18 = 72 \\ \text{White: } 33 + 24 + 16 = 73\end{array}\right\} 145$$

No case was seen of red among the offspring of plants which were expected to be pure white as regards pericarp, so that the proof that Mendel's law holds good for this pair of characters is established with considerable certainty.

The red colour is thus an ordinary Mendelian dominant; red and white are heterodynamous and schizogonous as Correns supposed in 1902, although the complete proof was then lacking. The intensity of the red colour varies however considerably from plant to plant, and it was not found possible to rear any certain extracted dominant for comparison.

B.—COMBINATIONS OF CHARACTERS.

The same remarks apply here as were given in Part I. under the same heading; the red, blue, and yellow allelomorphs appeared to segregate each from its corresponding allelomorph (absence of colour) in complete independence of the other pairs. In the following example, which shows a similar complexity in respect of the supposed yellow-white pair as did the complex cross described in the previous part, the starch-sugar pair is concerned as well as both pairs of endosperm colour characters.

F1.

Expt. 73.—A plant arising from a heterozygote grain, yellow × white flint, was crossed with pollen from Black Mexican sugar corn. There resulted nearly equal numbers of yellow, white, blackish yellow, and blackish white grains, the two last kinds showing a mottled pattern of bluish black overlying the ground colour.

The offspring of only the blackish yellow grains (heterozygotes presumably in all three pairs of allelomorphs concerned) were examined in detail.

F2.

22 plants were obtained from the blackish yellow grains, and these were allowed to mutually pollinate one another. The total number of starchy (flint) and sugary grains was given in Table 2 without distinction of colours. In Table 47 all the different kinds of grains obtained are enumerated separately. Grains with a blue (or blackish) aleurone layer may of course be either yellow or white in general endosperm colour, and when the blue colouration was faint, as it was in a

considerable proportion of cases, the yellow or white colour of the endosperm could often be distinguished. In other grains however the blue colouration was too deep for this to be possible. The blue grains in this generation did not show mottling.

That yellows are too numerous and whites too few as compared with the expected number is partly due to the fact that a small number of the palest yellows—counted as yellow—should really be placed among the whites, as the evidence of later generations shows. Compare Expt. 54, F_3 and F_4.

TABLE 47.

No.	Total Grains.	Per cent. Blue Starchy.	Per cent. Blue Sugary.	Per cent. Yellow Starchy.	Per cent Yellow Sugary.	Per cent. White Starchy.	Per cent. White Sugary.
1	549	37·3	14·9	30·8	9·7	5·7	1·6
2	609	37·7	13·8	31·7	7·5	7·2	1·5
3	498	38·3	13·0	25·7	8·8	11·8	2·2
4	397	42·8	15·6	16·9	7·0	14·4	3·2
5	291	43·6	12·0	28·2	8·9	5·5	1·3
6	502	45·0	9·7	27·7	9·7	6·7	1·0
7	459	42·3	12·9	25·9	10·2	6·8	1·9
8	423	39·0	10·9	30·5	10·4	6·6	2·6
9	210	40·6	11·4	20·0	9·5	11·9	1·4
10	418	43·5	10·3	29·4	9·6	5·9	1·4
11	304	39·4	15·1	27·3	7·9	9·2	1·0
12	470	45·1	15·1	27·6	9·1	5·3	1·9
13	221	46·2	17·6	19·4	8·1	8·1	1·4
14	354	43·5	11·0	27·9	9·6	6·2	1·4
15	301	41·2	10·9	22·9	9·6	11·3	3·6
16	331	42·0	10·3	28·1	7·8	9·7	2·1
17	381	44·1	12·1	26·8	8·1	7·6	1·3
18	484	44·8	13·1	21·7	8·2	8·9	3·1
19	457	45·7	11·4	22·7	8·3	8·7	3·0
20	238	45·0	16·0	21·4	7·6	6·7	3·4
21	380	42·3	12·9	26·6	8·7	7·3	2·1
22	352	48·3	12·2	24·1	6·8	6·8	1·4
Total	8,649	42·46	12·75	26·1	8·67	7·95	2·0
Expectation (taking Blacks as 55·22 per cent. the value found)		41·5	13·8	25·1	8·4	8·4	2·8

F3.

Grains showing each of the six combinations of characters were sown and pollination was effected from G. W. S. The plants were very weak and yielded for the most part only a few grains each, but the result so far as could be seen was in complete accord with those previously described, where simple pairs of characters were considered, with the exception of the behaviour of the pale yellow grains. The palest yellow grains yielded about 10 per cent. of pale yellow grains, the remainder of the grains on the same cobs being reckoned as white. A considerable number of white F_2 grains gave a similar progeny, whilst others yielded white grains only, c.p. table 29. Among the offspring of sugary blue F_2 grains the following plants were recorded :—

TABLE 49.

No.	White.	Yellow.	Black.	
1	123	135	157	All sugary.
2	43	39	82	
3	—	63	273	

The palest yellow grains were this time counted with the whites, but sown separately.

F4.

Offspring of No. 1 above. Pollination again by G. W. S.

TABLE 50.

Cob produced the following grains :—

Parent Grain.	W. only.	W.& y.	W.&Y. (&y.)	B.&W.	B.&W. & y.	B.&W. & Y. (& y.)	Total.
W.	13	—	—	3	—	—	16
Y.	—	—	22	—	—	—	22
y.	1	10	—	—	4	—	15
B.	—	—	—	15		14	29

W.= White. Y.= Full yellow. y.= pale yellow. B.= Blue.

( ) indicates presence of y in some of the plants.

The above *plants* can undoubtedly be separated in spite of the difficulty of distinguishing W., Y., and y. in individual *grains*.

SUMMARY.

The facts concerning "xenia" in maize, as well as those which refer to the offspring of the parallel process of true fertilization, have been worked out by Correns in the case of crosses between various strains of Indian corn, which differed in a large series of characters. The experiments showed that Mendel's law of segregation of characters in the heterozygote was approximately followed in the case of several pairs of allelomorphs. In other cases it appeared possible that germ cells bearing a blended character were produced, though here the evidence was much less complete. The specimens obtained, though quite sufficient for their purpose, were comparatively few and often imperfect, and Correns has himself pointed out the importance of examining the proportions of the germ cells in a larger series of plants, in order to discover whether those departures from the expected proportion, which are found in particular instances, have any special significance, or whether, on the other hand, they depend simply on the smallness of the samples examined.

This then was the main object of the experiments described in the present paper; and it may be stated at once that, so far as the numbers examined go, the following inference receives support, namely, that in the case of the allelomorphic characters concerned, it was an even chance whether one or the other member of a particular pair appeared in any given gamete of the heterozygote examined.

In the case of certain plant characters, which afford less simple material than seed characters do, for statistical treatment, and especially in those cases where the cross-bred form showed a blending of parental characters, there was doubt as to whether segregation took place or not; and in the case of the character height of plants it seemed certain that blended gametes were formed, though the proof of this is not so clear as in the Mendelian cases, partly owing to the great sensitiveness which such a character as height shows to the effect of external conditions.

We turn now to those cases in which seed characters were concerned and in which segregation was found to be of the normal type. In the foregoing account the description of crosses between supposed "definite" races has been placed first because this appeared to be the logical sequence. But in the case of the mongrel strain, of which the account stands second, a considerably larger number of individual plants was dealt with, and the characters considered were found to behave quite as definitely as in the former case. We may therefore deal here with the two sets of cases simultaneously, and furthermore may begin by taking together all those cases where there was (1) complete dominance, *i.e.*, most cases of starchiness crossed with sugariness,* or (2) where the heterozygote, though intermediate, was clearly distinguishable from one of the parental types, *i.e.*, most cases of yellowness crossed with whiteness; for in such cases no error will be introduced by treating the latter as recessive.

The summary which immediately follows includes then all the experiments described in this paper, in which, sugar and starch corn having been crossed together, the offspring was crossed with pollen from a sugar variety, together with the corresponding cases of (yellow × white) × white; with the exception (1) of those in which the black or blue character was also concerned, and (2) of those few complicated cases where an especially pale yellow character made its appearance, in the later generations, and thus rendered impossible an exact estimation of yellow and white. A small number of plants which bore grains showing both the yellow-white and the starch-sugar characters are counted twice over in the following summary —once for each pair of allelomorphs.

Throughout this series of cases Mendel's law seemed to be applicable as an approximation. 247 cases were available in which a heterozygote, having been crossed with the corres-

---

* Even in the cross starch × sugar, grains intermediate in appearance were to be seen in a small number of cases where certain strains were concerned. Such grains were distinguished by eye into one class or the other, and, on rearing their progeny, the classification adopted was almost invariably confirmed. In every case the behaviour of the offspring showed that the doubtful grain belonged in fact to one class or the other, and it is highly probable that if chemical tests had been applied to these grains the result would have been equally conclusive. The character actually used for discrimination is only an incidental one; the fundamental distinction lies in the chemical nature of the endosperm. See Experiments 20 and 54. The error introduced by including these few cases is probably inappreciable.

ponding recessive, yielded 50 per cent.—more or less—of the heterozygote and of the recessive types respectively. The results are expressed as percentages of the heterozygote (usually dominant) type throughout.

Grand total: 56,028 Het.: 55,669 R.; together 111,697.

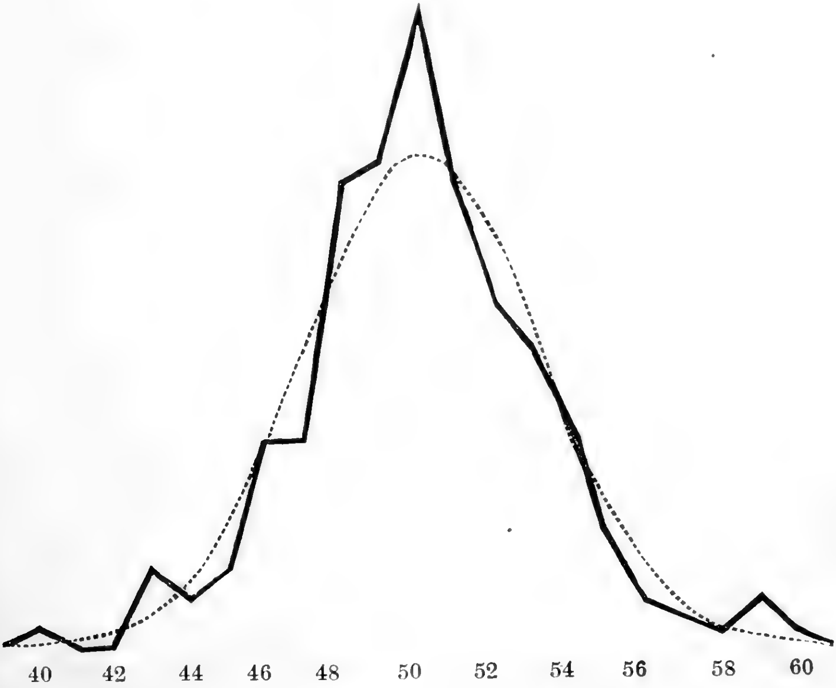
That is: 50·17 per cent. Het. (Expectation 50·11).±

The individual percentages shown by the 247 samples were as follows:—*

Per cent.	40,	41,	42,	43,	44,	45,	46,	47,	48,	49,	50,	51,	52,	53,	54,	55,	56,	57,	58,	59,	60
No.	1,	—	—	5,	3,	5,	13·5,	13·5,	30,	31·5,	41,	30,	22·5,	19·5,	14·5,	7,	3,	2,	1,	3,	1.

The series is shown graphically in the accompanying diagram:—

Fig. 4.



---

* The numbers are derived from Tables 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 28, 30, 31, 33, 35.

The above curve was thus obtained by plotting the actual errors or deviations from the value 50 per cent. shown by the percentage numbers of heterozygotes in 247 samples, each of which contained a known number of individuals (average number of individuals 450). The "mode" of the curve lies very nearly at 50 per cent., and the mid departure found graphically from the area of the curve is 1·9.

We have thus arrived by experiment at a value for the distance from the mode within which half the observed deviations lie. Now the theoretical probable error for samples containing 450 individuals is 1·6,* so that the experimental value is somewhat too high.† Certain possible sources of minor error, in addition to those pointed out in the footnote, have been alluded to in the case of the particular series in which they occurred (see Expts. 30, 54).

On the whole we may say that the experimental curve agrees with the theoretical one within reasonable limits of error, and the result is therefore the same as would be expected supposing the deviations from 50 per cent. to have no special significance, but to depend simply upon the size of the samples.

The above facts lead to the conclusion that in the case of any particular grain the chances of one or the other character being present are equal.

---

* An allowance for the fact that the samples are not all of the same size would presumably somewhat raise this value.

† The normal form of the unsmoothed curve in fig. 4 is somewhat spoilt by 5 extreme variants, which show deviations from the mode respectively of 10 in 2 cases and of 9 in 3 cases. It will be well therefore to look a little more closely at these variants: 1 of 40 per cent., 3 of 59 per cent., and 1 of 60 per cent. The sample showing 40 per cent. het. included only 218 individuals; the 1st sample showing 59 per cent. het. included only 138 individuals (Table 4); the 2nd sample showing 59 per cent. het. included only 296 individuals and was found among an unusually variable set of values (Table 10). 3rd sample showing 59 per cent. het. included 488 individuals (Table 31). The case of 60 per cent. het. occurred in Table 5, in which a possible source of error was noted, and the sample included only 305 individuals.

The statistical proof is not conclusive, because it is quite possible for a normal curve to be made up of a number of minor curves having independent modes different from that of the main curve. Still a certain interest attaches to this method of presenting the facts.

A portion of the above result was described in a letter to *Nature* (vol. 70, p. 601). The account was however expressed in such an imperfect manner that so astute a critic as Prof. Karl Pearson missed the main point of it, as appears from his letter in the following number. For this reason I feel constrained to deal here with one or two of the statements which Prof. Pearson's letter contains.

Like myself, Prof. Pearson headed his letter "Mendel's Law," but states: "The difficulty is to know what is understood by this term." What I personally understand by the term and what is in my opinion the only legitimate use of it since it was so first defined by Correns, I have stated on the 7th page of the paper from which Prof. Pearson quotes in his letter—I mean the law that the gametes of a heterozygote contain in equal numbers the pure parental allelomorphs completely separated from one another.* It is in evidence of this law that I believe that I have provided a "crucial experiment" by showing that in the case of both the male and female germ cells of the heterozygote produced by crossing strains of maize with a white and with a yellow endosperm respectively, this segregation in equal numbers is no theory but a fact.

The same proof was indeed afforded by Mendel himself in his classical experiment with peas, but too small a number of individuals was then dealt with for the evidence to be regarded as final.

The proof (as stated in *Nature*) consisted in crossing the female flowers of the heterozygote (each bearing one germ cell) with pollen from a recessive form. As the result of this

---

* And if the cross-bred plant is heterozygous in respect of more than 1 pair of allelomorphs, then all *possible* combinations of these allelomorphs occur in equal numbers of gametes.

process equal numbers of flowers yielded white endosperms (recessive) and yellow endosperms—evidently heterozygous since the male parent was white. The pollen of the heterozygote was tested in the same way and with the same result.

Prof. Pearson asks, Where is the other homozygote? In the last generation (as described in *Nature*) heterozygote plants were mutually pollinated and yielded a proportion of three yellow grains to one white. One out of every three yellow grains in this generation represents the other (yellow) homozygote.

A further series of cases, in which the presence and absence of a colour were concerned, require particular notice owing to the fact that the cross between heterozygote and white often yielded a sensible excess of whites over the expected 50 per cent. These were all found in crosses between parents one of which showed the blue or purple pigment in the aleurone layer; and the phenomenon was seen alike in crosses between definite strains and between mongrel plants. In the former case the reason of the phenomenon was at once apparent, since heterozygote grains arising from the cross white × blue might be either blue or white in colour, so that both kinds of grains were to be seen on the same cob, when the latter arose from the fertilization of a white strain with pollen from a blue (black).

At this point it is necessary to recall the methods of pollination employed throughout these experiments. In the one set of cases heterozygote plants were grown together in groups and allowed to intermingle their pollen, the pollen of other plants being excluded by distance. In the second set of cases which include the great majority, heterozygote plants deprived of their male inflorescences were exposed to the pollen falling from many plants of one particular strain (usually a recessive). Thus in no case can the exact individual parentage of the grains on the plant under consideration be arrived at. If this had been possible there is little doubt that the apparently complicated phenomena seen would receive their proper explanation, as has been the case with other plants when more precise methods were employed. This being understood, we may pass on to describe the phenomena actually seen in the present instance.

The account may be somewhat simplified by using a special notation. We may write :—bb for homozygote blue (or black): wb for heterozygotes, blue (or black) blue in appearance; w(b) for white grains among the offspring of which blue reappeared, *i.e.*, heterozygotes white in appearance; and ww. for homozygote white.

In F_1 from Black Mexican crossed with white dent—

b × w gave wb.
w × b gave wb and w(b).

The behaviour in F_2 may be stated as follows :—

$$\text{(1) wb} \times \text{wb gave } \underbrace{\text{bb wb w(b)}}_{3}\ \underset{:}{\text{and}}\ \underset{1}{\text{ww}}$$

$$\text{(2) wb} \times \text{w gave } \underbrace{\text{wb w(b)}}_{1}\ \underset{:}{\text{and}}\ \underset{1}{\text{ww}}$$

$$\text{(3) w} \times \text{wb gave } \underbrace{\text{wb w(b)}}_{1}\ \underset{:}{\text{and}}\ \underset{1}{\text{ww}}$$

The view embodied in this table is supported by the following evidence derived from the next generation (F_3), in which all the different kinds of grains were sown and the plants again fertilized with pollen from a white strain. Under these circumstances—

ww (white) × w yielded only white offspring.
w(b) (white) × w gave either (1) 50 per cent. black, or (2) some number of black less than 50 per cent.
bb (black) × w gave either (1) all black, or (2) a percentage of black much higher than 50, *e.g.*, 80 per cent.
wb (black) × w gave approximately 50 per cent. of blue, or sometimes slightly less.

It will be seen that certain assumptions are here made, of which the most questionable is the supposition that 80 per cent. of blue in the offspring indicates a homozygous parent.* A

---

* But the assumption is rendered almost a certainty when it is found that all the white grains (20 per cent.) of such a cob include some blacks among their offspring.

similar result was however obtained in F_1 (w × b); the whole fits in with Mendelian expectation, and there does not appear to be any other explanation of equal simplicity. The explanation given does not preclude the possibility that the difference between the plants yielding 100 per cent. b and those yielding 80 per cent. b may depend on a definite factor.

In F_2, in all three cases, the proportion of wb : w (b) was nearly 2 : 1 on the average. From this it seems likely that in case (1) the products of gametes w × b and b × w is the same. This differs from what took place in F_1 and is the contrary of what Correns supposes in the case of his cross "alba" × "cyanea."

According to the present view, among the offspring in F_3 of wb grains, blue was, in the case of most plants, dominant over white in every grain. But in the offspring of w (b) the result was more often like that which appeared in the case of w × b in F_1, blue being now dominant in certain cases. It is clear therefore that the degree of dominance (or valency) of blue is inherited to some extent, but the experiments are not precise enough to justify a more definite statement.

In the case of the offspring of the mongrel crosses in which the blue grains were of the flint form, whilst the white grains were derived at first from the same mixed flint strain, and later from a definite strain of dent corn, dominance of blue in all the grains of a plant was the exception even in the offspring of wb (or bb) grains. This is in accordance with Correns's view that the white character derived from a sugar strain is "weaker" in comparison with blue than the same character derived from a flint variety.

In the preceding case of a definite cross, the difference between the offspring of ww and w (b) was very distinct. In the example last described this was not the case, the distinction being doubtful in the case of one or two plants; but it is assumed that the two classes are distinct in fact, because in this way the simplest possible explanation seems to be arrived at.

There can be little doubt that had a precise examination of every individual been substituted for the examination in mass which was actually employed, the full explanation of the complexities seen would soon have been discovered; and the result of such an examination would without doubt repay the time expended upon it by any one situated in a suitable climate who should be disposed to take the matter up, in the light of Correns's results and of those detailed above. The results already obtained are however sufficient to show that in all probability there is here no exception to the ordinary course of Mendelian segregation.

It is to be noted that in the above descriptions the term blue (or black) is applied to all grains which showed any trace of the blue (or black) character. The intensity of colour varied considerably from grain to grain and in different parts of the same grain, and it seemed not unlikely that in the case of the cross with Black Mexican a definite factor for mottling was concerned, and possibly a definite intensity factor as well. These are points which might also be profitably studied by the process of individual pollination.

In the case of the mongrel flint corn a truly piebald character made its appearance in about one per thousand of the blue grains. Two piebald yellow and white grains were seen among about 50,000 presumably heterozygote grains which were examined.

Finally attention may be directed to those curious cases, exemplified in maize by the mealy and hyaline characters of the endosperm associated respectively with the indent and flint types of grain, in which characters of the endosperm (seed generation) behave on crossing as if they were characters of the maternal plant. Other instances are seen in the indent character of pea seeds (Tschermak), and in the soft and hard endosperm of wheat grains (Biffen). Unlike the last mentioned case the corresponding characters in maize do not show the phenomenon of dominance, and owing to the great variability of the cross-bred plants the existence of segregation is only to be inferred from analogy. It is clear that in the case of these definite characters of the endosperm the difference cannot be simply impressed upon the grains by the form of the pericarp, and if this is so it is quite possible that the case of the indent pea is of a similar kind. Tschermak's conception of a correlation between a vegetative and a sexual character must therefore hold good, at least provisionally.*

In bringing this paper to a conclusion, I desire to take the opportunity of once more expressing my indebtedness to Mr. Bateson for a great deal of valuable advice.

APPENDIX I.—EXPERIMENTS WITH KIDNEY BEANS.

Experiments with kidney beans, in which attention was paid especially to the colour characters of the testa, have been carried out on a large scale by Tschermak, who obtained results of great interest and complexity. In some of the most typical of Tschermak's experiments the plants obtained in F_2 from self-fertilization showed a great variety of types of colour in the testas. The main groups of these showed usually the Mendelian ratio of 3 : 1, but sometimes a ratio of 1 : 1 was seen, a result not yet fully explained. Within the main colour groups, sub-groups, differing in the particular shade of colour or in the presence or absence of mottling, were found to exhibit similar numerical ratios.

Results of a similar nature have been obtained by Emmerson, who observed also cases of irregularity in dominance, which may possibly be comparable with those shown by the blue aleurone layer in maize.

---

* C.p., Annals II., p. 327.

The results here shortly described confirm those of Tschermak in a qualitative manner; quantitatively the results were uncertain owing to bad conditions, which only a few plants survived.

A considerable number of crosses were made at Peradeniya between strains of beans which differed chiefly in the colour of the testa. Unfortunately the greater number of the progeny of these crosses were lost owing to drought and other causes. The number of plants which survived was in no case sufficient to afford complete evidence of the manner of inheritance of the characters examined, and the phenomena observed will only be very briefly indicated.

Besides the case of atavism described on page 340, the only example of a bean cross which survived more than two generations was one between "Golden Wax Butter" and "Ne Plus Ultra;" the former of these had yellow pods and testas of a dark blackish purple colour, whilst Ne Plus Ultra had green pods and dark yellow seeds.

The seeds of the cross bred plants (F_1) resembled those of Golden Wax Butter, or were perhaps of a slightly darker tint, but the pods were green. And from the evidence of later generations it was clear that the green pod colour behaved as a simple dominant to yellow.

As regards the characters of the testas, a great variety of types were obtained in F_2 and F_3. The number of plants obtained was small, but the facts appear to be as follows. The self-fertilized heterozygote gave rise to two principal groups of plants—a group (A) with seeds showing various shades of purple, including sub-groups with reddish purple, bluish purple, and chocolate testas—the whole group being probably three times as numerous as the second group (B) which included different shades of yellow, mottled yellow and white, and pure white seeds. On further self-fertilization members of group B never gave rise to any form of group A, but apparently any of the A types might produce some form of B.

APPENDIX II.—EXPERIMENTS WITH CANAVALIA ENSIFORMIS.

This was the only strictly tropical plant with which satisfactory crosses were obtained, but only a few were successful out of many attempted. The plants possessed a very large climbing habit, and it was consequently impossible to grow many specimens, and when grown the individual plants were difficult to disentangle. The first cross plants moreover failed almost entirely owing to their having been sown out of the proper season.

The following points were determined :—

Tall habit dominant to semi-dwarf.

Pink colour in the flowers dominant (or nearly) to white, the latter reappearing in F_2.

Absence of red pigment in the testa dominant to red. In F_2 red reappeared, but in nothing like its former intensity. Some of the plants of F_2 bore mottled grains, but in these also the pigmented patches were of a very faint reddish colour.

In F_2 plants with no red pigment in the testa were more numerous than (probably three times as numerous as) those with reddish and those with mottled testas taken together.

No mottled strain was heard of as previously existing.

The behaviour of the red character as described above is remarkable, and possibly at present unique. It is unfortunate that the difficulty already mentioned in combination with want of time prevented further experiments.

APPENDIX III.—RECENT PROGRESS IN THE EXPERIMENTAL STUDY OF HEREDITY.

Since the time of writing the account of the progress of Mendelian studies, which appeared as Part I. of these studies, steady advances have been made in the directions there indicated.

The most interesting event of the year which has elapsed since that account was written has been the publication by Correns of Mendel's letters to Nägeli, written between 1866 and 1873. These illustrate in a remarkable way Mendel's astonishing activity as a hybridizer, and show that his publications on peas and on Hieracium represent only a small section of the experiments he had in hand—experiments which confirm the conclusions drawn from the study of pea crosses by similar observations on a wide range of different plants.

We find moreover that the idea—recent subject of much discussion—that sex may be a Mendelian phenomenon was present to Mendel himself, having been suggested by the existence of the proportion 151 female : 52 male plants in F_1 from a cross between Lychnis diurna and L. vespertina.

Correns points out in an appendix that this particular case cannot indicate the existence of simple dominance and of Mendelian segregation. He contends further that the "Anlagen" for the separate sexes are never fully segregated, but it seems doubtful whether he has successfully excluded all possible explanations involving a Mendelian segregation of the sexes.

The second report to the Evolution Committee of the Royal Society, by Bateson, Miss Saunders, Punnett, and others, though published in the present spring, contains complete records of their work only to the end of 1903, with some reference to that of 1904.

The account of the inheritance of characters of the comb in fowls raises points of considerable interest. Put very briefly the facts are as follows :—

"Rose" comb (r) behaves as a simple Mendelian dominant to single comb (s).

"Pea" comb (p) crossed with single does the same.

r crossed with p gave a comb of characteristic appearance (rp), known as "walnut" and similar to that of the Malay breed.

rp × rp gave 9rp + 3r + 3p + 1s; rp × s gave equal numbers of rp, r, p, and s; and in a particular case true Malay × single gave the same result.

The authors express these results by supposing a "compound allelomorph" rp, which splits up giving off equal numbers of gametes rp, r, p, and s; in a manner identical with that suggested by Bateson* in his criticism of De Vries,† who had explained similar proportions obtained with colours of the flowers in Antirrhinum in a purely Mendelian fashion.

It appears to me that the formula of De Vries (which is also that of Mendel) is to be preferred in both these cases, and that the idea of "resolution of a compound allelomorph" is quite unnecessary in either of them.

Quite recently Bateson and Punnett have published a suggestion as to the nature of the "walnut" comb ‡ of which the following paragraph (which was written however before the appearance of their note) may serve as a summary.

If we write: r=Ab; p=aB; s=ab. A and a being a pair of allelomorphs of which A is dominant, and B and b in like manner, the artificial Malay will be ABab and the pure Malay ABAB. The whole phenomenon then resolves itself into a simple case of dihybridism.

This view is further supported by the following consideration. The single comb being the primitive form, it is almost necessary to suppose that both rose and pea have arisen from it separately by mutation; there seems therefore to be no inherent difficulty in treating rose—single and pea—single as separate pairs of allelomorphs; and the rp appearance would then be induced by the simultaneous presence of A and B, whilst in the absence of both of them the primitive single comb would be expected to appear.

---

* Bateson, W. Note on the resolution of compound characters by cross-breeding. Proc. Camb. Phil. Soc. XII., p. 50.

† De Vries, H. Mutations-theorie II., p. 197.

‡ Bateson, W., and Punnett, R.C., in Proc. Camb. Phil. Soc., October 25, 1905.

Among the experiments with sweet peas phenomena of remarkable interest are recorded. The following case is of particular importance.

The white-flowered strain Emily Henderson includes plants with long and with round pollen. When the two forms were crossed together plants with purple flowers and long pollen were obtained in F_1 (reversion in colour).

In F_2 the proportion of coloured flowers to white was 1·42 : 1, that of long pollen to round 3·36 : 1 (probably Mendelian). The coloured flowers included several different types. As regards colour the phenomena are clearly of greater complexity than those described by Cuénot in the case of mice, but it is probable that the explanation is to be looked for along similar lines.

An apparently new class of fact appears in the association of long pollen with certain colours and of round pollen with others. This coupling was not complete, but in some cases long pollen was found on plants of the colour usually affected by round pollen. The definiteness of the characters concerned makes the partial coupling in this case a more remarkable phenomenon than, for instance, the coupling found in the case of peas between floral colour and time of flowering, which was described in Part I. of this series.

Somewhat similar phenomena are described in the case of the floral colours of stocks. In these plants a complication is introduced by the fact that the characters hoariness and glabrousness are associated with the colouring in a manner not completely understood.

Recently published experiments by Biffen on the crossing of wheats and barleys show that simple Mendelian phenomena occur over a wide range of characters in these species. The evidence of these experiments does not appear to lend any confirmation to the elaborate formulæ enunciated by Tschermak for the purpose of describing the supposed results of crossing in cereals.

Correns has recently described dominance of the "hose-in-hose" form over the normal type of flower in the cases of Campanula and Mimulus.

He has also put forward a formula to describe the phenomena shown by the colours appearing when certain strains of Mirabilis are crossed together, which involves the interaction of definite factors—factors which individually follow Mendel's law.

Castle has described at length the occurrence of Mendelian phenomena on crossing strains of guinea-pigs and rabbits which differed in the structural and colour characters of their coats.

Cuénot, continuing his experiments with mice, has been able to obtain the expected pure strains both of coloured mice and of albinos carrying particular colour factors. The author was however unable to obtain a pure race bearing the yellow colour. CJCG × CJCG was expected to give in F_1 :—1 CJCJ : 2 CJCG : 1CGCG, but as a matter of fact this cross yielded no pure yellow dominants at all (out of a total of 81 offspring). No absolute explanation of this phenomenon is forthcoming, but Cuénot suggests an analogy with the curious case described by Correns in maize, in which the heterozygote crossed with the recessive gave equality, whereas self-pollinated it gave 84 per cent. of the dominant type.

Emmerson's results with kidney beans have been already briefly referred to in Appendix 1.

Hurst has published simple Mendelian results in the case of peas, and the confirmation of Mendel's classical experiments with these plants seems now to be complete. In the case of experiments with poultry, this author has found certain exceptions to the usually simple Mendelian phenomena, and these are to be made the object of further experiments.

McCracken has in all probability found simple dominance of a spotted type over the melanic form in the beetle Lina lapponica. And Schuster has published results of crossing mice, which so far as they go are in complete accord with Mendelian expectation.

De Vries, in his "Species and Varieties : their Origin by Mutation," has republished the account of some of his experiments, and has added a certain number of new ones.

On the cytological side much work has also been done. A discussion of such work, together with a full list of literature, is to be found in the paper by Allen in the Annals of Botany for April 1905.

APPENDIX IV.—LIST OF LITERATURE.

1. Allen, C. E. Nuclear Division in the Pollen Mother Cells of Lilium canadense. Annals of Botany, Vol. XIX., p. 189 1905
2. Bateson, W. Presidential Address to the Zoological Section of the British Association .. 1904
3. ——, Miss E. R. Saunders, R. C. Punnett, and C. C. Hurst. Reports to the Evolution Committee of the Royal Society, II. .. 1905
4. Biffen, R. H. Mendel's Laws of Inheritance and Wheat Breeding. Journal of Agricultural Science, I., 1 1905
5. ——. The Inheritance of Sterility in the Barleys, *Ibid* I., 2 1905
6 Castle, W. E. Heredity of Coat Colours in Guinea-pigs and Rabbits. Carnegie Institution of Washington 1905
7. Correns, C. Ein typisch spaltender Bastard zwischen einer einjahrigen und ein zweijahrigen Sippe des Hyoscyamus niger. Berichte d. d. bot. Ges. XXII., 8 1904
8. ——. Zur Kenntnisse der scheinbar neuen Merkmale der Bastarde. *Ibid.* XXIII., 2 .. 1905
9. ——. Einige Bastardierungsversuche mit anomalen Sippen und ihre allgemeinen Ergebnisse. Pringsheims Jahrbucher, 48, 458 .. 1905

10. ——. Gregor Mendel's Breife an Carl Nägeli. Abhandl. d. Math-Phys. Klasse d. konigl. Sachs. Ges. d. Wissenschaften XXIX. .. 1905
11. Cuénot, L. Les races pure et leur combinaisons chez les souris. Arch. de. Zool. exp. et gen. Notes et revue. CXXIII. 1905
12. Emerson. Heredity in Bean Hybrids. Agric. Expt. Sta. Report, Nebraska .. 1904
13. Hurst, C. C., Experiments in the Heredity of Peas. J. R. H. S. 1904
14. McCracken, Isabel. A Study of the Inheritance of Dichromatism in Lina lapponica. Journ. Exp. Zool. II., 1 1905
15. Schuster, E. H. J. Results of crossing Gray (House) Mice with Albinos. Biometrica IV., p. 1 1905
16. Tschermak, E. Weiterer Kreuzungsstudien an Erbsen, Levkojen und Bohnen. Zeit. f. d. landwirtsch. Vers. in Oest.. .. 1904
17. De Vries, H. Species and Varieties: their Origin by Mutation. Chicago .. 1905
18. Bateson, W. and R. C. Punnett. A Suggestion as to the Nature of the "Walnut" Comb in Fowls. Proc. Camb. Phil. Soc. October. .. 1905

Cambridge, October, 1905.

The Fungi of certain Termite Nests.

(*Termes redemanni, Wasm.; and T. obscuriceps, Wasm.*)

BY

T. PETCH.

With Plates V. to XXI.

THE knowledge of the existence of fungi in the nests of termites antedates Belt's observations on the habits of the leaf-cutting ants of South America by nearly a century; yet, though the "fungus gardens" of the latter have been fully described, no attempt seems to have been made to give a complete account of the corresponding structures in the former. On further inquiry, however, it is found that many of the chief points have been noted at one time or another in scattered articles by botanists or entomologists, though it is evident that in many cases the writers have not had an opportunity of confirming their first impressions by a reference to fresh material.

Smeathman (1) in 1781, after investigations in Tropical Africa, stated that some species of termites had chambers in their habitations in which grew a kind of fungus used by the insects for food. The nurseries were always covered with a kind of mould, and sprinkled all over with small white bodies which under the microscope were found to consist of oblong spore-like cells. This statement is true of the nests of the Ceylon ground termites, though exception may be taken to the apparent suggestion that special chambers are reserved

Annals of the Royal Botanic Gardens, Peradeniya, Vol. III., Part II., Nov., 1906.]

for "nurseries." Every chamber in the nest is an actual or potential nursery, and there is no chamber without fungi except the royal cell.

In 1847 Berkeley (2) described several species of fungi which had been collected by Gardner in Ceylon, and among them an agaric which he named *Lentinus cartilagineus ;* this grew from termite nests, sometimes from a depth of four feet. The record appears to have been overlooked by later workers ; probably the association was regarded as purely accidental, if indeed any one ever did consult these pioneer lists.

In 1875 Berkeley and Broome (4) published a further account of Ceylon fungi based on a far larger collection made by Thwaites in 1860, &c. Two of Thwaites' numbers, 176 and 554, labelled "On Termes' Nests" and "On White Ant Nests" respectively, are grouped by Berkeley and Broome with several others as "conidiiferous forms of unknown species" of Xylaria, and are said to "occur on the nests of termites when exposed to the light." This statement is only true for No. 554. No. 176 bears no resemblance to Xylaria, and occurs on combs in the nest.

It is rather surprising to find that neither Gardner nor Thwaites sent the actual fungus on the comb alluded to by Smeathman : at least this cannot be traced in the specimens or descriptions. Both of them must have handled the termite comb to obtain the specimens already referred to.

These three records include all the forms that are at present known to occur regularly on termite combs : indeed, collectively they are in advance of recent accounts, none of which deals with all three structures.

Of recent years the subject has again attracted attention in Java and Ceylon. Penzig and Saccardo (5) in 1897 described a Xylaria from a termite comb in Java. Holtermann (6) in 1898 figured an agaric growing on a termite comb which he called the sclerotium of the fungus : in a brief note he says that he found it in Ceylon, Borneo, Java, and Singapore. In 1899 the same observer (6) published the most complete account that has yet been written on the subject, though it has not been found possible to confirm many of his statements. He named the agaric *Pluteus Rajap*, and figured what purports to be the comb. In the same year Hennings and Nyman re-described Holtermann's agaric as *Pholiota Janseana* (9), and later as *Flammula Janseana* (1) : they recorded in addition *Pluteus bogoriensis* (9) and *Pluteus Treubianus* (10) from termite nests. All these were found at Buitenzorg.

Hennings (12) in 1904 also described *Pluteus termitum* from termite nests in Brazil.

Döflein (13) in 1905 published an account of the termite nests from an entomological standpoint, and recorded feeding experiments with the fungi growing normally on the comb. His investigations were conducted in Ceylon.

In the present paper I have endeavoured to give an account of the various fungi and their relation to each other and to the termites. On several important points the necessary evidence is still incomplete, but although experiments are still in progress there appears to be no immediate prospect of supplying the missing links.

The Nest.

Termite nests, or hills, are common in all except the highest districts in Ceylon. They occur at Bandarawela (4,000 ft.), but not at Nuwara Eliya (6,200 ft.) or Hakgala (5,600 ft.). There is however a current impression that termites are gradually extending their range into these higher districts.

There is not in Ceylon, as far as is known, that variety of form and size which is found in Australia and Africa : all the hills are roughly conical, and the largest are only about six feet high. They are built of earth and grains of sand brought from the interior of the nest and cemented together by the secretions of the termites. The upper part of the hill is continued into one or more conical hollow structures which may be styled chimneys. The outline varies considerably : the hill may slope gradually to the top of the chimney, it may fork into several chimneys, or it may even have a solid apex. and bear chimneys at the side. (Pl. V.).

A section of the hill (Pl. VI.) shows that it consists of a large number of separate cavities or chambers roughly oval in shape, each 5–25 cms. in diameter and 5–15 cms. high. The outer wall of the hill may be 20 cms. thick in large nests. The floor of a chamber is more or less flat, and its arching walls are smooth. The chambers are united to one another by numerous passages, sometimes a centimetre in diameter, but generally only large enough to permit the entrance of two or three termites at once. Similar minute passages connect the chambers laterally with the chimney shafts which run down to the base of the nest. These shafts are at first vertical, but when they reach the area occupied by the chambers, *i.e.*, the body of the hill, they pursue a tortuous course between them : they do not open directly, or merge into, the chambers, but are connected with the latter by narrow horizontal side passages : they are circular or oval in cross section with a diameter of 4–9 cms. (generally about 6 cms.).

The chambers are not confined to the hill, but occupy also the ground beneath and round it ; in fact the part of the nest below ground is usually much more extensive than that above.

Each chamber is almost filled by a brown or grayish structure which resembles in form a coarse bath-sponge, and consists of a labyrinth of galleries opening into one another by perforations in all directions. It is built entirely of vegetable substances, and is covered with a fine fungus mycelium which bears innumerable minute white spheres. This is the termite "comb," which serves the insects as a fungus garden, a nursery, and a living room.

The size of the comb varies with that of the cavity: some are only about 5 cms. in diameter; others may be 20 cms. long, 15 cms. broad, and 10 cms. high. They lie quite free in the chamber, with a clear space 2–3 cms. broad between them and the roof and sides. The smaller ones have a flat base, are more or less hemispherical, and are equally perforated on the sides and top: the larger (? older) are irregularly oval in plan and concave below. The under portions of these larger combs are soft, and can easily be removed with a brush: the upper part is firmer and somewhat brittle. There may be more than one comb in a chamber: if so, they are piled up on one another like inverted basins.

The larger combs of *Termes redemanni*, Wasm. (Plate VII.) show in the upper part a series of gradually diminishing plates with few perforations. In their earlier stages they contain eggs, larvæ, workers, and soldiers: the eggs are always in the lowest passages, while the living insects swarm throughout the comb. Many combs, especially those which are producing agarics, contain workers and soldiers only. It is not however probable that any chambers are specially reserved as nurseries: each in its turn contains eggs and larvæ.

In nests of *Termes obscuriceps*, Wasm. (Plate VIII.), the larger combs show on the top a complex series of roofless galleries which give them a resemblance to pieces of "brain coral." The combs of this species contain larvæ even when they are producing agarics. In these respects only do they differ from the combs of *Termes redemanni*.

Somewhere in the centre of the nest and invariably (?) below ground level is a single thick-walled earthen cell just large enough to contain the enormously distended queen and her smaller consort. Its walls are perforated everywhere by minute holes through which the workers remove the eggs and bring food to the royal pair.

Holtermann (7) refers to the single combs as the "nests" : it seems preferable to retain the latter term for the whole collection of chambers and combs which are dependent on (usually) one queen : this is sometimes called a Termitarium. The queens found by Holtermann in the combs would be supplementary or reserve queens : these are not always present.

In obtaining material for the present paper the nests investigated were usually in the earlier stage, when all the comb chambers are below ground. Their presence is then indicated as a rule by three or four small chimneys, 10–20 cms. high, surrounded by the scattered earth which has been brought up in excavating the chambers. It has not been determined at what age or under what conditions the mound nest is constructed, or why the termites in many cases appear to be content with a subterranean nest only. It seems probable that the termite hill was originally only a convenient method of disposing of the earth excavated in making subterranean chambers. Even at the present day the hill is always built as a solid structure and the chambers are excavated in it as required. True ants bring up earth in the same way, but they do not cement it together, and it is consequently washed or blown away : an extension of the nest above ground does not therefore occur in their case.

The chimney shafts of a subterranean nest run down to a depth of 50 cms. in an average nest and below the level of the chambers arranged round them. These nests are not as compact as the mound nests : a large one in a bank occupied a space 10 metres long, 4–5 metres wide, and over 1 metre deep : in the centre of this area the chambers were close together, but sections nearer the outer limits exposed chambers sometimes thirty-six centimetres apart. In many cases there is no chimney : an area 12 metres long and 6 metres wide in the Royal Botanic Gardens, Peradeniya, which has provided a number of specimens of the agaric shows no external sign of a termite nest except a small hole at one corner. The chambers in this area appear to be arranged in a single layer, and are only indicated by the agaric which grows from them. When the chambers, as in this case, are hollowed out in fairly loose earth, the walls are of a clay-like consistency, and often break away in sections like pieces of newly moulded pottery.

Both combs and cavities vary in size and shape in different nests, but the variation is not greater than that in a single nest. Combs near the periphery of large mound nests may be only one-twentieth the size of those in the interior. The three combs figured (Pl. VII.) were taken from the same nest of *Termes redemanni* : that on the right is exceptional in having an oblong ground plan and almost perpendicular sides.

Holtermann (7) evidently investigated the underground nests, since he states that he was guided to them by the agaric. He names the termites *Termes fatalis*, König, and *Termes taphrobanes*, Walker, and says that he found the same species in Borneo and Java. Döflein (13), who appears to have studied chiefly the mound nests, assigns the occupants of the latter to *Termes obscuriceps*, Wasm. It was at first thought that the difference in the kind of nest, *i.e.*, entirely subterranean or mound forming, was due to difference in the species of termite, but this view has proved incorrect. The same species forms both kinds of nests, the first being merely a preliminary stage of the second. The species which occur more commonly and have been the subject of investigation at Peradeniya are *Termes redemanni*, Wasm., and *Termes obscuriceps*, Wasm. The fungi accompanying these two species are identical.

Since investigations into the relations between plants and animals invariably lead to digressions from the main subject, I need offer no apology for recording a few observations which do not really fall within the scope of this paper.

Döflein (13) in discussing the mound nests figures and describes a termite hill : he omits the underground portion and figures an upwardly-directed opening at the foot of the hill. On this he bases his explanation of the use of the chimneys. He says : "Was aber das Wichtigste ist, die ganze Bauart der Hügel sichert die ausgiebige ventilation seiner Innenräume : die Termitenhügel mit ihren Kaminen sind hygienische Bauten. Jene Aufbauten sind Luftschächte, welche Feuchtigkeit und Kohlensäure und andre schädliche Gase ableiten, wahrend durch die unteren Öffnungen des Baues frische Luft eindringen kann. Diese Ventilationskamine können aber jederzeit, je nach den Vergrösserungen des Stockes, nach klimatischen Schwankungen usw. verändert und angepasst werden. So erklärt sich die ganz verschieden grosse Anzahl von Kaminen, welche auf den Termitenhügeln sich erheben, und es wäre von Interesse eine vergleichende Untersuchung anzustellen, welche Grösse und Zahl der Kamine, Grösse des Hügels, Zahl der Pilzkammern, Klima und Örtlichkeit, Material des Baues, Volksreichtum und systematische Stellung der betreffenden Termitenart berücksichtigte."

While admitting that the chimneys may serve such a purpose, it may be pointed out that this ignores the difficulty of ventilating chambers which are not all connected in series. In order that a current of air passing up the chimney should draw out the air in the side chambers through the narrow side passages it would need to be so strong as to be readily observable ; but no draught has yet been detected.

But apart from this, the essential part of the arrangement, the lower opening, is never present except by accident, and then exists only for a short time. All openings at the base or sides of the hill are immediately blocked up by the inhabitants to prevent the raids of predatory (true) ants. Sections of nests are very common, especially on roadsides, but in no case is there any connection between the exposed chambers and the still-inhabited part. If the comb is left in an exposed chamber, a fresh wall is built in the position of the old one: if only a small fragment is left, this is enclosed by a new chamber built within the former one; but if all the comb is removed, the termites simply stop up the small passages which lead to an adjoining chamber. Döflein's explanation fails also in the numerous cases in which the nest is entirely underground.

There is no apparent relation between the number of chimneys and the size and situation of the nest, species of termite, &c. Underground nests of *Termes redemanni* consisting of only a dozen chambers may have three or four chimneys, while mound nests of the same species, six feet high with an extensive underground portion and in the same locality, have only one. In general, mound nests have the greatest number of chimneys in their earlier stages, when the number of their chambers is comparatively small and the hill is inconspicuous. This lends support to the view that the chimney is merely a permanent scaffold to guide the direction of further additions to the hill. Any ventilation which takes place is more probably due to an exhaustion effect produced by the wind blowing across the opening of the chimney.

There are no doubt narrow passages extending underground for long distances from the subterranean part of the nest, though these have not been actually traced. It is easily seen that this must be the case, since the narrow covered galleries of the termites appear on the surface of the ground or on the trunks of trees at long distances from the hill. Except when the winged termites leave the nest,* the insects do not use the chimneys as a means of exit, but advance underground until they reach dead wood or other suitable food, when

---

* See Appendix.

they emerge and attack it, building galleries if necessary. Even cow dung on the bare road is devoured by them in this way.

The construction of these galleries has given rise to the idea that the termites only work in the dark, but anyone who has witnessed the raids of the small red ant (*Plagiolepis longipes*, Jerdon) on a temporarily unprotected termite colony will agree that the primary object of the galleries is to afford protection from the attacks of other insects, &c. Danger of exposure to a dry atmosphere and consequent too rapid evaporation is quite a secondary matter in most districts of Ceylon. The construction of the nest is sometimes carried on in the full mid-day sunshine.

In order to ascertain the effect of this assumed ventilation, a series of temperature observations were made in a mound nest at Peradeniya. The nest chosen (Pl. V.) was in every respect suitable for the investigation. It was 2 metres high and 4½ metres in circumference at the base. A single chimney emerged at about 60 centimetres from the solid apex and rose almost to the level of the latter. This chimney was united to the nest by a solid buttress of clay : its opening, which was oblique and extended almost to the junction with the hill, faced north-east. This construction made it possible to take temperatures in the shadow of the chimney, while the solid buttress diminished the direct heating of the latter. The one chimney was the only possible means of ventilation, and any effect might be expected to be intensified by the size of the nest. The surrounding vegetation was cleared away so as to expose the nest to full sunshine from 7 A.M. till shortly after 6 P.M., practically from sunrise to sunset. Readings were taken at a depth of 20 cms., *i.e.*, just within the body of the nest, and with a maximum and minimum thermometer at a depth of 80 cms. The results are given in the following table, the temperatures being given in degrees Fahrenheit.

Date.	Time.	Temp. at depth 20 cms.	Shade Temp. Outside.	At depth of 80 cms.			R. B. G. Thermometers.		Notes.
				Actual Temp.	Max.	Min.	Max. in Shade.	Min. in Shade.	
March. 13th	6.15 P.M.	84·2	70·9	—	—	—	89·2	—	Heavy rain during afternoon
14th	7 A.M.	80	70·2	—	—	—	—	70·5	
	1 P.M.	84·6	84·6	—	—	—	89·4	—	
	6.15 P.M.	81·9	76·1	—	—	—	—	—	
15th	7 A.M.	80	69·3	—	—	—	—	70·2	
	1 P.M.	86·8	89·1	84	84	—	89·6	—	Maximum in the nest about 6 P.M.
	6.15 P.M.	83·2	79·6	86·5	86·5	—	—	—	
16th	7 A.M.	81·2	69·8	84·5	86·5	84·5	—	69·9	Minimum in the nest between 7 A.M. and 1 P.M.; maximum after 6.15 P.M.
	1 P.M.	89·6	91·4	84·5	84·5	83	92·4	—	
	6.15 P.M.	84·6	76·7	87	87	84·5	—	—	
17th	7 A.M.	81·4	70·2	84·5	87·5	84·5	—	70	Morning dull. Minimum in the nest at 1 P.M.; maximum after 6.15 P.M.
	1 P.M.	82·4	83·2	83·5	84·5	83·5	85·1	—	
	6.15 P.M.	82·4	76·7	84·5	84·5	83·5	—	—	
18th	7 A.M.	80	72·7	84·5	85·5	84·5	—	71·2	Minimum in nest at 1 P.M.: maximum at 6.15 P.M. Rain in afternoon.
	1 P.M.	86·4	86·8	84·5	84·5	84·5	89·8	—	
	6.15 P.M.	84·6	81·4	86·5	86·5	84·5	—	—	
19th	7 A.M.	81·7	69·8	84·5	86·5	84·5	—	70·1	Minimum in nest between 7 A.M. and 1 P.M.; maximum at 6.15 P.M. Rain in afternoon.
	1 P.M.	88·2	89·6	84·5	84·5	84	91·6	—	
	6.15 P.M.	83·9	75·2	86·5	86·5	84·5	—	—	
20th	7 A.M.	80	71·6	83·5	86·5	83·5	—	69·5	Minimum in nest between 7 A.M. and 1 P.M.; maximum (85·5) after 6.15 P.M.
	1 P.M.	84·6	88·2	83·5	84	83	89·2	—	
	6.15 P.M.	81·4	78·8	84·5	84·5	83·5	—	—	

Considering the temperatures near the mouth of the chimney we find that the daily variation is considerably less than the variation of the external temperature. The internal temperature never reaches the external shade maximum, and its minimum is about 10° F. above the external minimum. A sudden fall of temperature in the afternoon due to heavy rain causes no corresponding variation in the nest. An external daily variation of about 20° F. is accompanied by an internal variation of only 5–8° F. The internal temperature only falls about 2° F. during the night, except when the previous afternoon is cloudy, when it may fall 4° F. The results at the depth of 80 centimetres show only a daily variation of 2–4° F. The minimum is about 14° F. above the external minimum, and is sometimes not reached till mid-day if the morning is dull. The maximum is several degrees below the external maximum, and is not reached till about sunset or later. This remarkable lag of the internal maximum and minimum seems to indicate a gain and loss of heat by direct radiation only.

The maxima and minima in the last two columns are not strictly comparable with the other readings as they were not taken in the immediate neighbourhood of the nest : they are included merely to give a general idea of the daily range of temperature at Peradeniya during the hottest and driest month of the year.

An interesting point with regard to the chimneys was raised by observations on constructions made by true ants. One large species, *Myrmecaria brunnea*, Saunders, brings up from its nest underground grains of sand and particles of earth through a small hole about a centimetre in diameter : it is generally observed on footpaths. These particles are at first arranged on one side of the hole in a crescentic mound about 3 centimetres high which curves round and slopes away to nothing on either side of the hole, the distance between the vanishing horns of the crescent being about 12 centimetres. The ants run up the slope from the hole with their burden and drop it over the ridge down the steeper outer side. The most striking feature of this is that when the hole is situated in the middle of a path, away from any bank, the ridge is always on the windward side of the hole. A smaller ridge of the same shape and in the same position is constructed by *Phidole* (? *nietneri*, Emery). If undisturbed *Myrmecaria* eventually constructs a complete funnel round the hole.

As the rim of the termite chimney is never horizontal, several were examined in order to determine whether there was any constant higher side, but it was very evident that no such relation could be established. Some of the chimneys are closed at the top and have an opening just below at the side: in these cases also there was no constant orientation of the openings even in the chimneys of a single nest. Of three chimneys on one nest, one was open at the top, another on the side facing south-west, and another at the side facing north-east.

The mode of construction pursued by the Ceylon termites (*Termes redemanni* and *Termes obscuriceps*) appears to differ from that which has been described in other countries. The workers bring up from the interior of the nest particles of soil and sand which have been covered with saliva and place them on the new work, where they adhere even if put on at the side. In some cases the workers have been observed to move their heads a few times over the joint and cement the particles more firmly by a fresh secretion of saliva. Froggatt (14) in describing the termites of Australia says: "The workers return with grains of earth which they place on the fracture, then turn round (and) void a drop of what looks like liquid mud." Dudley and Beaumont (15) agree with this statement, but I have never seen this process in Ceylon. The material dries to a firm stone-like mass, but if evaporation is prevented it remains soft. This property of drying like cement has no doubt prompted the use of earth from termite nests for top-dressing lawn tennis courts.

Earth from a newly built addition to a nest, taken when the termites were building, lost 26·5 per cent. of its weight in drying over sulphuric acid. This was in the dry season. In many cases more moisture than this is present, *e.g.*, in a wall newly built in an exposed underground chamber.

The process of building varies, apparently with the nature of the work to be constructed. In the early stages of mound building, when the work is carried on more or less on the level, small pillars are built about a centimetre high and the same distance apart. A partial roof is then constructed from pillar to pillar and the work commences again on this new foundation. The new structure bears at first an exact resemblance to the comb, which is probably built in the same way. When work ceases a continuous roof is built, and the spaces between the pillars are subsequently filled in so as to make a solid mass of earth. In making new chambers in the hill this mass is re-excavated.

In making additions to a hill the termites emerge from a hole purposely made in the side and proceed to build small overlapping dome-shaped cells. These cells are not complete, and the arrangement is not at first sight very obvious: they are afterwards filled up with earth. In repairing a wall or building a chimney the work is often solid from the beginning. When combs are left exposed they are usually enclosed, at least temporarily, by a close-fitting layer of earth, though cases have been observed where the new covering was supported by pillars resting on the comb.

The combs exposed in the nest figured on Pl. VI. were all enclosed within three hours. The covering was then only a thin layer resting on the combs. This was afterwards strengthened by the addition of fresh material externally, and the inner layers of the new walls were removed, so that the combs again lay free in the chambers. In some cases the temporary wall was abandoned and a new one constructed level with the general surface of the section.

The first care of the termites was to protect the combs and larvæ from the attacks of red ants as quickly as possible: the restoration of the chambers to their normal condition was deferred.

A similar secretion to that emitted by the workers is poured out by the soldiers when they bite. Döflein (13) says it causes a brown stain which is "schwer abwaschbare." It really affects the skin to some depth, and does not disappear for several days: I have known the stains to persist for eight days. Handling the comb is one of the best ways of getting rid of the soldiers. They attach themselves firmly to the skin, launch themselves free from their previous support, and remain at right angles to the fingers, waving their legs vigorously in the air and pouring out their sticky saliva. They are so firmly fixed by their mandibles that pulling them off usually separates the head from the body. Their bite is scarcely felt.

As the termites, at least in some stages, are dependent upon the fungi growing on the comb, it was thought that the destruction of these by the use of copper sulphate might involve the death of the insects. As a preliminary experiment 18 gallons of water were poured quickly into a nest of *Termes redemanni*. This disappeared without filling the entrance, as had been expected. Another more recent nest was then selected and water was poured down for two hours through a pipe delivering 15 gallons per minute. This appearing equally fruitless, a small new nest was tried. Unfortunately it was only possible to run in water at the rate of 2 gallons per minute. The water rose in the chimney to a depth of 3 inches only, and maintained that level the whole time. After two hours the nest was opened. The earth round the lowest chambers was damp, but no water had entered any of them. It is evident that rain entering the chimney will have no effect on the combs, and that the fungi cannot be destroyed by pouring in fungicides. In no case were the termites disturbed by this treatment.

The Comb and Spheres.

As previously stated, the comb resembles a coarse bath sponge. The colour of the actual comb-substance varies from yellow-brown to dark brown, but it usually appears gray or glaucous owing to its covering of fungus hyphæ. In combs which contain only workers and soldiers this covering is universal, but when larvæ are also present the upper layers are generally dark brown and show very little fungus growth. The difference in colour is well marked in the combs figured. These darker layers are firmer and more brittle than those covered with fungi, and it seems probable that they are added to the comb as it disintegrates below.

The surface of the comb is rough with minute rounded hillocks which suggest that it is composed of closely packed balls. This is verified by a cross section : the individual balls, about ·75 mm. diameter, can be clearly distinguished without the aid of a microscope since their outer layers are darker than the interior. These balls consist entirely of finely divided vegetable substances : irregular pieces of ringed and pitted vessels up to 250 μ long, sclerenchymatous cells, tracheides, can be distinguished, together with the hyphæ and spores of *Helminthosporium*, *Diplodia*, &c., embedded in a ground substance from which all structure has disappeared. The wood elements still give their characteristic reaction with phloroglucin. The same substances are found in the stomach and intestine of the workers and soldiers, and this, together with the regular arrangement of all the material in small balls, makes it quite clear that the comb is built up exclusively of the excreta of the termites, cemented together in the same way as the walls of the hill.

Holtermann (6) referred to the combs as the sclerotia of an agaric, and the translator of Döflein's paper unconsciously perpetuates the error by calling them "Termite truffles." It must be emphasized that the actual comb is not of fungus origin.

The mycelium on the comb is composed of interwoven hyphæ, 3–4 μ diameter, often united into strands 5–15 μ

broad. The hyphæ are markedly septate, the septa being sometimes only 5 μ apart, and often form oval expansions. From these creeping hyphæ arise upright branches of the same diameter, 20–120 μ long: they do not however develop any different structure individually, but unite into small groups to produce the "conidial" formation which has been noted by all investigators into the habits of termites (Pl. XII. B).

These "conidial" formations are seen all over the comb as small white stalked, or almost sessile spheres up to 1·25 mm. diameter. Few or none are found on the dark brown outer surface when the comb contains larvæ, but elsewhere they may be closely crowded as many as 120 to the square centimetre. In the interior of the comb they are more abundant on the roof and sides of a passage than on the floor. In some cases comparatively extensive tracts are almost destitute of spheres, though the hyphæ are present, and in these areas there often occur long narrow bare patches from which the hyphæ also have been eaten away. When viewed as opaque objects under a low magnification they appear to be a cluster of spherical conidia on a short stalk. They are largest in combs which do not contain larvæ: I have not been able to confirm Holtermann's observation that they vary in size according to the size of the comb and the size of the termite inhabiting it. Combs vary enormously in size in a single nest. The white spheres arise directly from the superficial mycelium by the combination of several of the upright branches into a loosely-built stalk in which the individual hyphæ can be clearly distinguished. The stalk expands upwards, and at the height of about a millimetre the hyphæ separate and bifurcate repeatedly, each branch ultimately terminating in one or two oval expansions (which may be 60 × 20 μ) on which "conidia" are produced. The head, which was at first oval, is now almost exactly spherical, and the stalk is in many cases hidden by the reflexed lower branches (Pl. XVII. B).

The conidia-like cells are of two kinds: on the exterior hyphæ only spherical cells, 20 μ diameter, are formed, while in the interior the majority are oval or cylindric, 8–20 × 5 μ. In the latter case the inflated apical cell of the hypha usually bears at first two primary "conidia": these elongate and divide transversely, the process being continued indefinitely by the terminal cell. Meanwhile new cells arise by budding immediately below each septum and divide in the same way, so that a branched system of united "conidia" is finally produced. Steps of this process are shown in fig. 9.

On the other hand, the spherical "conidia" are generally arranged in chains of three or four which increase by the apical budding of the terminal cell: the production of the side buds appears to be less prevalent than in the oval form (fig. 3).

The two branches of one hypha may give rise to spherical and oval cells respectively (fig. 1), or a branch which is producing spherical cells may bud off side branches which form oval cells only. Hyphæ in the middle of the sphere often produce a succession of oval swellings before forming "conidia" (fig. 4): these are not separated by cross walls, and resemble the swellings on the creeping mycelium.

The sphere is easily teased out into its component branches, or by slight pressure on the cover glass these may be caused to radiate and thus make clear their internal arrangement. The extremities only of these branches are shown in the figures, the dichotomous branching of the original stalk hyphæ being omitted. The cells are filled with protoplasm, vacuoles not being observable. Some of the youngest spheres appear to consist of oval cells only.

If a piece of comb is placed in a damp chamber the spheres become semi-transparent and acquire a halo-like fringe of short radiating hyphæ. In the course of twenty-four hours they turn yellow, shrink to about half their former size, and decay. Occasionally some growth is obtained. In one experiment all spheres above ·25 mm. diameter were removed: on the following day some of the small ones left had increased to ·4-5 mm. diameter, but by the next day all had become yellow and commenced to decay. Variations of moisture and light apparently make no difference : the result is always the same, and it has not been found possible to develop the spheres further.

On the other hand, when a sphere is suspended in a hanging drop of water, hyphæ grow out from it in all directions and convert it into a tangled mass in which the original regular arrangement of the conidial branches is quite obscured. A better growth is obtained by using an extract of the comb : if the latter is soaked in water at the ordinary temperature, a deep brown, feebly acid liquid is obtained, which after sterilization by boiling is an excellent medium for the cultivation of the comb fungi. The addition of a small quantity of tartaric acid hinders the development of bacteria which otherwise stop all growth in three or four days.

If the sphere is separated into its component cells and these are suspended in a hanging drop, it is found that growth arises exclusively from the oval conidia ; and a careful examination of an uninjured sphere shows that if the conidia are not separated only the terminal cell of a chain produces a hypha.

Growth from the separated conidia is far more rapid in comb extract than in water : the number of cells formed is about the same, but they are shorter in the latter case and the resulting hyphæ appear more moniliform. Figures 7 and 8 show four days' growth in water and comb extract respectively. At the end of twenty-four hours the original cell (marked by a cross in the figures) has produced a hypha at both ends, and effected a total growth of sometimes 500 μ : these hyphæ frequently emerge obliquely and curve into line with the spore. The growing apex is somewhat inflated. In many cases the original spore gives rise later to one or two additional hyphæ on either side. Branching arises by side buds immediately below the septa, as in the sphere, but through the further growth of the hypha the branches are ultimately at right angles to it.

The conidia germinate readily in comb extract agar, with or without dextrose. The best results were obtained by using thin films of this on cover glasses, and inverting them over damp chambers. Growth at first was identical with that in the hanging drops of comb extract. At the end of a fortnight several hyphæ formed terminal pear-shaped swellings, 18 × 9 μ, rather like the conidia of *Phytophthora*, but not cut off by a cross wall immediately below them. Instead of forming conidia, growth continued as a hypha from the apex of the swelling and left an intercalated oval cell. During the following month this frequently occurred. The terminal swellings were oval, pear-shaped, or almost spherical, and two or three were often produced in succession, but the hypha invariably reverted to its original mode of growth after a short distance. Neither on ærial branches or creeping mycelium was it possible to reproduce the "conidia" of the sphere. Cultures on sterilized comb were also tried but were equally fruitless.

The spherical "conidia" of the sphere do not germinate. No growth has been obtained from these on any medium, fluid or solid. This negatives the idea that the oval conidia are identical with the spherical form, but modified by their crowded growth in the interior of the sphere.

There is not in the actual comb substance that abundance of mycelium which might be expected to exist judging from the luxuriance of the external growth. At a depth of 200 μ (the wall is 1–2 mm. thick and strengthened at the angles) hyphæ are scarce. Near the surface are hyphæ about 3 μ in diameter which emerge to form the superficial mycelium ; and deeper, but apparently continuous with the former are very fine hyphæ, 1·5–2 μ diameter. Sections of the comb do not fall to pieces, but may be disintegrated by dilute potash.

It is improbable that this small quantity of mycelium acts as a binding material, as suggested by Holtermann (7). The firmest combs are those which have hardly any fungus growth, and their fragility increases with the increase of the fungus : indeed, it is often impossible to remove from its cavity (except in small fragments) a comb which has produced an agaric. This deterioration of the comb substance is probably caused by the growth of the fungus, and sets in after some definite period, and observations tend to show that when this condition is reached the whole structure is removed, probably re-eaten, by the termites.

Döflein (13) suggests that the fungus on the comb is one which is common on dead wood in the neighbourhood of the nest, and is made use of unwittingly by the termites. He supposes that the chewed wood is partially sterilized by the treatment it undergoes, and converted into a medium suitable only for the growth of this particular fungus, so that practically a pure culture is assured : the partial sterilization, it is suggested, destroys the spores of all fungi except the one in question.

But during an exhaustive search for micro-fungi at Peradeniya, involving the examination of a large quantity of dead wood and leaves, I have not met with any fungus resembling that on the termite comb, though the general resemblance of the latter to a sporangium would undoubtedly have led to its further examination : if such occurs it is certainly not common. It is also scarcely probable that thin-walled spores should be uninjured by their passage through the alimentary canal of the termites seeing that the thick-walled spores, *e.g.*, of Diplodia, are completely destroyed. Diplodias are ubiquitous in the Tropics, but they do not grow on the comb, either before or after removal from the nest, though spores may be found in its substance. The question whether the fungus cultivation on the comb is pure will be dealt with later. That the termites "understand" the value of the fungus seems to be indicated by the re-enclosure of small pieces of comb exposed in a broken chamber even when they contain neither eggs nor larvæ.

This conidial formation with its mycelium is all that occurs in a normal comb. The above account differs so largely from the description given by Holtermann (7) of the fungi of the same nests that it was considered necessary after the receipt of his paper to make a further examination of fresh material.

He says that the erect branches of the creeping mycelium end in swollen cells which may be 16–32 μ thick, and that here and there are found small groups of hyphæ inclined to one another, with the same swollen tips, but that they do not occur in all nests. In these he sees a resemblance to the "Kohlrabi heads" of Möller.

I have not found anything of this description on fresh combs. If they are kept for a few days under a bell glass, such structures do arise as will be described later, but they do not occur on the comb *in situ*. Another possible explanation, remembering that Holtermann was guided to the combs by the agaric, is that these collections of hyphæ were aborted agarics. These nearly always occur on combs producing agarics and would to some extent answer the description given; they are not otherwise referred to by Holtermann.

I am also unable to confirm Holtermann's description of the sphere. He recognizes the branching at the top of the stalk, but says "the outer cells have a less active growth than the inner, and after a short time become completely passive: they constitute thereby a cover which later appears as a kind of peridium. The limits of this cover are exactly indicated by the drying of the outer cells. There begins in the interior an active development of conidia, in which the mycelium divides into short oval cells. The destruction of the hyphæ is almost complete, and it needs only a slight pressure on the cover glass to split the dried peridium and liberate the thousands of conidia."

I have not been able to find or develop spheres with the peridium described, or any in which the conidia were free. The sphere consists of branches radiating from a common stalk, some of which produce spherical conidia, and others oval conidia. In alcohol material there is sometimes a brown amorphous deposit (derived from the comb) overlying parts of the sphere, but there is no sign of drying in the nest.

It is remarkable that one never finds on the comb a free conidium or a stalk from which the conidia have fallen. This however is in agreement with the behaviour of homologous structures connected with other agarics below. Nor is there ever an injured sphere. If they are eaten by the termites—and there is hardly any doubt of this— they must be consumed at one bite. From this standpoint it is scarcely probable that the termites would leave a structure which Döflein says is just a mouthful until it formed a sack of loose spores.

Döflein (13) relates that he found great difficulty in wetting the comb, and therefore supposes that the termite secretion waterproofs both the comb and the nest. When a comb is covered with hyphæ water naturally runs off it in drops, but I have never found any difficulty in moistening the actual comb substance or the earth of the nest.

The Agaric.

An agaric which grew from termite nests was collected by Gardner at Peradeniya in 1844. This species is the chief edible fungus of Ceylon, and on that account there is some difficulty in procuring perfect specimens, since the native who gathers them for food does not trouble to dig out the stalk, and unfortunately he does not overlook many.

Gardner says that they grow sometimes from a depth of 4 feet, and Holtermann gives a depth of 1 metre: the majority of my specimens have been from combs 25 cms. or less below the surface. It generally appears within a few feet of the low chimneys of an underground nest of *Termes redemanni* or *Termes obscuriceps*, but it is often found in places where there is no outward indication of a termite nest. As Holtermann (7) states, the agaric indicates the nest, or rather that comb of it which has arrived at the stage at which agarics are produced.

I have not yet found it connected with a mound nest, though the termites and their other fungi are identical with those entirely underground. It may be that the latter are sometimes damper or that the agaric is unable to pierce the thick, firmly cemented, outer wall of a hill. There is no reason however why it should not develop from the combs of the subterranean base.

Though easily recognizable, it varies greatly in size, form, and colour, and hence it is not surprising that it has received at least six names, especially as these have with one exception been bestowed on dried specimens. Gardner sent two forms to Berkeley, both apparently immature, for Berkeley named one *Lentinus cartilagineus* and the other *Armillaria eurhiza*. Twenty-five years later, Thwaites sent the first form again to Berkeley: this time it was named *Collybia sparsibarbis*. It is really a pink-spored agaric, as Holtermann (7) decided when he named it *Pluteus Rajap*, the specific name being that by which it is known to the Malays.

In its most frequently occurring form it is at first sight a *Pluteus* (Pl. XI. and XII. A). The pileus is at first conico-campanulate, then almost plane with a strongly developed umbo, smooth or radially rugose, glabrous, viscid when moist, blackish brown at the umbo becoming gray towards the edge, sometimes wholly livid brown, sometimes gray. The pileus of smaller specimens may be wholly pale brown when dry. The margin is very irregular, and the pileus is usually split in several places almost to the centre. The outline may be circular, oval, or irregularly lobed, the greatest irregularity occurring in the wet seasons. The white flesh is differentiated from the stalk and is very thin towards the margin. The diameter varies from 6 to 15 centimetres. The gills are free, equal, crowded, about 5 mm. broad, at first white, then pink from the spores, and finally pinkish yellow in decay.

The solid stalk is on the average about 30 centimetres long and 1–2 centimetres in diameter. From one-third to one-fifth of this is above ground. Of the part below ground, the lower half, or sometimes the whole, is black. The upper white portion is equal, often twisted, fibrous, slightly striate longitudinally, glabrous or with a few scattered fibrils, especially at the transition from white to black, with sometimes a bulbous swelling at this point. The black rooting base is horny externally and tapers to a diameter of about 2 millimetres. When it is found in contact with the comb it terminates in a small brown solid campanulate swelling (fig. 14), but one often finds on digging down to the comb chamber that the termites have eaten off the connection with the comb, and the stalk terminates in a slender black thread at the wall of the cavity.

The spores are pink, elliptic with a sublateral apiculus, 8-10 × 4–5 μ : immature spores may be sub-globose, and 6–7 μ diameter. The basidia are 28–33 μ long, 8 μ diameter near the apex, narrowing to 4–5 μ at the base, clavate; the cystidia are pear-shaped, 27–40 μ long, 14–19 μ diameter at the widest part, and 6–7 μ diameter at the base.

The above is the form described by Berkeley, first as *Lentinus cartilagineus*, and later as *Collybia sparsibarbis*.

The first indication of the agaric on the comb is a small white patch, from 1 to 3 millimetres in diameter, composed of erect, rather thick-walled hyphæ which have a diameter of 4–5 μ when they emerge from the comb but increase rapidly to 6–8 μ and terminate in clavate heads 10–12 μ in diameter. As growth proceeds, other hyphæ are added exteriorly and a conical mound is formed. The hyphæ in the centre arise perpendicularly from the comb, but some of the oblique exterior ones appear to be continuous with the superficial sphere-producing mycelium.

The developing agaric grows in all cases to a height of 1–2 centimetres. It is then a brownish-white, somewhat conical, tomentose column, 3–5 mm. in diameter. The exteriorly-pointing hyphæ end for the most part in spherical spore-like heads, resembling the spherical "conidia" of the "sphere." The interior hyphæ tend to separate into short cells, and the column therefore breaks readily at any point. The apex becomes black.

Examples of this stage may be found in abundance on digging down to combs which have produced agarics. In some cases as many as fifty have been counted on one comb. But in no case does more than one *Pluteus* develop from a comb. The remainder are arrested at this stage and will not grow further. The exterior of these aborted agarics becomes feebly cartilaginous and the interior hyphæ form thick-walled cells. In old specimens the walls of the original cells are thickened until the cavity is almost obliterated, and a section from such a specimen separates readily into its component cells. These are 40–100 μ long and very irregular in shape: H connections and branched cells are common (fig. 16) and many of the narrower cells are U-shaped. The cell wall is faintly laminated and in many cases the thickening takes an annular form (fig. 17) : indeed, a tendency to the production of this annular thickening may be traced in nearly all the larger cells, but even in the best examples the rings are not sharply defined like those figured for *Battarrea*, but are rounded off on either side. These sclerenchymatous cells do not stain with phloroglucin.

Several experiments have been tried with these aborted agarics to see whether under any conditions they would re-commence growth or produce other structures, but in all cases they merely decayed. No growth resulted from the separate cells when these were suspended in hanging drops of water or comb extract.

These aborted agarics constitute Thwaites' specimen No. 176, but they do not, as stated by Berkeley, develop on combs exposed to the light. There is no apparent reason why they should not develop further in the nest: as a rule, they do not reach the wall of the chamber, and the majority are larger than the one from which the agaric has developed. There is no trace of a pileus in these aborted agarics, but that they are really such is shown by the similar structure at the base of the *Pluteus* stalk, in which the thick-walled cells are even better developed. It seems probable that these in their earlier stage were the collections of concurrent hyphæ noted by Holtermann and that the sclerenchymatous cells of the agaric led him to remark that the mechanical elements (in the comb) occur sometimes in discs as if they had been arranged by an expert anatomist.

Considering the depth from which these agarics arise, and the number which commence development on a single comb, it might be thought an easy matter to obtain a series of stages showing all the different periods of growth. This however is not possible. It is extremely rare to find a specimen which has only partly penetrated the soil. One appears above ground and all the rest remain aborted in the chamber, and there is no way of ascertaining that a comb has reached the agaric-producing stage until this solitary mature agaric is fully expanded. The surrounding combs may then contain eggs and larvæ, and show no trace of an agaric. Digging up nests at random has never yielded any results as far as the agaric is concerned.

In the mound of hyphæ which grows on and produces an agaric, the apex is continued into the soil as a narrow black thread with a white tip. For a distance of one or two centimetres it is only one or two millimetres in diameter, but afterwards it increases rapidly to the thickness of the agaric stalk. Unfortunately it has not been possible to obtain stages which would illustrate the development of the pileus: no immature specimen has yet been found between this thin black thread and the stage in which the white portion of the stalk is visible. The youngest available specimen of the latter stage has a black stalk about 18 centimetres long, followed by about 4 centimetres of white stalk which tapers to a point capped by a small pileus 1 centimetre in diameter. The pileus fits closely over the apex of the stalk, but the margin is free. In most cases, however, there are a few broken fibrils at the point where the stalk becomes white, and in favourable instances a distinct collar, partly cartilaginous and partly in separate fibres, is present. This, and further evidence which will be adduced later, supports Berkeley's statement that the stalk is covered with a cartilaginous stratum which is continuous with the universal veil, though it may be doubted whether his specimen warranted the assumption. The black layer of the stalk is not as amorphous as the outer layer of the pileus.

De Bary (16) states that in the species of agaric he examined the increase in length and breadth of the stipe was almost exclusively due to the extension of the original cells. In the present species the length of the stipe may be more than a metre, while the breadth changes from 2 millimetres to 1 or 2 centimetres and the upper portion is more solid than the lower. It is very evident that the number of cells in the cross section increases enormously. The internal hyphæ are of two kinds, the thicker about 30 μ in diameter and the remainder about 5 μ. The latter arise as side branches immediately below the septa of the larger hyphæ exactly as the medullary hyphæ are formed in the rhizomorphs of *Armillaria mellea*, and, as in the latter, they branch repeatedly. There is not, however, in the present case any distinct medullary tissue. In this way the number of cells in the cross section constantly increases upwards, branching internal hyphæ being produced even near the top of the stalk. As the agaric ripens, the black portion of the stalk shrinks considerably, as is shown by its longitudinal furrows.

At irregular periods, but probably only in the wet season, apparently another agaric develops from the termite comb. It emerges as a gray, oval structure whose outer wall is continuous with the white stalk. Several may develop from one comb, and at the same time many immature specimens, all capable of further growth, may be present within the comb chamber, though, as in the case of the *Pluteus*, none are found partly through the overlying soil.

As the stalk of this second form elongates, the outer covering splits away from it and curves slightly outwards, and when the pileus expands a fresh rupture occurs at its margin so that part of this universal veil is finally left as a ring on the stem. On tracing the stalk down to the comb it is found to be pale brown below and of the same diameter throughout, except at the base, where it narrows to about half the width (fig. 15). The lower portion of the broad stalk is of a loose texture internally, and its shape is only preserved by a thick cartilaginous wall: the smaller base is on the contrary solid. The upper white portion of the stem usually bears horny squamules to a varying extent.

Pll. IX. and X. show this form in various stages. The stalk of the five egg-shaped agarics which appear above ground in Plate IX. are at the back of the cavity and are somewhat curved: the structures in front are developing agarics which have just reached the roof. Plate X. shows various stages in the formation of the ring, and numerous developing agarics.

The development of this form agrees with that of the apparent *Pluteus* in the formation of the first mound of hyphæ, but when the mound is about 5 mm. high, the exteriorly-pointing hyphæ develop twisted ends which intertwine and fuse together, ultimately forming a thick cartilaginous coat in which the outlines of the individual hyphæ are obliterated. When dry this coat is seen to be slightly hairy.

On the completion of this process the agaric is a brown cylindrical column slightly inflated upwards (fig. 18). If it is broken off, the outer cartilaginous coat separates from the comb with an abrupt edge and the base of the column is seen to contain some of the comb substance ; but if a section is made through comb and agaric, it is found that the outer coat is continuous with the superficial mycelium, which has also become feebly cartilaginous, at least near the agaric, and where the section crosses a perforation in the comb substance this thinner coat continues to the under surface as a sheet of interwoven hyphæ (figs. 19, 20).

The whole of the internal tissue is at first loose and brownish, but becomes whiter and more compact towards the apex when the column has attained the height of about 1 centimetre (fig. 20): at the same time a slight constriction appears about half way up. These features increase until the column is about 2·5 centimetres high, when the formation of the gills begins at the lower edge of the compact white tissue. An increase in diameter then takes place a short distance above the base, leaving the well defined narrow foundation observed in the mature agaric, and with the extension of the upper constriction there results the flask-shaped structures of figs. 21–23. When the roof of the chamber is reached, the pressure of the developing agaric distorts the head to some extent.

Before the agaric has appeared above ground, the universal veil splits at some distance below the level of the margin of the pileus, and the oval upper structure is carried up above ground by the elongating stem. There is no collar at the point of separation, but the subsequently developed portion of the stalk is white and lacks the cartilaginous covering: it frequently bears horny scales which are obviously part of the universal veil.

When the agaric first appears above the ground, the covering of the pileus is apparently continuous with the stem, but partial drying causes an outward curl of the lower edge which shows that this at least is free: fig. 11 is a section through an unexpanded agaric: on one side the universal veil is apparently continuous with the stem, but on the other it has a free lower edge. When the pileus expands, a free upper edge is also left.

The ring thus formed differs widely from the usual agaric ring; it is a thin horny structure with irregularly laciniate edges, usually encircling the stem obliquely and united to it by a narrow band in the middle (figs. 10–13).

The scales on the stem are of the same horny texture and are evidently part of the same layer (fig. 10). They are composed of modified hyphæ as in the outer layer of the young agaric, but the amorphous layer is thinner and the individual hyphæ (partly modified) beneath it are long and straight instead of being crooked and intertwined. The greater part of the ring is derived from the covering of the stalk: part also comes from the covering of the pileus, and these two parts are either joined to the stem by a projecting collar or are continuous with it where they merge into one another.

The irregularity of the ring will be seen from the figures. In some instances the outer layer divides into fibres so that the expanding agaric appears to have an arachnoid veil. In one case, where the agarics grew through a gravelled path, fragments of the pileus and gills remained attached to the ring.

These two agarics are apparently quite distinct, and it is therefore not surprising that the second was placed by Berkeley in another genus under the name *Armillaria eurhiza.* But except for the ring there is nothing to distinguish them in the parts which appear above ground : they are identical in size, shape, structure of pileus and gills, size and colour of spores, &c. Both too have the curious base of sclerenchymatous cells and a cartilaginous universal veil. The colour of the pileus is usually paler in the *Armillaria* form, but this is easily explainable. It is quite clear that the two are merely forms of the same species. Under certain conditions, the original mound of hyphæ acquires a cartilaginous coat when it is only about 5 mm. high, and there then results the *Armillaria* form in which the universal veil clearly extends as a thick covering down to the comb. More generally, however, the universal veil is not developed over the part in the comb chamber : the mound of hyphæ produces at its apex a thin black cord which penetrates the soil, and the development of the pileus takes places in a cartilaginous covering in the earth above the chamber ; the mound of hyphæ at the base lacks this covering or shows only a slight tendency towards the production of it. The presence or absence of a ring is a more or less accidental phenomenon brought about merely by a difference in the point of dehiscence of the universal veil, and we find accordingly that the *Pluteus* and *Armillaria* forms are linked by specimens possessing the ring of the latter and the black rooting base of the former.

It is noteworthy that while only one black-stalked agaric develops out of the large number of mounds of hyphæ which originate on the comb, several examples of the other form may appear above ground from one comb, and all, or nearly all, the immature examples in the chamber are apparently capable of further growth. The conditions which result in the production of the *Armillaria* form are therefore the more favourable to the growth of agarics.

The colour of the pileus depends on the attenuation of the universal veil. In *Pluteus*-like examples with a small pileus, on which this layer is relatively thick, the colour is often entirely pale brown or tan when dry, becoming livid brown when wetted; and the deeper tint of the umbo in the usual form is due to the greater thickness of the cartilaginous coat at that point. In specimens which appear in the drier periods the covering is often so thin that the pileus seems almost silky and some are pure white, while in the wet season pilei with a thick, radially-corrugated upper surface are common. Ringed examples on the other hand have only a thin covering and are usually pale gray like the outer half of the ordinary form. The structure of the outer layer of the pileus is identical with that of the ring. If a smooth pileus be allowed to decay under a bell jar, the cartilaginous layer absorbs moisture and swells, wrinkling and "frilling" at the same time like a photographic plate.

The combs which have arrived at the agaric-producing stage are soft, have a strong fungus smell, and require very careful handling to avoid their falling to pieces. In nests of *Termes redemanni*, combs in this stage contain neither larvæ nor eggs, but only a few workers and soldiers. In the case of *Termes obscuriceps*, they usually contain a few larvæ also, but in the observed instances of this the lower layers only of the comb were decayed and the agarics developed from these layers.

In no case has it been found possible to develop further specimens of the agaric from combs which have produced them in the nest. All treatment invariably results in a copious growth of the structures dealt with in the next section. In the same way agarics cannot be made to grow from normal combs under any conditions.

The growth of agarics in the nest is a direct consequence of the condition of the comb, and their appearance above ground depends partly on the humidity of the soil and partly on the termites themselves. There is no doubt that a large number are aborted in all cases : this is not from inability to penetrate the ground, for one from each comb pushes through, and the aborted specimens do not reach the roof of the cavity. A comparatively slight rainfall is sufficient to favour their growth, in striking contrast to the majority of tropical agarics which only respond to a prolonged soaking of the soil. It is remarkable that the termite agaric appears almost throughout the year, even at times when no other species can be found. It is therefore to some extent independent of the conditions which control the growth of agarics in general.

The following data relate to a few of its occurrences. It must be remembered that several days' continuous rain is necessary to produce even a few specimens of other agarics. In the specially dry months, January and February, it has not been observed. It has been found in March and August, which have generally a small rainfall. No exhaustive search, however, has been made, and therefore no conclusions can be drawn from the absence of records for particular months. 1905 was an exceptionally dry year. In June–July, 1906, the *Pluteus* form was abundant at Peradeniya.

Peradeniya, May	23,	1905 ..	Rainfall, 22nd, 1·85 in. 17th–21st, 2·28 in.
Peradeniya, June	16,	1905 ..	Rainfall, 14th–15th, nil ; 1st–14th, ·95 in.
Peradeniya, July	6,	1905 ..	Rainfall, 2nd–6th, nil ; 1st, ·02 in.; June, 15·26 in.
Peradeniya, Sept.	18–19,	1905 ..	Rainfall, 10th–17th, 1·17 in.; 1st–10th, 4·94 in.
Peradeniya, Oct.	12,	1905 ..	Rainfall, 11th, 4·5 in.; 1st–11th, 7·98 in.
Peradeniya, Oct.	29,	1905 ..	Rainfall, 19th–29th, nil ; 1st–18th, 15·93 in.

Peradeniya, Nov.	26,	1905	.. Rainfall, 25th, ·01 in.; 1st–25th, 4·8 in.
Peradeniya, Dec.	7–8,	1905	.. Rainfall, 6th, ·29 in.; 1st–5th, 1·83 in.; Nov., 5·05 in.
Matale,	March 6,	1906	.. Rainfall, Feb. 27th, ·46 in.; Feb. 1st–26th, nil.
Peradeniya,	March 31,	1906	.. Rainfall, 27th, ·06 in. 1st–26th, 3·23 in.
Peradeniya,	May 30,	1906	.. Rainfall, 20th–30th, ·24 in. total, May, 3·29 in.
Peradeniya,	June–July,	1906	.. Rainfall, June, 6·13 in.; July, 11·23 in.

Peradeniya is in the wet zone (Central Province) at an elevation of 1,560 feet; Matale is in the wet zone (Central Province) at 1,200 feet. The agaric has also been found at Badulla in the Eastern wet zone (Uva Province) at 2,220 feet, at Telulla (Uva Province) below 100 feet, at Undugoda (Sabaragamuwa) at 800 feet, and at Trincomalee (Eastern Province) at sea level, while Mr. E. E. Green informs me that it is common in Pundalu-oya at 4,000–4,300 feet.

The *Armillaria* form occurred only on September 18th–19th and October 12th: in the first instance seventeen were found in a very small area. At Matale, March 6th, 1906, I was informed that in addition to the *Pluteus* form then collected, the coolies ate an "egg-shaped" mushroom, *i.e.* the *Armillaria* form. It was at first thought that the difference in these two forms was due to the difference in depth of the combs from which they arose, but the *Pluteus* form has since been found growing from a comb only 10 centimetres below the surface. The production of the ringed form may depend on the humidity of the comb chamber, but observations are not yet numerous enough to afford any solution of this question.

I have not been able to germinate the spores of the agaric in any solution, nor has the addition of pieces of the tissue to the hanging drops containing the spores induced any growth. Experiments with portions of the developing agaric on various media did not result in the production of any mycelium, but it is probable that the tissue employed was too old. The stages figured on Pl. XIX. were not available when these experiments were attempted.

Holtermann in 1899 (7) says that the spores germinate in a particular solution which he will describe elsewhere, but in his account of this solution (of palm sugar) in 1901 (8) he states that he had no success with the spores of pink-spored agarics.

The history of the agarics figured on Pl. IX. is instructive. The chamber was opened in the afternoon, and after a photograph had been secured the fungi were left to develop further. Next morning it was found that the opening had been closed and that the agarics were still unexpanded. On the third day two of these fell over, followed on the fourth day by the other three. On reopening the chamber it was found that all the developing agarics had disappeared and the termites had eaten away the stalks of those above ground, following them up to the surface until they collapsed and then closing up the hole. A fortnight later I reopened the cavity to extract some of the comb ; as before, it was closed again by the termites before the next day : at the end of another fortnight I reopened it again for the same purpose, but found that all the comb had been removed. Thus it is certain that the termites may eat the agarics and that they remove the comb probably by eating it also. In another instance a wall was built round the stalk of a mature agaric, and the whole of the stalk and part of the pileus was devoured.

With reference to Döflein's suggestion that the termite fungi are common in the neighbourhood of the nest on dead wood, it may be stated that in every case where this agaric has been found, it has been determined that it proceeded from a termite comb.

There remains for consideration the systematic position of the fungus. The following descriptions undoubtedly relate to this species:—

Armillaria eurhiza Berk. Decades of Fungi, No. 146.

Pileo carnoso, e subconico expanso, fortiter umbonato, cute gelatinosa, rugosa vestito : stipite sursum attenuato, extus cartilagineo radice fusiformi : annulo e strato externo orto evanescente : lamellis adnexis, albis arcuatis. *Armillaria mucida* proxima : habitus *Collybiæ radicatæ* similis. Pileus 9 cm. circ. latus : stipes 5 cm. altus, 1·3 cm. medio latus.

Lentinus cartilagineus Berk. Decades of Fungi, No. 167.

Cæspitoso-gregarius, é communi basi enascens : pileo albido subsericeo : stipitibus validis, contortis, strato crasso, cartilagineo-viscoso, in velum universale producto tectis, intus spongiosis : lamellis integris, liberis, pallidis.

E profunditate 1·30 m. sub terra erumpens in valle Thermitum Ceylon (Gardner).—Pileus 5 cm. latus : stipes 20–26 cm. longus. Forte novi generis typus.

Collybia sparsibarbis B. and Br. Linn. Trans. 27 (1870), p. 151.

Esculentus : pileo carnoso fortissime umbonato convexo virgato-striato marginem versus floccis liberis aspero, umbone glabro fusco, carne alba : stipite valido subradicante, præmorso, basi marginato bulboso hic illic sulcato : lamellis angustioribus postice rotundato-adnexis pallidis. (Thwaites, Ceylon, No. 697).

"On the ground, Peradeniya. July and August, 1868. Pileus 5½ inches across, deep brown in the centre, then paler : stem white (including the bulb, half of which is buried in the soil), 4 inches high, ⅔ inch thick half way up ; gills ¼ inch broad, rounded behind, free."

" Evidently nearly allied to *Agaricus eurhizus* Berk. Lond. Jour. Bot., 1847, p. 483 (Gardner No. 43), but differing in the hairy margin of the pileus and the absence of a long root and ring. The Himalayan *A. napipes* Berk. with its long root, is also very nearly related."

Agaricus (*Pluteus*) *Rajap* Holtermann.

In " Mykologische Untersuchungen " (1898) Holtermann figures an agaric on a termite comb, natural size. It is 3 cm. high, with a fusiform stem 5 mm. diam. in the widest part, the pileus is 2·5 cm. diam., split almost to the centre, umbonate ; the origin of the stalk is obscure.

In " Botanische Untersuchungen. S. Schwendener " (1899), he says, " the spores are rose-red, the pileus—5 to 20 cm. broad—is distinct from the stalk, at first villous, arched, later expanded circular, umber brown. Stem above ground 10 or more cm. long, up to 2 cm. thick, gray : gills free, rounded at the inner end, moderately crowded, gray-white. Spores elliptic (4–5 μ long ?) : the lower part of the stem which is in the earth is altogether black."

It is obvious that the agaric figured by Holtermann could not have grown from a comb *in situ*, since it is only 3 centimetres high and could not therefore have appeared above ground.

Flammula Janseana, P. Henn. et E. Nym. Monsunia I.(1899, p. 154. *Pholiota Janseana*, P. Henn. et E. Nym. Naturw. Wochenschr. *XIV*. (1899), p. 1899 (*sic*) : Monsunia I. (1899) p. 18. *Agaricus* (Pluteus) *Rajap*, Holtermann in Festschrift für Schwendener (1899), pp. 411–421.

Pileo carnoso, primo viscoso, conico-campanulato, dein convexo-explanato, 4–6 cm. diam., vertice rotundato, radiatim striato, sericeo, pallide brunneo, margine primo involuto dein revoluto ; stipite subfusiforme, tereti, pallido, ca. 2½ cm. crasso, basi bulboso, 3½ cm. incrassato, radicato, atro, usque ad 15 cm. elongato, medio annulo submembranaceo, evanido prædito : lamellis adnatis, subconfertis, primo pallidis, dein brunneis ; cystidiis late clavatis, 30–40 × 15–22 μ ; basidiis clavatis, fuligineis 25–30 × 8–9 ; sporis subglobosis, levibus, 8 μ diam., intus granulosis, sordide flavobrunneis.

Ad nidos termitum in horto Bogoriensi ins. Javæ (E. Nyman).—In speciminibus evolutis annulus haud conspicuus, hinc species melius Flammulæ adscribenda. *Flamm. filipendula*, P. Henn. et E. Nym. l. c. cujus diagnosis ab auctoribus vitiosa est data, verisimiliter est tantum forma *F. Janseana.*

With the exception of the third and fourth the above descriptions are copied from Saccardo, Sylloge Fungorum : I have not had an opportunity of consulting the originals. Berkeley's diagnoses were drawn up from dried specimens and drawings (chiefly the latter), and the specimens were immature. Among Ceylon fungi this can be paralleled by *Armillaria rhodomala*, B. & Br., which is an immature *Pholiota.*

The length of stalk of *Armillaria eurhiza* is probably an error, since 5 centimetres would scarcely call to mind *Collybia radicata*, and in describing *Collybia sparsibarbis*, with a stalk 10 centimetres long, Berkeley states that it differs from *A. eurhiza* in the absence of a long root. The rugose pileus is a common feature of specimens developed in the wet weather. It may be noted that Berkeley's specimen was the ringed form with a black rooting base, not with an equal stalk like those figured on Pl. IX.

The description of *Lentinus cartilagineus* is remarkable for the fact that Berkeley recognized what has been overlooked by subsequent describers, viz., that the agaric has a universal veil. The silky pileus is an inaccuracy due to the extreme attenuation of this veil. It is difficult to understand how it could be described as "gregarious, rising from a common base," unless by some extraordinary chance Gardner found two or more examples growing from one comb. This has never occurred to me except in the case of the *Armillaria* form.

The figure of *Collybia sparsibarbis* which was sent to Berkeley is decorated on the margin of the pileus with a few wavy pencil marks. They do not suggest that the margin was hairy, and were probably only intended by the draughtsman to indicate a few broken fibrils. The pileus had evidently only a thin cartilaginous coat, and is therefore apparently striate ; the gills (in the figure) are free. An examination of the herbarium specimen shows that it is cartilaginous and smooth up to the margin, and that the stalk is " præmorsus " because it has been cut off just below the commencement of the black rooting base. The bulb at the base of the stem is abnormal, though it is included also in the description of *Flammula Janseana*.

Holtermann's description (not his figure) applies to the Ceylon specimens, except that the pileus is not truly villous.

Exception may be taken to the size of the pileus, description of the margin, and relative thickness of the stalk of *Flammula Janseana*. The gills may be styled adnate in some specimens, especially if the pileus is depressed and the stalk expanded at the apex: they are brown on old, dried, decayed specimens. Hennings and Nyman, however, say that it is the same as *Agaricus Rajap*, and the latter is undoubtedly the Ceylon termite agaric.

It would be interesting to determine whether Thwaites collected the ringed form and what name was bestowed on it, or whether either he or Gardner sent either form to Berkeley in the pink-spored condition.* Presumably there should be five more names in the Ceylon list, but up to the present I have not been able to trace more than the three descriptions quoted above, either from specimens or drawings.

With regard to the colour of the spores, which Hennings and Nyman say are yellow-brown, one or two facts may be adduced to show how similar mistakes could arise. A *Lepiota* (probably *zeylanica*, Berk.) has spores which are white when fresh, then pale yellow, while those which remain in contact with the gills and stalk are deep red ; "*Lepiota flavidorufa*" has spores which are pale yellow, ochraceous, or light or dark slate, according to age and the mode of deposition ; and there is not much doubt that many Ceylon Lepiotas have been classed as *Psalliota* through the change in colour of the gills. *Chitoniella poderes* (B. and Br.), P. Henn., too, which is identical with *Chitonia pedilia*, B. and Br., is said by Hennings to have purple-brown spores, whereas they are really olive green. This statement however appears to be a pure assumption, for Berkeley's specimens, the only examples ever sent to Europe, were immature, and he does not mention the spores. The same species further illustrates the possibilities of error in describing dried agarics : *Chitonia pedilia* is said to differ from *Chitoniella poderes* in the absence of a secondary veil, but the figure from

---

* Both sent "*Pluteus cervinus* Schaeff," which was more probably the present species.

which it was described shows the secondary veil clearly. Another error arises in the transcription into Saccardo, where the stem thickness, 1 inch, is changed to 2 millimetres. There is probably a similar error in the length of the stem of *Armillaria eurhiza*.

This digression may serve to mitigate doubts which must arise as to the validity of the supposition that the quoted descriptions refer to the same species. Instances might be multiplied almost indefinitely from the Ceylon fungus flora. It must be remembered that the describer of dried agarics works with a limited number of specimens and that these are often abnormal : he may too, when dealing with tropical fungi, meet with changes of form and colour which he would not expect from his previous experience and so create two or three species from one gathering.

With these facts in mind, the following descriptions may be considered. The only points which throw doubt on their inclusion with *Pluteus Rajap* are the small size of the pileus and the diameter of the stalk. With regard to the former there is the parallel case of *Flammula Janseana*, whose pileus is said to be 4–6 cm. diameter, whereas it may be "the size of a dinner plate." Can we suppose that the collector merely gathered those which were convenient for transport ?

Pluteus Treubianus, P. Henn. et E. Nym. Naturw. Wochenschr. *XIV*. (1899), p. 28 : Monsunia I. (1899) p. 19.

Pileo carnuloso, campanulato-explanato, vertice conico-umbonato, radiatim substriato, subsquamuloso, pallide brunneo, 4–6 cm. diam.: stipite farcto, cylindraceo, gracili, glabro, levi, interdum flexuoso v. curvato, usque ad 12 cm. longo, ½–1 cm. crasso, albido : lamellis subliberis, latis, pallidis, dein flavo-carnescentibus ; basidiis clavatis ; sporis subglobosis, grosse 1-guttulatis, 5½–6½ μ diam., incarnatis.

Ad nidos Termitum in horto Bogoriensi ins. Javæ (E. Nyman). Odor et sapor grati.

Immature spores of this size and shape are frequently found among the larger spores of *Pluteus Rajap*, and there is nothing else in the description to separate it from that species: the spores of *F. Janseana*, which is identical with *Pluteus Rajap* and has "pip-shaped" spores, are also styled subglobose by the same authors. This probably removes the chief difference between *P. Treubianus* and the following species.

Pluteus bogoriensis, P. Henn. et E. Nym. Monsunia I. (1899), p. 19.

Pileo membranaceo-carnuloso, convexo, centro mammoso, subacuto, luride brunneolo, 3–3½ cm. diam. stipite farcto, tereti, gracili, æquali, levi, glabro, albo, basi radicante elongata, attenuata, ca. 10 cm. longo, 2–3 mm. crasso: lamellis adnatis, confertis, tenuibus, angustis, e pallido flavescentibus v. subcarnescentibus; cystidiis ovoideo-clavatis, ca. 30–36 × 18–22; basidiis clavatis, guttulatis, 22–25 × 5–6; sporis ellipsoideis, basi apiculatis, 5–6½ × 4, episporio levi, flavo-carnescente.

Ad nidos termitum in horto Bogoriensi ins. Javæ (E. Nyman).—*Pl. treubiano* affinis: differt autem lamellis adnatis, stipite tenuissimo et præsertim sporis ellipticis.

Only the thin stalk separates this species from *Pluteus Rajap*. The thinnest stalk I have seen of the latter was 5 mm. in diam., the pileus being 6 × 5 cms. It seems quite probable that *Pluteus bogoriensis* was only a small specimen of *Pluteus Rajap*. The stuffed stalk may be neglected as I have had several specimens of *Pluteus Rajap* in which the upper portion of the stalk was longitudinally split internally and therefore hollow.

Pluteus termitum, P. Henn. F. Amaz. I. in Hedw. (1904), p. 183.

Pileo carnuloso, campanulato, vertice umbonato-obtuso. brunneolo, radiatim substriato, albido, 3–4 cm. diam.; stipite fistuloso, tereti, substriato, levi, basi interdum curvulo, incrassato, pallide brunneolo, 4–5 cm. longo, 2–3 mm. crasso; lamellis liberis, confertis, ventricosis, 3 mm latis, pallidis dein flavidis; sporis ellipsoideo-fusoideis, utrinque acutiusculis, 1–2 guttulatis, episporio pallide incarnato, levi, 7-10 × 4·5.

Ad excavationes Termitum, Fortalezæ Amazoniæ. Nonnulis notis ad Lepiotas nutat.

Holtermann's name, *Pluteus Rajap*, appears to have priority. But is the fungus a *Pluteus?* Its development enclosed in a universal veil is that of *Volvaria*, and the mature agaric appears to differ only in slight degree from *Volvaria gloiocephala*, DC., in which the volva is "adnate to the base of the stem except a short torn margin." On the other hand *Pluteus* is said to have neither volva nor ring at any stage. It appears to be really a *Volvaria*, probably modified by its peculiar habitat ; and this view is supported by a single specimen in which the covering of the pileus is split into thin, brown, gelatinous patches, with a curved edge, arranged concentrically. I propose to call it *Volvaria eurhiza*.

Döflein (13) states that if the comb be exposed to the light the fructification of the termite fungus can be easily induced. This does not refer to the agaric, but to the structures dealt with in the next section. It has not been found possible to grow the agaric from the comb under any conditions.

Attempts to grow the sphere-producing mycelium from the spores or tissue of the agaric have been uniformly unsuccessful, and the connection between the two is not proved. The available evidence appears to indicate that they are parts of the same fungus, and further facts in support of this supposition will be given later.

The synonymy as far as can be determined is :—

Volvaria eurhiza (B. and Br.) : *Armillaria eurhiza*, B. and Br. Hooker's Journ. Bot. 6 (1847), p. 483 : *Lentinus cartilagineus*, B. and Br. Hooker's Journ. Bot. 6 (1847), p. 496 : *Collybia sparsibarbis*, B. and Br. Linn. Trans. 27 (1870), p. 151 : *Agaricus* (*Pluteus*) *Rajap*, Holtermann. Festchrift für Schwendener (1899), pp. 411-421 : *Pholiota Janseana*, Henn. and Nym. Monsunia I. (1899), p. 18 : *Flammula Janseana*, Henn. and Nym. Monsunia I. (1899). p. 154.

The Xylarias.

Thwaites' specimen No. 554 is labelled "White ants' nests," and was grouped by Berkeley (14) with other numbers as "conidiferous forms of unknown species" of *Xylaria*: he adds that the fungi of No. 554 occur on the nests of termites when exposed to the light. It includes about two dozen thin, xylaria-like structures of varying shapes, simple, bifid, or repeatedly forked, from 1 to 6 centimetres in height, but they show no trace of conidia or conidiophores.

My attention was directed to these apparent *Xylarias* by Mr. E. E. Green, who has repeatedly exhibited the phenomenon of their production to entomologists, &c., who have visited Peradeniya.

If a fresh termite comb from which the insects have been removed is placed under a bell jar, the spheres decay, and after two or three days are succeeded by small groups of erect hyphæ which grow rapidly into tall thin structures resembling the conidial forms of *Xylaria*.

These arise from the interior of the comb substance, and are apparently continuous with the mycelium in it. If the termites have not been completely removed from the comb, the survivors in a short time eat off all the spheres and also the external hyphæ: this however does not affect the production of the *Xylaria*-like structures, though the latter are eaten off also as they appear. They are not therefore dependent upon the external mycelium.

The hyphæ are indistinguishable from those which arise to form the agaric: they are hyaline, septate, rather thick-walled, branching, with swollen heads, and filled with granular protoplasm. They are about 4–5 μ in diameter on emergence, and increase to 6–8 μ, swelling at the extremity into a clavate head, 10–12 μ in diameter: they unite to form a loose column with free ends projecting on all sides. Hyphæ about 3 μ in diameter are present in the comb substance: from these the ærial hyphæ emerge perpendicularly and bend together from a breadth several times the diameter of the subsequently developed stroma.

In the simplest form this stroma is an upright rod 5–10 cms. in height and about 2 mm. in diameter. It is at first white and loosely built, but as it increases in length the lower part becomes greenish and finally black. This change of condition travels upwards until, at the end of a week or so, only the apex is white. It then has a solid white core of parallel hyphæ, enclosed by a black outer layer formed by interwoven twisted hyphæ ends which give it the appearance of an epidermis with wavy cell walls. In general a few hyphæ remain unchanged outside this layer and give the stroma a scurfy appearance.

Branched stromata generally occur in abundance, though it sometimes happens that all on a given comb are simple. In most cases in which the comb contained larvæ when in the nest, *i.e.* the brown topped combs, these stromata are weak and divide into a brush of single hyphæ at the ends of the branches. As a rule, they do not bear conidia, and soon collapse under their own weight.

The production of branched stromata appears to depend on the degree of moisture in the comb. If the termites are merely brushed out of the comb as far as possible and the latter placed under a bell jar, the survivors gradually descend to the lower surface and may be removed at intervals, though the process may occupy a week and the comb in the meantime becomes rather dry. The stromata which develop subsequently are almost invariably small and simple, and may bear conidia.

The removal of all the termites in such a way that the comb retains its original degree of moisture is a matter of considerable difficulty. The use of poisonous gases is undesirable, since it would kill them in the comb : it may be mentioned that carbon dioxide appears to have very little effect. Workers and soldiers are fairly easily got rid of, but the larvæ are extremely sluggish and take refuge in the inner passages, where they cannot be reached. Perhaps the best method is to put the comb in the track of a colony of the small black bungalow ant, or any of the red ants, and leave it partly covered with a bell jar for a night. The ants carry off the termites, and if the former remain in the comb they may easily be removed by shaking it, or a few may be left in order to prevent the attacks of other insects. *Œcophylla smaragdina*, Fabr., has been employed in this way, but any (true) ant will serve. *Myrmecaria brunnea*, Saunders, cleared out the termites from combs placed on a sink in the laboratory, entering through the waste pipe from a nest twelve yards away.

It has not been found possible to develop these stromata further. After three or four weeks they die off. As a rule, however, unless special precautions are taken, cultivation is limited to about fourteen days, for at the end of that time comb and fungi alike are reduced to a mass of excrementitious matter by the larvæ of two tineid moths, *Opogona flavofasciata*, Stt., and an allied species, which appear to be peculiar to termite combs. The culture is resolved into a mass of black pellets. Though the moths are apparently confined to this habitat, it is remarkable that no trace of the larvæ or their work has been observed in the nest.

In order to determine further the nature of these xylarioid structures, and to avoid as far as possible the attacks of the caterpillars, pieces of comb were planted in pots. Several marked differences resulted. The fungi took a much longer time to develop: in general they did not appear above the soil until ten or fourteen days had elapsed, though the pots were kept well watered, and in no case did they grow more than a centimetre high.

The pot-grown stromata from normally inhabited combs have always been simple and, like other pot-grown forms, have always borne conidia. This production of conidia appears to depend in all cases on the compactness of the stroma: those produced under a bell jar are often loosely built and non-conidiferous. In the present case, the conidiferous hyphæ bend out horizontally from the developing column to a length of about 200 μ and form a continuous outer layer. In diameter they vary from 8 to 20 μ, most of them increasing towards the extremity and being therefore somewhat funnel-shaped. They terminate in a four-lobed head on which are borne closely packed, flask-shaped basidia bearing catenulate spores, 4–5 μ diameter (fig. 26). The entire conidiophore with its basidia and spores forms a somewhat flattened spherical head. In some instances the hypha divides into two short branches each of which bears four lobes: in other cases, a second whorl of lobes is produced below the apex of the hypha (fig. 27). In general there are no septa cutting off the separate lobes, but the whole head is isolated by a cross wall just below it. At the apex of the stroma are found undifferentiated hyphæ in the centre, and all stages of the developing conidiophore immediately beneath them.

The contrast between the areas in which the spores have or have not been shed makes the stroma at first sight resemble a small developing agaric. Fig. 24 shows one of these pot-grown stromata: the apparent cap is formed by the conidiophores which still bear conidia, and the small clear area at the apex represents the non-conidiferous central hyphæ. No further development has been obtained: the whole structure turns black and finally decays. Whether the comb is planted at a depth of 1 or 6 inches makes no difference in the height above ground of the stromata. The underground portion is an extremely fine black thread, and is not easily traced to the comb. The whole of the stroma above ground bears conidia eventually: there is no barren stalk except the part under ground.

If the comb is wetted before being placed under a bell jar, growth is more rapid, but the resulting stromata are loosely built. In many cases the hyphæ arise in an erect brush and do not coalesce, and sometimes they merely spread over the surface of the comb. In this condition they are quickly overrun by species of *Mucor* and *Thamnidium*.

A conidiophore from a loosely built stroma is shown in fig. 29. It branches repeatedly in planes at right angles to each other, each branch ultimately terminating in a four-lobed head smaller than that of the compact pot-grown form. Each lobe now bears only two basidia. As a rule, each basidium bears one chain of spores, but instances of two chains on a single basidium can be found.

The preceding account refers to the growth on normally inhabited combs, but the greatest production of these stromata always occurs on combs which have previously produced an agaric. These however generally differ from the forms already described. If the comb is allowed to become somewhat dry. simple stromata are obtained (Pl. XIII. A) : these grow to a height of 4 to 5 centimetres. They are stronger than the simple stromata from normal combs, and have a firmer core of thickened hyphæ enclosed in a well-developed black cortex. They bear conidiophores of the type of fig. 26 or 29, but these are generally scattered instead of forming a continuous layer. As a rule, however, the stromata branch dichotomously after attaining a height of a few centimetres and produce the structures illustrated on Pl. XIII. B and C. If the comb is fairly moist, the ultimate branches divide into single hyphæ without producing conidiophores and collapse on drying. Pl. XIII. B. and C. show the growth of the same group at the end of four and five days respectively. A portion of an agaric-bearing comb was placed under a bell jar on 30th October (afternoon). On 1st November loose developing stromata up to 2 centimetres high were present, together with an abundance of white spreading hyphæ on the comb. On 2nd November the stromata were up to 3 centimetres high and 2 to 3 millimetres in diameter ; the larger had become firm and showed indications of branching, but the majority resembled loosely twisted locks of wool. On 3rd November when the first photograph was taken, the largest stroma had formed a tree-like structure with branches dividing into single hyphæ ; on the previous day this was growing obliquely, and terminated in a slender glabrous projection, only about one-quarter the diameter of the lower part and springing abruptly from the truncate apex, but by 3rd November new growth had taken place vertically and had branched into the tree-like structure photographed. Thus from the bend upwards represents fourteen hours' growth. The former whip-like apex is seen to the right of the bend. The bell jar was removed for about twenty seconds: during that time the branches collapsed slightly and the looser stromata commenced to droop, as shown on the right of the photograph. They doubled over completely immediately the photograph had been taken. On the following day nearly all had assumed the tree-like form and the stalks had turned black. The delicate radiating hyphæ are not well seen in the photograph (Pl. XIII.C): the stroma on the extreme left especially shows their collapse. The main stalk hyphæ were about 12 μ diameter with frequent septa, some only 30 μ apart; some of the ultimate branches were only 5 μ in diameter. This cultivation was continued until 17th November, but no conidiophores were observed. The mass of spreading hyphæ on the comb is chiefly a *Mucor*.

The corresponding pot cultivation will be dealt with later. It gave results which have not been confirmed by any other experiment, but which agree exactly with those obtained by observation of the combs in the nest.

A diminution of moisture results in the formation of similarly branched stromata in which the branches are rigid, taper to a point, and bear scattered conidiophores along their whole length. These conidiophores branch repeatedly, and are identical with those of figs. 29 and 30.

It is possible when the comb is producing simple stromata only, to cause the formation of branched ones with rigid conidiferous branches by the addition of water. This was done in one instance with a semi-deserted comb, *i.e.* it contained workers and soldiers only. It was placed under a bell jar on 23rd February without removing all the termites. These were removed as they appeared beneath the comb, and during that time all developing fungi were eaten. The last two termites were taken out on 1st March. A development of simple stromata now took place, and by 4th March these were about 4 centimetres high and had turned greenish. The comb was now watered, and on 6th March showed several rigidly branched forms.

Another example is figured on Pl. XIV. A. This shows six days' growth, two-fifths natural size, from a comb which had produced an agaric. These commenced to develop on the second day and showed signs of branching on the third. In this case spores were developed on the spreading branches of those which rested on the sides of the bell jar. The conidiophore was more branched, recalling in the regular dichotomous arrangement of its widely spreading branches the conidiophore of *Piptocephalis*. The radiating basidia were also more divergent: the end of one branch of a conidiophore is shown in fig. 31, half the basidia of each group being omitted.

The pot cultivation from the same comb did not produce anything for eight days. Branched stromata then appeared, but they did not grow higher than 1 centimetre. The photograph Pl. XIV. B was taken at the end of fourteen days. The stromata subsequently turned black, and at the end of six weeks decayed. The conidiophore was the same as that of the simple pot-grown form (figs. 25, 26).

One more example may be cited out of the dozens of cultivations which have been made. A semi-deserted comb was deprived of termites, and wetted by plunging it into a bucket of water. In two days loose stromata developed, and on the third day some broadened out into palmate expansions. These are shown on Pl. XV.: owing to their exceptional thickness, only a few collapsed on removing the bell jar. On the fourth day, the largest was 9 centimetres high, and the expanded portions had split into from three to ten upright branches. On the seventh day several were removed and photographed: many of them had arisen from the lower layers of the comb and had penetrated the upper layers. The broadest in Pl. XV. is on the right of Pl. XVI. The black epidermal layer had developed on the lower parts, but was hidden by a white coating of conidia. Apparently this was yet another form, but on the following day the upright branches of the remaining stromata (which were identical with those photographed) forked dichotomously into long rigid acute branches identical with those previously described. They fell over and adhered firmly to the sides of the bell jar, and fused completely with one another wherever they came in contact. After fourteen days all were devoured by caterpillars.

No pot cultivation was made in this case, but combs from the same nest left piled together under a box outside (and therefore drier) bore only stromata with unexpanded stems branched dichotomously at the apex. When, as in this case, the supply of water gradually diminishes, the stromata are often short and thick and only slightly branched at the apex, resembling pieces of white coral.

The spores germinate readily in water or in comb extract. The resulting hyphæ are easily distinguished from those developed from the "sphere" conidia: they are more irregular in diameter and branch always at an acute angle, the branches following the same general direction as the main hypha. Only in one case were conidia obtained directly from the creeping mycelium in a film of comb extract agar on a cover glass, and in this the conidiophore was identical with that described below.

When the conidia were sown on slants of comb extract agar, with or without dextrose, simple stromata developed at the end of eight days. They only came above the surface in contact with the glass. The largest projected above the agar for about 5 millimetres, but the black stalk could be traced in the medium for a centimetre or more. The ærial portion was rather loose, and the scattered, spreading conidiophores could easily be seen with a simple lens. The structure of the conidiophore had undergone further variation. The basidia were still more widely separated, and now appeared as side branches as in Brefeld's figure of the conidiophore of *Peziza (Sclerotinia) tuberosa* (20): they had lost the regular flask shape, and were practically of uniform diameter with a somewhat truncate apex and often irregularly bent (fig. 32).

As may be seen, the form of the stroma varies widely : illustrations of different shapes might indeed be multiplied indefinitely, but in general two types may be distinguished—(1) an upright simple stem ; (2) an upright stem branching dichotomously at the apex. These may be produced by altering the degree of moisture in the comb if this was in the semi-deserted condition with an abundant growth of mycelium : the brown-topped combs which contain the termites in all stages usually show stromata with less regularity of branching, and these are generally non-conidiferous. A determination of the amount of moisture in fresh combs is desirable, but up to the present has not been found possible. The larvæ are extremely sluggish and take refuge in the central passages, whence they cannot be dislodged. It is therefore impossible to get the weight of a fresh comb without including the larvæ at least.

The conidiophore varies directly with the conditions under which it is grown. That of the pot-grown form is at first sight an *Aspergillus*, and that of the simple stroma is often only slightly removed from it by the greater development of the four lobes of the simple head. With increase of moisture it becomes branched, but retains the four-lobed head on each branch, though each lobe now bears only two basidia. In a further stage the branches are more regularly dichotomous and diverge at a greater angle, and the separate basidia are also more divergent. Finally, in agar cultivations the conidiophore becomes altogether irregular, the basidia appearing as somewhat truncate, often crooked, side branches.

It is noteworthy that the simple stromata have conidiophores with comparatively simple heads, while the dichotomous stromata repeat the dichotomous branching of their conidiophore.

It is not necessary for the development of these conidial forms that the comb should be exposed to light : they will grow equally well in a dark chamber. They are strongly positively heliotropic, and respond readily to slight differences in illumination.

Sclerotia may be formed in these cultivations, either before or after the production of conidia, though in the latter case they are irregular. In one instance a piece of comb placed under a bell jar in the usual way developed upright stromata in a few days. As these were not particularly required, the cultivation was put aside. At the end of a fortnight small, white, depressed, circular tufts of hyphæ were observed: these bore no conidia, and were regarded as an intrusive growth. At the end of the third week they had become spheres, 2 or 3 millimetres in diameter, at first with a silvery coat, and then black. They were allowed to remain on the comb for another week, though they were not then united to it by any mycelium. They were then removed, and two were placed on damp filter paper in a sterilized dish. I was unfortunately absent during the next five days, but on returning I found that one had produced two slender stromata 2 or 3 centimetres high and 1 to 2 millimetres in diameter, and that the same structures were just developing from the other. The conidiophores were identical with those formed on simple stromata on the comb, and a further point of agreement was afforded by the fact that one sclerotium bore unbranched stromata, while those of the other were feebly branched (fig. 28).

A less regular sclerotium may also be formed after the stroma has produced conidia; *e.g.*, in old cultivations which have escaped the attacks of caterpillars, the bases of the stromata frequently become thickened. The best examples of this occurred in a piece of comb, fully inhabited when taken from the nest, which had been lying on the verandah for about three months. Under such conditions the comb dries gradually without producing fungi, and the external mycelium is eaten off by cockroaches. The piece in question was 8 centimetres long, 5 centimetres broad, and 2 or 3 centimetres thick in the centre. After being moistened and placed under a bell jar, an extensive development of simple stromata occurred, some of them 14 cms. high: the stoutest was 8 cms. high and 3 mm. in diameter. A month later the stromata were counted, and in the process the comb was broken up. Neglecting very thin hair-like growths, there were three hundred and seventy stromata. The larger were found to possess irregularly thickened bases corresponding in structure to the usual sclerotium type, and in one case the sclerotium retained the shape of the comb passage round which it had been formed, being U-shaped in section with the arms of the U one centimetre in length.

Though the shape and size of these precluded the idea that they were built into the comb by the termites, numerous fresh combs were broken up to see whether there was any trace of them, but nothing of the kind was found in fresh combs, nor in dried combs which had been subjected to the same conditions as the one described above. It seems quite evident that these irregular sclerotia in the comb are developed during or after the growth of the stromata, and from their absence from the numerous cultivations which have been stopped at an earlier stage, the latter supposition is most probable.

The conidiophores of these stromata appeared to throw doubt upon their classification as conidial forms of *Xylaria*, and this doubt was not removed by any of the cultivations already cited, nor was it possible until recently to obtain any similar structures from termite combs in the nest. It was however at last discovered that under favourable conditions apparently two *Xylarias* grow from deserted termite combs, the first to appear being *Xylaria nigripes*, Klotzsch, and the second the one under consideration.

Xylaria nigripes, Klotzsch, is a not uncommon fungus at Peradeniya, but for a long time I was unable to find the conidial form. All the specimens seen in 1905 bore perithecia only, even in cases where they could not have been a day old. These stromata are from 5–15 centimetres high, with a sharply defined black stalk, 1 or 2 centimetres high and about 3 millimetres in diameter, and an upper cylindrical fertile portion, twice this diameter, at first brown, then yellowish gray and rough with the black projecting ostiola. They occur singly or in groups, arising from long black rooting cords only slightly thinner than the stalk. Occasionally the apex of the root divides and produces two or three stromata, and rarely a stroma may be branched, but in general the stromata are unbranched and only one arises from each root. Their growth is remarkably rapid, and it is not uncommon to find full-sized stromata in localities where it is certain that their development has only occupied a few hours. On the other hand the perithecia ripen very slowly, and one cannot be certain of obtaining ripe spores until they have been ejected and form a black glutinous coat over the yellowish gray clava. The spores are broadly cymbiform, 4–5 × ·3 μ, black with a thick, slightly transparent wall: apparently the ascus is expelled from the perithecium and is resolved into a gelatinous coat which binds the eight spores together. The size given above agrees fairly with Berkeley's measurement, 5 × 4 μ. Berkeley says that *Xylaria nigripes* grows on dead wood, obviously a somewhat peculiar position for a species which has a root several feet in length. I did not follow up the roots of my earlier specimens, nor did I attribute any special significance to the fact that they were all within a short distance of termite nests.

At the beginning of August, 1906, towards the close of the monsoon rains, my attention was directed to several patches of conidial Xylarias in various places in the Royal Botanic Gardens and elsewhere. These conidial forms were long and slender, usually simple, of all lengths up to about 15 centimetres, and 1–2 millimetres in diameter. They had a distinct black stalk and a long, black, thin, rooting base. The conidia were narrow-oval, 6–7 × 2 μ, on simple conidiophores.

These stromata occurred in scores, growing closely together on well defined areas up to 60 cms. in diameter which were whitened by the myriads of conidia. On the second or third day the perithecial stromata of *Xylaria nigripes* appeared, not in such abundance but only a dozen or so on each patch. At the end of a week all the conidial forms decayed, leaving only the still unripe perithecial form. Thus the conidial and ascus stages of *Xylaria nigripes* are borne on different stromata: they are probably united to the same rooting base, but this has not been determined with certainty: they are alike in their distinct stalk and the possession of a black central core about ·25–1 mm. in diameter. Apparently in moderately dry seasons only the ascus stage is produced.

When all the conidial forms of *Xylaria nigripes* were dead, the conidial form of the other *Xylaria* appeared. The majority of these were only 5–10 millimetres high, but some reached 3 centimetres; most of them branched dichotomously. They slowly turned black at the base, but had little or no distinct stalk except the rooting base in the soil. The conidiophores of these were identical with figures 29 and 30, and in every respect the stromata resembled those developed on the termite combs under cultivation. They are distinguished from the conidial stage of *Xylaria nigripes* by the different conidiophore, whiter colour, the absence of the black central core, and their flexibility, the conidial form of *Xylaria nigripes* being brittle. Nearly all these died without producing perithecia, but fortunately one or two of the larger developed further and thus demonstrated that they were really Xylarias.

On digging down at the edge of these patches, it was found that all these stromata grew from deserted termite combs 40–50 centimetres below the surface. The combs were thickly covered with fine mycelium which almost filled their inner passages also, and from this arose the black bases of the aërial structures. From the growth of the fungi it was evident that the combs had been deserted for some time, and only in one case was it possible to identify the species of termite by the discovery of part of a dead soldier of *Termes redemanni.*

In the cavities occupied by these deserted combs were found also large, black, irregular or fig-shaped sclerotia. These measured up to 8 cms. in length, 3 cms. in breadth, and were somewhat flattened, about 1 cm. thick. Some were united to the comb by a tangled mass of fine hyphæ, while others were apparently growing from the sides of the cavity. The question whether these were connected with *Xylaria nigripes* or the *Xylaria* whose conidial form appears in bell jar cultivations was settled by placing them under bell jars on damp filter paper where in the course of a fortnight they produced the ascus form of *Xylaria nigripes.*

As far as the conidial forms are concerned, the natural course of events agrees precisely with the results of that pot cultivation which was formerly regarded as abnormal. Part of the comb on which the branched stromata of Pl. XIII. were grown was planted 3 inches below the surface in a pot on 30th October, 1905. On 10th November three stromata appeared. They were longer, narrower, and more regularly cylindric than all previous forms, and did not show the apparent cap. Instead, they tapered off to a long point, which in course of growth became twisted, but finally they straightened out, becoming about 3 centimetres long and 1·5 millimetres broad, with a thinner black stem sharply defined from the conidiferous layer, and a central black core. The conidia were narrow oval, 4–6 × 2 μ, borne at the apex of simple horizontal basidia, and they did not germinate in water or comb extract. On 17th November three more were produced : these were rather thicker and one was bifid, but the structure and conidia were the same. On 27th November, however, a single simple stroma developed of the same type as those in other pot cultivations, and this was succeeded by another of the same kind on 4th December. The first of these were the conidial stages of *Xylaria nigripes*, while the later ones were the conidial form already described.

We now return to the later stages of the conidial forms which succeeded *Xylaria nigripes* from combs *in situ* at the beginning of August, 1906. Several specimens whose conidiophore had been determined to be identical with those in bell jar cultivations were marked and their development noted.

Very few survived, but those that did, except in one instance, developed perithecia. The first was gathered on August 15: it was unbranched and bore perithecia like small globules attached to a stem; the spores were not ripe. Others were gathered on September 13; these were simple, bifid, or forked into four branches, with a whitish, conidiferous tip, and a lower portion the colour of *X. nigripes*, rough with projecting ostiola. The spores of these were identical with those of *X. nigripes*. The largest marked stroma, some three centimetres high, was forked dichotomously: after appearing to cease growth with the others, it threw out new conidiferous branches in September, and again in October, during wet weather: it still (November 19) shows no signs of producing perithecia.

These results show that the mycelium of xylarias is always present in the termite comb. When a comb is taken from the nest and placed under a bell jar, a conidial form always develops, and the same appears when combs are planted in pots. In the latter case a second conidial form, that of *X. nigripes*, may appear first. From deserted combs in the nest, however, there arise, under suitable conditions, first, the conidial and ascus stages of *X. nigripes*, and subsequently the conidial form of the other species, which, when it develops further, has many points of resemblance with *X. nigripes*, *e.g.*, spores, ascus, perithecium, formation of sclerotia, and colour. The association and order of development are constant in all localities, and it may, I think, be inferred that there is really only one xylaria, viz., *Xylaria nigripes*, which possesses distinct conidial and ascus forms, and also an ascus-conidial form with conidia of a different type. Whether *Xylaria nigripes* is confined to termite combs or not is undecided. Its regular occurrence when the termites have been removed from or have deserted a comb indicates that the mycelium vegetates in the comb, and that all developing xylarias are "weeded out."

Two references to these *Xylaria* stromata have been noted. Holtermann (7) relates that the combs which he kept in crystallizing dishes produced an abundance of aërial hyphæ, some of which united into strands, "the thickness of a finger," but at the end of a week the walls and cover of the dish were completely over-grown by a thick, white web. He did not obtain any conidia, and the cultivation was probably kept too damp. Döflein (13) records the formation, under similar conditions, of long cylindrical fructifications, but does not describe them further.

A *Xylaria* has been described by Penzig and Saccardo (5) from termite combs at Buitenzorg under the name *Xylaria torrubioides*. They state that it resembles *X. Gardneri*, *var. minor*, but is still more slender. Their description is *Xylaria torrubioides*, Penz. & Sacc. Malpighia *XI.* (1897), p. 496.

Gregaria, stromatibus erectis, cylindraceis, sursum attenuato-acutis, sæpe curvulis, rarius furcatis, griseo-cinereis, 15–20 mm. long., 1–1·5 mm. diam., stipite sterili brevissimo, clava fertili vix tenuiore; peritheciis semi-immersis, ostiolo conico prominente, nigris, carbonaceis, 180–120 μ diam.; ascis cylindraceis, 18–20 × 3–3·5; sporidiis monostichis, minutissimis, 2·5–3 × 2–2·5, globoso-ellipticis, atro-brunneis.

In nidis termitidum in horto bot. Bogoriensi in Java.

The figure of this species in Icones Fungorum Javanicorum shows that it grew directly on the comb, the latter presumably being exposed. It is probably the ascus-conidial form of *X. nigripes* (= *X. Gardneri*).

The specimens here referred to as *Xylaria nigripes*, Klotzsch, agree exactly with those in the Peradeniya Herbarium marked *X. Gardneri* by Berkeley. The species is so strikingly distinct that the latter name was at first accepted without much doubt; the description of *X. escharoidea* suggested *X. Gardneri*, but as there are no specimens of the former in the Peradeniya Herbarium no comparison could be made. But the figures of *X. mutabilis*, Currey (Trans. Linn. Soc. 1875. Ser. 2, Bot. 1, tab. 21) exactly represent the conidial and perithecial forms of *X. Gardneri*, and the habitat, "on brick laid paths," can be matched by its frequent occurrence on footpaths at Peradeniya: the description differs in some particulars, but the discrepancies are not greater than those in the description of *X. Gardneri*, and there seems no doubt that it is the same species. On the same plate is figured *X. flagelliformis*, Currey: this is a conidial form only, and, except in the brown colour, it exactly represents the conidial stage of *X. Gardneri.* Cooke (Sacc., vol. 9., pp. 538, 539) says that *X. nigripes*, Klotzsch, is the same as *X. escharoidea*, Berk., *X. piperiformis*, Berk., *X. mutabilis*, Currey, and *X. flagelliformis*, Currey. He does not include *X. Gardneri* with these, which he calls "*simplices*," but places it amongst the "*furcatæ*," and says that its spores are 30 × 2 μ. But *X. Gardneri*, like *X. mutabilis*, is only rarely forked, and its spores are 4–5 × 3 μ: apparently Cooke measured the ascus which is 30 × 3 μ. Cooke's determination was based on an examination of the specimens at Kew, and accepting this as correct, *Xylaria Gardneri* must evidently be regarded as a synonym of *X. nigripes.* If allowance is made for the fact that the six descriptions were drawn up from dried specimens, it will be seen that they agree as well as could be expected. *X. Gardneri* is only "longitudinaliter rugoso-sulcato" when dry, and though it is always black within it is not black externally except when covered with extruded spores: except in these two points it agrees with the description of *X. nigripes.* *X. Gardneri, var. minor*, grows with, and often on the same base as, the longer form, and cannot therefore be separated as a variety.

The use of the Fungi.

The relation of the fungi to the termites has not yet been the subject of exact inquiry, at least in the case of Tropical species. It is however generally assumed that the conidial spheres on the comb are used for food.

Holtermann (7) rightly points out that a systematic feeding or starving of the insects does not lead to a correct conclusion, since when hungry they may eat many things which would under ordinary circumstances be rejected (compare Möller's experiments). He states that a solution of the question must be sought by an investigation of the contents of the intestine, &c., in which he found the oblong conidia of the spheres in great abundance together with numerous vegetable fragments. He does not say whether the insects examined were workers, soldiers, or larvæ, or if he investigated all forms.

Döflein (13) found the spheres in the crops of all the larvæ and nymphs which he investigated. He says that the crop was completely filled with them, there was no other food present, and the cells of the spheres were quite uninjured. He declares that this is true of the larvæ of the workers and soldiers as well as of the larvæ and nymphs of the male and female insects. The same observer fed all these forms with the spheres, after starving them for a day : the queen also ate the same, but he never succeeded in feeding a worker or soldier, and in these he found nothing but finely divided wood.

Döflein suggests that the spheres form the special concentrated food of all the larvæ, and the permanent food of the sexed insects, while the larvæ of workers and soldiers at a certain stage adopt other nourishment. From this he supposes that food plays an important part in the differentiation of workers, soldiers, and sexed forms. This is of course the conclusion of Grassi, who attributes the anatomical distinctions which arise between soldiers, workers, and winged forms (of *Termes lucifugus*) to differences of food. The life histories of the present species are as yet too imperfectly known to admit of much theorizing, but one objection to this view arises immediately. All the combs bear fungi, and it is difficult to understand how any larvæ could be prevented from eating them, if such had hitherto formed their normal food, especially in view of the fact that all these termites are blind. Such a method of differentiation would seem to require a segregation of the larvæ destined to be workers and soldiers in special combs destitute of fungi. It has yet to be decided whether the larvæ feed themselves, whether there is any production of proctodæal or stomatodæal food, or whether there is a constant succession of sexed insects.

When an inhabited comb is enclosed in a glass vessel, the termites eat off all the spheres and the superficial mycelium, and also the *Xylaria* as it develops. In the nest they eat the developing agaric and often follows the stalk of the mature form up to the surface. Cultivated plants attacked by fungi are soon discovered by them, and the diseased tissue is eaten away: in fact, the evidence at present to hand seems to indicate that *Termes redemanni*, *Termes obscuriceps*, and probably many other species, attack only diseased trees. They undoubtedly prefer wood which has been attacked by fungi. This raises the question whether the change in the wood through the action of the fungi renders it more palatable to the termites, and recalls the popular but most probably erroneous belief in their partiality for sugar.

The difference in colour between the larvæ on the one hand and the workers and soldiers on the other immediately suggests a difference in food. The former are milky white, while the abdomen of the latter evidently contains brown substances. In the intestine of the worker (*Termes redemanni*) I have found pieces of wood up to 250 μ long, fragments of violet-black hyphæ, and apparently the oval conidia of the spheres. The latter observation is open to doubt since so many spores of common fungi are of the same size and shape. If the workers eat the spheres, the spherical conidia should also be present in the alimentary canal, but I have failed to find any. In the soldiers I have only found wood and the violet-black hyphæ of saprophytic fungi. I was unable to find anything in the intestine of the larvæ : the probability that these are fed on proctodæal or stomatodæal food seems to have been overlooked. Winged termites (*i.e.*, sexed insects) captured as they left the nest have also been examined: in the peculiar intestinal pouch were found the spherical conidia of the spheres, fragments of wood, and violet-black hyphæ and spores, but these latter may have been obtained by eating some of the comb, and cannot be taken as proving that the sexed insects share the functions of the workers.

The non-occurrence of injured spheres on the comb suggests that each is devoured as a whole. If so, although the spheres are abundant, there does not appear to be at any time a sufficiently large number to supply food for the crowded hosts of larvæ, unless the growth of the fungus is abnormally rapid. There are however in most large nests a number of combs which contain only a few workers and soldiers, and the fungi on these might conceivably constitute temporary food reserves.

It may be mentioned that in the case of workers, soldiers, and larvæ enclosed in a damp chamber with the object of carrying out feeding experiments, the workers and soldiers died before the larvæ.

Other Fungi on the Comb.

The purity of the termite fungus cultivation has been remarked by all observers, though as has already been shown this purity is only apparent. On a normal comb just removed from the nest one never finds any fungus except the spheres and their mycelium, but the growth of *Xylaria* (*nigripes* ?) takes place regularly in bell glass cultivations after two days, before the development of any other fungi, and both its luxuriance and regularity of occurrence support the view that its mycelium vegetates in the comb substance, though it has not been found possible to distinguish it from the mycelium of the "spheres."

The comb material is probably at first sterilized by its passage through the alimentary canal of the termites. Döflein's suggestion that it is only partially sterilized, the spores of the cultivated fungus being uninjured, is scarcely credible : it would be more reasonable to suppose that the thick-walled ascospores of *Xylaria* escape injury. If the comb substance is sterilized, however, this would necessitate an inoculation of every new nest with fresh spores. Möller states that the leaf-cutting ants carry their fungus garden to a new nest, but the possible modes of establishment of new colonies by termites do not favour the supposition that a similar transference takes place in their case. Yet on the present evidence they could not obtain the agaric or "spheres" elsewhere: these have not yet been found apart from termite nests.

Assuming this supposed sterilization, there then arises the difficulty of maintaining a pure culture. Mites are quite efficient in introducing fungus spores into agar cultivations, and it is extremely unlikely that no spores should be similarly taken into the comb by the workers and soldiers. A system of weeding appears to be necessary to keep out other fungi, and it seems probable that *Xylaria* (*nigripes*?) is the one species which is kept under but not exterminated by this process.

Holtermann (7) states that in spite of all precautions *Mucor* and *Penicillium* appeared after one or two days on combs placed in crystallizing dishes. He considers that the spores are originally present in the comb, but are only able to develop under the altered conditions, and attributes the purity of the termite cultivation either to the fact that these foreign fungi cannot develop underground or that the termites adopt a system of weeding. The latter he considers improbable, since "if the comb before it is put in the dish is full of living termites, the growth under the influence of light still commences." This objection loses force when it is remembered that this growth is that of the Xylaria stromata, and that as previously stated these are constantly eaten off as long as a comparatively small number of termites is present. If the normal population could be retained, there would be no growth of *Xylaria*.

It will be shown later that for two forms at least Holtermann's first supposition is incorrect: other fungi than the agaric, spheres, and Xylarias can develop on the comb below ground.

Döflein (13) also remarks on the purity of the comb cultivation, but rejects the idea that it is due to the weeding out of foreign fungi: he suggests that the digested wood forms a medium on which only the spheres can grow. This view would necessitate a rapid change in the composition of the comb on removal from the nest, since other fungi then grow on it luxuriantly if allowed.

The production of the *Xylaria* is often accompanied by the growth of a parasitic *Mucor*, especially when the stromata are loose and collapse over the surface of the comb. When the culture is very moist, *Thamnidium* also occurs in abundance. In general these only appear after several days. *Aspergillus flavus* appeared on a rather dry comb at the end of five days.

The most regularly occurring foreign fungus, except the *Xylaria*, on exposed termite combs is a hyphomycete which forms red or yellow depressed tufts about 2 mm. diameter. These appear even on combs which are left to dry, but are then only on the damper under surface. They are visible at the end of four days, sometimes earlier. Apparently this is a species of *Cephalosporium*. When growing on combs from which the termites have not been removed, the insects eat the developing *Xylaria*, but, as far as I can judge, do not touch the red or yellow tufts. This mould developed under circumstances which show that it is quite capable of growing in the nest. In the earlier stages of investigation it was thought possible that the agaric might be cultivated directly by planting the termite combs. The latter were accordingly placed at the bottom of holes about a foot deep, and covered with earth. On re-opening one of the holes after fourteen days, it was found that the comb had collapsed into a light brown mass containing a large number of yellow tufts of the mould in question.

Another fungus whose development would not be prohibited by the fact that the termite comb is underground has been grown on six occasions on combs from nests of *T. redemanni* and *T. obscuriceps*: it has not been found on combs *in situ*. It first occurred in a pot cultivation in which the comb had been placed about two inches below the surface: the Xylaria appeared after four days and a number of small yellow discomycetes on the sixth day. The mycelium of these could not be traced to the comb and they were regarded as intruders.

In four other instances this discomycete appeared on combs under bell jars. On the fourth or fifth day a tuft of yellow hyphæ arose and spread in a tassel over the surface of the comb, passing thence to the glass and finally climbing for several centimetres up the side of the bell jar. Some of the hyphæ united into thicker strands, and the network of thick radiating threads with thinner cross-connections resembled at first sight the wandering plasmodium of a myxomycete. At the extreme edge of the network small yellow spheres developed, and on the tenth day the upper halves of these split away in the form of a hemispherical cap, leaving a small *peziza* in some cases with the shrivelled remains of the cap attached to the margin on one side. In one instance the tassel of hyphæ hung loosely down at the side of the comb without reaching the glass, and the discomycete was thus pendent at the tip.

In another instance the discomycete developed in clusters on combs left on the verandah and merely covered with a box. In all cases the combs were semi-deserted, *i.e.*, they did not contain larvæ when removed from the nest.

The ascophore of this species is pale yellow or bright orange yellow on the disc when fresh, and orange red when dry: externally it is paler and somewhat scurfy, being covered with a loose network of hyphæ which fix it below to the comb or bell jar. It often grows in clusters of about six. The diameter may reach 1 centimetre: the larger specimens are almost plane and have an undulating disc. The asci are narrow cylindric, 100–120 × 6–7 μ. with a slightly curved pedicel, and the spores, obliquely uniseriate, usually only occupy about one-third of the ascus: they are oval, continuous, 6 × 4 μ. The paraphyses are as long as the asci, slightly swollen upwards, septate, and in some cases branched. This agrees with the Herbarium specimens and Massee's re-description of *Peziza* *radiculosa*, B. and Br., which is said to grow on the ground with a long root or threads in the soil. This root is not developed in the specimens at present available. Whether there is any connection between the yellow mould and the *Peziza* has not yet been ascertained.

Mucor, *Thamnidium* and *Aspergillus* may be regarded as impurities which find access to the cultivations but are not present in the nest. The remaining two fungi are not easily accounted for. Both can develop underground, and it cannot be supposed that their spores would remain dormant in a medium and situation so admirably adapted for their growth. The presence of only two fungi on the combs *in situ* appears to demand a systematic process of weeding on the part of the termites.

Even this however would not quite explain the subsequent growth of these two fungi, since weeding would lead either to a complete extermination or to the development of a large quantity of yellow mycelium in the comb. If the yellow mould is exterminated its appearance in cultures is purely accidental; and there is no coloured mycelium to show that it vegetates in the comb material.

It seems most probable that the foreign fungi are weeded out by the termites, but that *Xylaria* (*nigripes* ?) defies their efforts to exterminate it. All the other fungi which develop in cultures are probably due to infection after removal from the nest. It should however be recorded that neither the hyphomycete nor the discomycete have been observed on the hundreds of diseased parts of plants which have been kept in the laboratory in the course of disease investigations.

Entoloma Microcarpum.

It had been hoped to place the relation of the conidial spheres to the agaric beyond doubt by growing them from the spores of the latter, but up to the present no germination of these spores has been obtained. The agaric appears to arise from the same mycelium, and the resemblance of the spheres to the "kohlrabi" heads of the mycelium of Möller's *Pholiota* (*Rozites*) *gongylophora* lends additional support to the supposition that they are stages of the same fungus.

The probability is increased by consideration of another Ceylon agaric which has no connection with termite nests. This species arises, not from the usual thread-like mycelium, but from a white mass which on examination is found to consist of innumerable small spheres. It was described by Berkeley and Broome from Ceylon specimens and figures under the name *Entoloma microcarpum.* Their description is:

"A (Entoloma) microcarpus. B. & Br. Caespitosus, edulis, albidus; Pileo convexo fisso acutissime umbonato; stipite farcto glabro; lamellis arcuatis pallide carneis liberis (No. 748, cum icone; Gardner, No. 71, cum icone).

"In large patches, on the flower borders and on grass. Peradeniya, September, 1868.

"Eaten by the natives.

"Caespitose: pileus $\frac{1}{2}$ inch across, dirty-white, darker towards the prominent umbo, soon split at the margin, even; stem $1\frac{1}{2}$ to 2 inches high, $\frac{2}{3}$ to 1 thick (*i.e.* lines, not inches), somewhat rooting, nearly equal, smooth, stuffed, at length partially hollow; gills about a line broad, rounded behind, free or nearly so; spores obliquely oblong, ·0002 to ·00025 in. long; mycelium forming little granular masses."

I found this species on April 26, 1905, after a rainfall of ·87 in. on the previous day and 6·33 in. for the month to date. It grew in profusion on the side of a mound of earth, part of which was occupied by a termite nest, at the base of a clump of palms. The heavy rain had washed away the surface of the mound and exposed the white, rounded, or linear masses of spheres. These completely filled small cavities which had no connection with the chambers of the termite nest. Lumps of mycelium which were placed on damp filter paper in a Petrie dish produced agarics by the following day, even if the cluster of spheres was only the size of a pea. It was seen that the balls of mycelium were not identical with the termite spheres, but as there was a termite nest in close proximity, the question of a possible connection was left open.

Unfortunately what should have been the wet season of 1905 was abnormally dry, and I did not find the agaric again until May 1, 1906. The rainfall for April was only 4·5 in., but 2·85 in. fell on the last five days. This time there was no doubt that the agaric was independent of termite nests. It occurred in various places on the flower beds, and in great abundance on a bank by the roadside. In the latter locality the mycelium was again exposed and some had been washed by the rain into the gutter, where it developed agarics among the dead leaves. The largest clump of mycelium formed a thin cake 15 cms. long and 6 cms. broad, but having been exposed was spoilt by the attacks of insects, especially a podurid, *Achorutes armatus*, Nicolet. The mycelium appears to lie generally at a depth of one or two centimetres and therefore when growing on a slope is soon laid bare by the rain. It seems probable that it is formed in this position at the beginning of the rains and is at once exhausted by the growth of the agarics. There are no strands of mycelium connecting adjacent clumps.

The spheres are ·4 to ·7 mm. in diameter and are massed together like fish roe : they lie in a compact mass, without any vegetable matter among them, and are bound together by fine hyphæ which run from each sphere to all others in contact with it : some of these hyphæ are united into strands like those which occur in the mycelium on the termite comb.

The interior of a sphere is a tangle of interlacing hyphæ swollen into irregularly oblong or oval cells, which may be produced in succession, or singly in the course of a hypha. There is no definite arrangement of the individual hyphæ in the interior, but radially-directed hyphæ near the circumference of the sphere show more regularity, and all these terminate at first in spherical or oval swellings (fig. 33). Some of these form single spherical cells 25 to 40 μ diam. which simulate a covering on the exterior : they are borne singly on the hypha and are at first terminal, but subsequent budding beneath makes them lateral; the new branches do not necessarily produce other spherical cells. Others form a succession of cells and after a short distance grow on again as a hypha (fig. 35). In rarer cases branching occurs in the chain of spore-like cells in the same way as in the spheres of the termite comb (fig. 36). Many of the radiating hyphæ with swollen ends grow out without producing special cells, and these appear to form the foundation of the next ball.

When the agaric develops, the spheres turn yellow and collapse. The large spherical cells are then indistinguishable and the ball appears to consist chiefly of hyphæ. The agaric is not formed in the interior of a sphere as in *Coprinus stercorarius*, but grows on the top of a cluster.

Though at first sight dissimilar, a close resemblance can be traced between the parts of the sphere of *Entoloma microcarpum* and those of the sphere on the termite comb. In both cases there is an outer covering of comparatively large spherical cells: these are borne in branched chains in the termite sphere but singly in *Entoloma;* in both cases also the same hypha may produce different cells on a side branch, and in neither do the spherical conidia give rise to hyphæ. The oval conidia of the termite sphere are matched as far as their branching is concerned by those of fig. 36 from the sphere of *Entoloma.* A more striking resemblance is seen when the termite sphere is placed in water or when it grows for a short time after the insects have been removed, for then radiating hyphæ with swollen tips are produced from the ends of the oval conidial chains just as they are from the chains of cells in the *Entoloma* sphere. Similar production of a chain of swollen cells which terminate again in a hypha has been shown to occur in the mycelium developed from these oval conidia of the termite sphere on agar.

The *Entoloma* spheres constitute a perfectly normal mycelium. Möller's "Kohlrabi" heads have been regarded as special structures evolved under the influence of ants. Küster

(17) regards them as galls, and Schimper (19) states that they represent a new structure which has arisen as a result of artificial selection exercised by the ants. Möller himself says "Die Kohlrabikopfe sind neue, morphologisch bestimmte Gebilde geworden, welche ihrer Fadennatur bereits so weit entfremdet sind, dass sie nur in seltenen Fällen noch nachtraglich zu Fäden auszuwachsen vermögen," and he traces in the species of ants investigated by him a gradually increased specialization of these structures. In the lowest form (nest of *Cyphomyrmex auritus*, Mayr. fig. 38) the swellings occur irregularly in the course of the hyphæ; they vary in size, and all stages from normal hyphæ to strongly swollen ones are found entangled together. A higher development is seen in the nest of *Cyphomyrmex strigatus*, where the size of the swellings is more regular though their shape and position is still variable. In *Apterostigma Wasmanni* they are cylindrical, but occur at the tips of the hyphæ. Finally, in the genus *Atta* (*Acromyrmex*), the swollen hyphæ ends are spherical and are grouped in more determinate heads than in the other three cases (fig. 37).

As long as the only recognized type of agaric mycelium consisted of a system of filamentous hyphæ sometimes united into strands, it was reasonable to regard the spheres of the ant nests as special structures evolved by cultivation in a mycelium which exhibited a strong tendency to produce irregular swellings on the hyphæ. Schimper states: "These peculiar structures are a product of cultivation comparable with Kohlrabi. The phylogenetic starting point of their evolution is to be found in the tendency of the fungus to produce all kinds of swellings."

But the re-discovery of the fact that a normal mycelium may consist of a mass of small spheres built up of swollen cells affords another explanation. It seems most probable that Möller's "Kohlrabihäufchen" are part of the *normal* mycelium of an agaric, and that their form is due to cultivation by the ants only in a small degree, if at all. The stages of development in the nests of different species may then be attributed to differences in the agarics cultivated, and not to differences in the intelligence of the ants. The intervention of the latter need only be demanded to limit or prevent the growth of those hyphæ which emerge from a sphere to form others connected with it, and if the spheres are eaten as soon as they are fully formed, this condition is attained. It may be re-stated that such hyphæ do grow from the termite spheres just before they decay, and it is conceivable that if the necessary conditions could be realized a mycelium similar to that of *Entoloma microcarpum* would be produced.

The spheres of the termite comb show a far higher development than any of the similar structures which occur in ants' nests. They possess a distinct stalk, are of definite shape, and consist of definitely arranged hyphæ bearing conidia of two kinds. But this may be considered to be due to an advance in complexity of the fungus rather than to any specialization induced by the termites.

Seeing that these "conidia" when *in situ* only produce a hypha from the terminal cells, it is probably incorrect to style them "conidia." They are never thrown off from the termite sphere. It might be argued that the insects eat the spheres before they are ripe, but in that case we should expect them to develop further when the termites are removed, instead of producing only hyphæ. The cells of the sphere of *Entoloma microcarpum* behave in exactly the same way. It seems most probable therefore that the termite spheres are part of a normal mycelium and not a conidial formation.

Entoloma microcarpum arises directly from the mycelial cluster of spheres and is gymnocarpous. Its pileus is at first conico-campanulate with an acute umbo, then almost plane; its colour is livid grey when moist, becoming darker towards the umbo; when dry it is dirty white. Young examples are slightly silky and striate; older ones may be radially streaked owing to the splitting of the surface layers. The margin is irregular, at first incurved, and in old specimens sometimes reflexed. The pileus is often split to the centre, and the flesh is thin. When fully expanded it measures 1·75 to 5 cms. in diameter. The stalk is white, longitudinally striate, somewhat bulbous and tomentose at the base, solid, slightly twisted, cartilaginous, 3—5 mm. thick, 2·5—3·5 cms. high. The gills are rather thick, white, ventricose, forked, with an irregularly lobed edge: they may be adnexed and separating, or free.

The spores are 5—7 by 3—4 μ, elliptic with a sub-lateral apiculus. Their colour has been variously estimated by different people I have consulted as pinkish-buff, dull salmon, or pink. The predominating hue is pink, and I have therefore left the species under Berkeley's name. *Entoloma stylophorum* B. & Br. appears to be an abnormal form of the same species.

Comparison with the "Fungus Gardens" of leaf-cutting ants.[*]

The "Fungus Gardens" of the leaf-cutting ants which were investigated by Möller resemble the termite combs in structure though they may attain a much greater size. Like the latter they lie free in the chambers of the nests.

The material of which the garden is built consists entirely of finely divided leaves. Pieces cut out of living leaves are carried into the nests, and after having been further bitten into small fragments are kneaded by the ants into small balls about $\frac{1}{2}$ mm. diameter. The upper and more recent part of the garden is bluish black, while the lower older portion where the leaf material has decayed is yellowish-red. The leaf balls are permeated by hyphæ which bind the whole structure together, and scattered over the surface of the passages are round white bodies consisting of groups of hyphæ which terminate in spherical heads. These groups are $\frac{1}{4}$—$\frac{1}{2}$ mm. diameter, though they sometimes occur so close together as to appear to form a single group about 1 mm. diameter : they are the "Kohlrabihäufchen" of Möller, the single swollen heads being "Kohlrabikopfe."

---

[*] The description of the fungi of the nests of the leaf-cutting ants is taken from Möller's account.

On the other hand, the material of the termite comb consists entirely of balls of finely divided wood and other vegetable substances which have passed through the alimentary canal of the insects, and these balls are cemented together by the secretion of the termites. The fungus is not abundant in the interior of the comb material and does not serve to bind the individual balls together. There seems to be more mycelium, both internal and external, in the garden of the leaf-cutting ants than in the termite comb. A difference in colour between the old and new material is also to be seen in termite combs. Apparently there is no difference in the distribution of the "Kohlrabihäufchen" in the garden, except that, as in the termite comb, these are less abundant in the more recently built part.

There is however a wide difference between the "Kohlrabihäufchen" and the termite "spheres." The former are merely tufts of hyphæ, each hypha terminating in a single spherical swelling, which is not cut off from the hypha by a cross wall. There is no regular arrangement of the individual hyphæ, and normal hyphæ occur intermingled with them. The termite sphere differs in having the primary hyphæ united into a distinct stalk, at the apex of which regularly arranged branches are produced. The formation of two kinds of cells in regular series has no parallel in the "Kohlrabihäufchen."

Möller succeeded in growing from the "Kohlrabikopfe" of *Atta discigera* a mycelium on which the "Kohlrabihäufchen" were reproduced. Only in rare cases did the spherical heads give rise to a hypha : instead, the new growth generally arose from the original hypha at some distance below the swelling. In the termite sphere the spherical conidia do not germinate, while the oval conidia produce abundant mycelium, but in no case has it been possible to reproduce the sphere. The growth of a hypha immediately beneath the swollen "Kohlrabikopf" resembles that in the spherical cells of the sphere of *Entoloma microcarpum*. The oval cells of the termite sphere in their natural position produce a hypha at the apex of a branch, and this also obtains in the chains of cells in the *Entoloma microcarpum* sphere, as well as in the less determinate "Kohlrabikopfe" found in the nests of *Apterostigma Wasmanni*, *Cyphomyrmex auritus*, and *C. strigatus.* In general there is a close resemblance between the behaviour of these various "conidial" formations.

The occurrence of agarics appears to be a much rarer phenomenon in the nest of the leaf-cutting ants than in those of the termites. When the fungus garden develops them, the upper surface is covered with a continuous layer of brown hyphæ. The growth of mycelium is more abundant, though the remains of the leaf balls can still be found amongst it. The hyphæ of this upper crust are continuous with the white hyphæ in the more loosely built "garden." The agaric is a Pholiota (*Pholiota gongylophora*) and grows in clusters directly on the upper layer, from which it is impossible to remove them without at the same time breaking away a considerable mass of the "garden." This condition seems to resemble *Entoloma microcarpum* more nearly than the termite agaric : in the former the agaric arises directly from the cluster of spheres and these remain attached when it is uprooted. There is no continuous sheet of hyphæ over the termite comb when it produces agarics, though the mycelium is then more abundant. The nests of the leaf-cutting ants are often covered merely by leaves, sticks, &c., and consequently an enormous development of the stalk of the agaric does not take place. Möller was fortunately able to germinate the spores of *Pholiota gongylophora* and to grow from them a mycelium which developed the "Kohlrabihäufchen."

T. redemanni and *T. obscuriceps* belong to the same subgenus, and all the fungi of their nests are identical. Möller found *Pholiota gongylophora* on one occasion on the nest of *Atta discigera :* three other occurrences are noted but the species of ant is not recorded. He states, however, that the "Kohlrabihäufchen" in all species of the genus *Atta* which he investigated are the same. Similarly those of *Apterostigma* are identical with each other but differ from those of *Atta*. The available facts seem therefore to indicate that the same fungus is cultivated by all species of the same genus.

A piece of the fungus garden of *Atta discigera* when placed in a sterilized crystallizing dish and moistened produced an abundant growth of erect hyphæ, 2 cm. high ; these ultimately covered the garden with a white mass of mycelium. Side branches of this mycelium bore club-shaped conidiophores over which were scattered flask-shaped basidia bearing chains of spores. After a few days strands 1 mm. broad were formed, and their component hyphæ produced irregular swellings. Single hyphæ also bore small spherical outgrowths along their whole length and subsequently ended in, or produced on side branches, a second type of conidiophore.

Möller styles these later hyphæ " Perlenfäden ": the conidiophore appears to be only a modification of the first, but the conidia differ in colour and shape, and in their growth on germination. The conidia of the first type produce a mycelium with spherical swellings and finally the original shape of conidiophore, while those of the second type give " Perlenfäden," mycelial strands with irregularly swollen hyphæ, and finally their particular conidiophore. It was not possible to grow one form from the conidia of the other. Saccardo says that these conidial forms are intermediate between *Aspergillus* and *Spicaria*.

If the termite comb is moistened and placed in a small vessel the resulting growth of mycelium fills the receptacle with a white mass of hyphæ, but, given sufficient space, the *Xylaria* previously described invariably arises. The conidiophore varies with the conditions under which it is grown, but all are easily seen to be modifications of one type, and no difference is observable in the colour or shape of the spore or in the mycelium produced on germination.

Möller conducted an extensive series of feeding experiments with the " Kohlrabihäufchen " of different nests, and found as a rule that after starvation for a few days any ant would eat the fungus taken from any nest, no matter to what species the nest belonged. This result, and the fact that they would also eat the conidiophore of any mould which was available, supports Holtermann's view that feeding experiments carried out with ants or termites in captivity are unreliable in forming a true estimate of their normal food.

A weeding out of other fungi as assumed by Möller appears to be a necessity in the case of leaf-cutting ants, since the leaf material is merely bitten into small fragments and is not digested as in the case of the termites. The passages of the fungus garden become narrower towards the upper layers and finally are only large enough to admit the smaller workers. For this reason, since foreign fungi are equally absent from large and small galleries, Möller assigns a special weeding function to the smaller workers alone.

In the termite comb a sterilization of the comb material probably occurs in its passage through the alimentary canal. This would not, however, prevent the subsequent growth of foreign fungi, and as these do not appear in the nest, a weeding process is equally necessary in this case also. There is no appreciable difference in the size of the comb passages, and hence the assumption that this function is allotted to special workers is superfluous. Two sizes of workers have however been observed in a nest of *Termes redemanni*.

Summary.

1. The existence of fungi in some termite nests is a matter of common knowledge. In Ceylon fungi are found in the nests of ground-inhabiting species, but have not yet been demonstrated in the nests of those which inhabit trees. The species here dealt with are *Termes redemanni*, Wasm., and *Termes obscuriceps*, Wasm.—both are ground-dwelling and mound-forming species.

2. The termite hill is built of the earth excavated in making subterranean chambers, and was originally only a convenient method of disposing of this material. The chimneys

form a permanent scaffold and have little effect on the ventilation of the nest: they are not correlated to the size of the nest in any degree.

3. The particles of earth used in constructing the hill and chimneys are covered with saliva in the nest, and are then brought up and placed on the new work.

4. The fungus grows on a comb which consists exclusively of the excreta of the termites. These combs occur in every chamber except the royal cell. There is no allocation of different chambers for special purposes. Combs vary in form according to the species of termite inhabiting them.

5. The mycelium on the comb bears small, white, stalked or almost sessile "spheres." These consist of branching hyphæ bearing either spherical or oval cells. The spherical cells do not germinate. The oval cells germinate readily, but it has not been possible to reproduce the "spheres" from them.

6. When the comb is old an agaric grows from it. This agaric appears in two forms, one of which has been assigned by various mycologists to *Lentinus*, *Collybia*, *Pluteus*, *Pholiota*, and *Flammula*, and the other to *Armillaria*. It develops in a cartilaginous, almost gelatinous, universal veil and is a modified *Volvaria*.

7. Sclerenchymatous cells occur at the base of the agaric stalk and in aborted agarics.

8. It has not been possible to germinate the spores of the agaric or to grow the sphere-producing mycelium from its tissues.

9. When the comb is enclosed in a bell jar, *Xylaria* stromata are produced. Sclerotia may also be formed: the same stromata grow from these. This *Xylaria* is probably *X. nigripes*.

10. The shape of the stroma and conidiophore depend on the age of, and amount of moisture in, the comb.

11. When sown on agar the spores of these reproduce the Xylaria stromata.

12. These stromata occur most abundantly on combs which have produced an agaric.

13. After continued rain *Xylaria nigripes* grows from deserted termite nests.

14. Other fungi which grow on combs removed from the nest include Mucor, Thamnidium, Cephalosporium, Peziza. As these are not found in the nest, though some of them are capable of development underground, it is probable that the termites " weed out " foreign fungi from the cultivation of the comb. The comb material is probably sterilized by its passage through the alimentary canal.

15. That the spheres form the food of the termites is probable, as in the case of the leaf-cutting ants: neither case can be considered definitely proved. *Termes redemanni* and *T. obscuriceps* undoubtedly prefer fungi, or wood which has been attacked by fungi.

16. Whether a difference in food causes the differentiation of termites into workers, soldiers, and sexed insects is not decided.

17. A Ceylon agaric, *Entoloma microcarpum*, possesses a mycelium composed of spheres of swollen cells : the details of these spheres resemble the parts of the termite spheres, but are not so highly developed.

18. It is most probable that the " spheres " in the termite comb and the "Kohlrabihäufchen" of the leaf-cutting ants investigated by Möller are parts of a normal mycelium, and that their shape is modified by the insects only in a very slight degree, if at all.

19. The available evidence appears to show that the " spheres " are part of the mycelium of the *Volvaria*, but it has not been possible to connect these forms experimentally.

My thanks are especially due to Mr. E. E. Green for the determination of the species of termite, assistance in the actual investigation of the nests and in the entomological details of the paper, and valuable criticism of the whole: and also to Mr. H. F. Macmillan for the photographs reproduced on Plates IX. and X.

BIBLIOGRAPHY.

1. *Smeathman.*—Phil. Trans. Roy. Soc., **71** (1781), pp. 139–192.

2. *Berkeley, Rev. M. J.*—Hooker's Journal of Botany, **6** (1847), p. 479.

3. *Berkeley & Broome, C. E.*—Journn. Linnean Soc., **11** (1870), pp. 514, 537.

4. ——— Journ. Linnean Soc., **14** (1875), p. 119.

5. *Penzig, O., & Saccardo, P. A.*—Malpighia, **11** (1897), p. 496.

6. *Holtermann, C.*—Mykologische Untersuchungen aus den Tropen (1898), p. 107, & pl. 12, fig. 5.

7. ——— "Pilzbauende Termiten," in Botanische Untersuchungen, S. Schwendener (1899), pp. 411–420.

8. ——— "Fungus Cultures in the Tropics." Annals Roy. Bot. Gard. Peradeniya, **1** (1901), pp. 27–37.

9. *Hennings, P., & Nyman, E.*—Naturw. Wochenschr., **14** (1899), p. 28.

10. ——— Monsunia, **1** (1899), pp. 18, 19.

11. ——— Monsunia, **1** (1899), p. 154.

12. *Hennings, P.*—Hedwigia (1904), p. 183.

13. *Döflein, F.*—" Die Pilzkulturen der Termiten." Verhandl. d. Deutsch. Zool. Gesellschaft (1905), pp. 140–149. Translation in "Spolia Zeylanica," 3 (1906), pp. 203–209.

14. *Froggatt, W. W.*—" White Ants." Dept. Agr. New South Wales. Misc. Publications, No. 874 (1905).

15. *Dudley & Beaumont.*—Trans. N. York Ac., **8** (1889), p. 91.

16. *De Bary.*—Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria (English Translation).

17. *Küster, Dr. Ernst.*—Pathologische Pflanzenanatomie (1903), p. 124.

18. *Möller, A.*—Die Pilzgärten einiger sudamerikanischer Ameisen (1893).

19. *Schimper, A. W. F.*—Pflanzen-Geographie (English Translation), pp. 137, 138.

20. *Brefeld, O.*—Botanische Untersuchungen uber Schimmelpilze. Heft. 4.

21. *Berkeley & Broome.*—Trans. Linn. Soc., **27** (1871), p. 151.

22. *Massee, G.*—Journ. Linn. Soc., **31,** p. 480.

EXPLANATION OF PLATES.

Plate V.—Mound nest of *Termes redemanni*, with a solid apex, and a single "chimney" on the right. The nest was built round a branch of a rose bush: this emerges just below the chimney. The branch was not attacked by the termites, and bore healthy shoots and leaves. Herbaceous plants are growing on the nest.

Plate VI.—Section of the same nest. The apex (above the chimney) is solid, the apparent hollows being caused by the tool used in cutting the section. The chimney shaft runs down on the right, and the orifices of the small lateral galleries may be seen on its wall. The subterranean portion and the royal cell are not shown.

Plate VII.—Three combs from a nest of *Termes redemanni*: the upper layers are newly built, and have no "spheres" on the outside: the latter are seen at the edges of the galleries. × $\frac{1}{3}$

Plate VIII.—Two combs from a nest of *Termes obscuriceps*: the lower one bears numerous aborted agarics of the *Pluteus* form. The open galleries on the top distinguish this comb from that of Plate VII. × $\frac{1}{2}$.

Plate IX.—Developing agarics (*Armillaria* form) on the comb of an underground nest of *Termes redemanni in situ*. The stalks of the five which have appeared above ground are at the back of the cavity. × $\frac{1}{4}$.

Plate X.—Developing agarics (*Armillaria* form) on a comb of *Termes redemanni*. × $\frac{1}{2}$.

Plate XI.—Mature agaric. The Pluteus form with a thin cartilaginous covering on the pileus; developed in moderately fine weather. × $\frac{1}{2}$.

Plate XII. A.—Mature agaric. The Pluteus form with a radially rugose pileus; developed in rainy weather. A portion of the comb remains attached to the stalk. × $\frac{1}{3}$.

Plate XII. B.—Horizontal section of the comb of *Termes redemanni*, showing "spheres" on the roofs of the passages. At the edge the individual balls of comb material may be distinguished. Slightly magnified.

Plate XIII. A.—Simple stromata, six days old, developed on a piece of comb under a bell jar, curving towards the light. On the addition of water this produced branched stromata. The mycelium on the right is that of *Peziza radiculosa*, and bears a single ascophore at the lower edge of the largest white patch. × $\frac{1}{3}$.

Plate XIII. B.—Branched stromata (non-conidiferous), grown under a bell jar on comb which had produced an agaric. 4 days' growth. The diffuse mycelium is chiefly a *Mucor*. × $\frac{1}{2}$.

Plate XIII. C.—The stromata of XIII. B., 5 days' growth. × $\frac{1}{2}$.

Plate XIV. A.—Stromata developed in 6 days on comb which had produced an agaric. × $\frac{2}{5}$.

Plate XIV. B.—Stromata developed from the same comb as XIV. A, when planted in a pot. 14 days' growth. Photograph taken from above. × $\frac{1}{2}$.

Plate XV.—Developing stromata: 3 days' growth. × $\frac{2}{3}$.

Plate XVI.—Seven days' growth of the stromata of Plate XV. The remainder subsequently branched dichotomously at the apex. × $\frac{1}{2}$.

Plate XVII. A.—*Entoloma microcarpum*, B. & Br.; with mycelial mass of spheres. This mass is continuous, but is stained in places by the red earth, and therefore obscured in the photograph. × $\frac{2}{3}$.

Plate XVII. B.—Part of a termite "sphere": the hyphæ on the upper margin have been displaced in mounting. × 65.

Parts of the "Sphere" on the Termite Comb.

Plate XVIII.—Fig. 1. Hypha producing spherical and oval cells. × 300

Fig. 2. Another, showing branching in the chain of spherical cells. × 300.

Fig. 3. Hypha from the exterior of a sphere, with spherical cells only. × 300.

Fig. 4. 5. Hyphæ from the interior of a sphere, bearing oval cells only, with aseptate swellings on the hypha. × 300.

Fig. 6. Hypha from a sphere, showing developing side branches. × 300.

Fig. 7. Four days' growth of the detached oval cells in water. × 300.

Fig. 8. Four days' growth of the detached oval cells in comb extract. × 300.

Plate XIX.—Fig. 9. Stages in the branching of the chains of oval cells. × 300.

The Agaric.

Fig. 10. Ring of the "*Armillaria*" form of *Volvaria eurhiza*: the stem bears scales of the same texture below. Nat. size.

Fig. 11. Longitudinal section of a developing pileus of the "*Armillaria*" form. Nat. size.

Fig. 12. Section of stem, showing ring : on one side it is apparently continuous with the lower portion of the stem, on the other united to it by a collar. Nat. size.

Fig. 13. Section of stem, showing an oblique ring. Nat. size.

Fig. 14. Base of stem of the "*Pluteus*" form. Nat. size.

Fig. 15. Base of stem of the "*Armillaria*" form. Nat. size.

Fig. 16. Sclerenchymatous cells from an aborted agaric. × 30.

Fig. 17. An annular cell from an aborted agaric. × 300.

Plate XX.—Fig. 18. A developing agaric, "*Armillaria*" form enclosed in a cartilaginous coat which is continuous with the superficial comb mycelium. Nat. size.

Fig. 19. An older stage, broken off the comb and showing the edge of the cartilaginous coat. Nat. size.

Fig. 20. A developing agaric showing differentiation of the internal tissue at the apex. Nat. size.

Fig. 21.–23. Developing agarics, showing formation of the gills and the solid base. Nat. size.

XYLARIA (*nigripes?*).

Fig. 24. A pot-grown conidiferous stroma. × 6.

Fig. 25. A developing conidiophore of fig. 24. × 300.

Fig. 26. A fully developed conidiophore of fig. 24: most of the bassidia omitted. × 300.

Fig. 27. A developing conidiophore of fig. 24, with two whorls of basidia. × 300.

Fig. 28. Two conidiferous stromata growing from a sclerotium formed on the comb in a damp-chamber cultivation. Nat. size.

Fig. 29. Part of a developing conidiophore from a loose, simple stroma. × 300.

Fig. 30. Ripe branchlet of a conidiophore of the type of fig. 29. × 300.

Fig. 31. A branchlet from a conidiophore of the stromata of Plate XIV. A. Half the basidia omitted. × 300.

Fig. 32. Terminal branch of a conidiophore from a stroma grown on comb-extract agar. × 300.

ENTOLOMA MICROCARPUM.

Plate XXI.—Fig. 33. Terminal swellings of the hyphæ of the sphere of *Entoloma microcarpum*: these grow out to form new spheres. × 300.

Fig. 34. Spherical cells from the exterior of the sphere of *Entoloma microcarpum*. × 300.

Fig. 35. Chains of swollen cells from the sphere of *Entoloma microcarpum*; growth continuing as a simple hypha. × 300.

Fig. 36. Branched chains of swollen cells from the sphere of *Entoloma microcarpum*. × 300.

Fig. 37. "Kohlrabihäufchen" from the nest of *Atta (Acromyrmex) discigera*. Mayr. × 270. After Möller.

Fig. 38. "Kohlrabihäufchen" from the nest of *Cyphomyrmex auritus*, Mayr. × 150. After Möller.

APPENDIX.

The exit of winged termites, *i.e.*, the male and female insects, from the nest usually takes place at night, and, therefore, although the fact is well advertised by their appearance in large numbers round the lamps of the bungalows, the actual circumstances connected with their departure are not often observed.

On leaving the bungalow at eight o'clock, one morning, large numbers of winged termites were observed flying along the road and over the adjoining tea in full sun. A quarter of a mile away, the nest from which they had come was found by the roadside. It was a subterranean nest with six small chimneys from which the termites were still emerging in scores. The chimney openings had been narrowed, in some cases to mere slits, so that the insects came up side by side in a single row. On reaching the edge they flew off immediately. Several lizards which had been snapping them up as they emerged ran off at our approach, but one which had apparently eaten too many sat gazing stupidly across the mouth of a chimney, his mouth fringed with termite wings. The workers and soldiers were running about inside and outside the chimneys, and numbers of them were wandering among the surrounding grass. They were not engaged in building, as they usually are when seen at the mouth of a chimney, nor did they seem to be making any endeavour to prevent the escape of the winged insects. The latter fly to a considerable distance, and in this case were observed more than half a mile from the nest. On returning, four hours later, it was found that all the chimneys had been closed, and when they were broken open no winged termites were found inside. This was a nest of *T. obscuriceps*.

A flight of *T. redemanni* was observed about two months later from a similar nest. This time it took place shortly after 6 o'clock in the evening during heavy rain. There was the same narrowing of the exits, the same assembling of workers and soldiers outside the nest, and the closure of all openings when the winged termites had departed. Another smaller flight from the same nest was observed three weeks later.

This flight usually occurs at night, and generally after or during rain. On one occasion when a day and night of tropical showers had succeeded several weeks of dry weather, I travelled at dawn the next day through miles of winged termites.

Another flight of *T. redemanni* was watched under more favourable conditions. The nest was under the floor of a verandah, and the termites emerged through about a dozen widely separated openings between the bricks which formed the sloping face of the gutter. It was raining heavily the whole time. The exodus began at 5.45 P.M. was at its height at 6, and was completed at 6.15. By 6.30 all the openings but one had been closed, but the closure was not complete; in each case a row of small openings was left, large enough to admit workers or soldiers, but too small for the winged insects. The remaining hole was closed at 7.10 P.M. This was the one which was being particularly watched, and it is very probable that the constant illumination altered the normal course of events to some extent, as the winged insects would be thereby induced to remain longer in the neighbourhood of the nest than they would under ordinary conditions. As in other cases, the workers and the soldiers were congregated outside the nest. Most of the sexed insects dropped their wings soon after emergence, but one which was imprisoned in a glass tube retained them until it died thirty-six hours later. They began to pair at once, some before they had shed their wings, following one another about in strings, but I did not see any actual pairing. When the exit of winged insects had ceased, some of them re-entered the nest. This occurred at every opening, but at the one especially observed more than thirty entered. Most of these had shed their wings, but many still-winged insects went in, and of these only two came out again. One was prevented from entering by a soldier, and flew away with the soldier attached to its head, but this was the only instance which suggested any selection. Some, which attempted to enter when the workers were closing the entrances, were walled up in the clay.

When all the holes were thus closed, except for the small openings previously mentioned, the workers and soldiers organized processions which wandered apparently aimlessly in the neighbourhood of the entrances. At 8.50 all the holes were completely closed, but there seemed no diminution in the number of insects outside, and at 10.45 P.M. several hundreds were still wandering about within a foot of the nest, accompanied by four wingless and two winged males or females. There was no trace of them next morning.

Though these two nests of *Termes redemanni* are on either side of the entrance to my bungalow, I had not observed any flight of termites from them during the previous 18 months.

The importance of this flight in the economy of the termites is unexplained. The majority of the insects are undoubtedly eaten by lizards, toads, birds, &c., and those which escape this fate cannot found a new colony without the assistance of workers. Froggatt suggests that they are adopted by wandering bands of workers. But what purpose is served by this enormous waste of individuals is not clear. There can be no question of overcrowding in a termite colony. It is however not yet ascertained whether the production of winged insects is a regular phenomenon, or whether it depends on some condition in the nest which only recurs at irregular intervals. The frequent occurrence of these flights immediately after rain is another obscure point which seems to suggest that the winged termites are retained in the nest until the weather is favourable, but out of the large number of nests which I have opened only two contained winged insects, and these were not quite mature.

The Flora of Ritigala, an isolated mountain in the North-Central Province of Ceylon; a study in Endemism.

BY

J. C. WILLIS.

SO far as I am aware, the only investigation of the botany of this remarkable mountain hitherto made is that of my predecessor Dr. Trimen in 1887, described in his "Note on the Botany of Ritigala," in the Journal of the Royal Asiatic Society (Ceylon Branch) for 1888. As this interesting little paper is practically inaccessible to botanists, I propose to incorporate the bulk of it in the following notes, and begin with a quotation of the first few paragraphs, which will help to explain my own object in further investigating the flora.

"The main object of my ascent of Ritigala was to investigate its vegetation and collect specimens of its plants. I had often, during my journeys along the North road, looked with interest at the striking outline of this fine hill, and determined to take the first opportunity that offered of examining its flora, which I knew had never yet been seen by botanically trained eyes, and at length I availed myself of some leisure in July, 1887, and of Mr. Green's companionship. Unfortunately, owing to the prolonged drought for several previous months, vegetation was then in a very torpid state. Many trees and shrubs were dried up and nearly bare of leaves, and very few were in flower or seed; thus some were indeterminable, and the present notes give doubtless but an imperfect account of the flora. Another visit is needed soon after rains to complete our knowledge of the botany of this hill, but so far as it goes, the following may be considered to convey an accurate idea of the subject.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. VIII., Pt. II., November, 1906.]

"Though actually itself of no great altitude, Ritigala is the highest ground intervening between the central mass of the Ceylon mountain system and the very similar hills of Southern India. From its complete isolation and abrupt rise on all sides, directly from the low country, it presents a more imposing appearance than would be expected from its real height (2,506 feet); and this is always over-estimated by those endeavouring to fix its altitude by the eye alone.

"The nearest ground of equal height is to the south, about 40 miles, in the foothills of North Matale, where however, the hills run up to over 4,000 feet, and thus enter our real mountain zone. None of the numerous other hills which stand up out of the great forest-covered plain of central Ceylon attain so great a height as Ritigala; the peak called Friar's Hood, in the Eastern Province (2,147 feet) being the nearest approach. The hills known as "Westminster Abbey" (1,829 feet) and "Gunner's Quoin" in Tamankaduwa (1,736 feet) come next; and the better known ones, Dambulla, Sigiri, and Mihintale, are all much below this last elevation.

"Now, though the botany of these lower rocky hills is often very interesting, and they are the home of many curious, rare, or very local species, the general character of their vegetation does not differ in type from that of the great dry forest tract spread out around their bases; and it was one of the principal points in the ascent of Ritigala to find out whether, as reported, there occurred any vegetation of a different character at its summit. It was the confirmation of this rumour, that the cap of Ritigala really does present a characteristic little oasis of vegetation distinct from the dry country type surrounding it, that has made it worth while to write this botanical addendum to Mr. Green's paper.

"The interest of this remarkable little flora lies in its small extent. It all occurs, I suppose, within 100 feet of the summit, and though I am unable to give its actual area, it cannot be many acres, as the ascent is steep. In this small space are found a number of species belonging to the flora of the wetter districts of Ceylon, and it is obvious that their existence here must depend on an atmosphere often heavily charged with moisture. The complete isolation of this summit causes it to be frequently surrounded with and bathed in mist, especially during the south-west monsoon, which is a time of drought over the country below. It is indeed striking evidence of this to observe that, at this comparatively low elevation, the branches of the stunted trees are draped with pendent masses of Meteorium moss and lichens, like those on our high mountains.* "

To myself, as a student of geographical distribution, the interest of this flora rather lies in the question of how it got there. Ritigala is a fine three-peaked narrow ridge, several miles long, running north and south, and separated by about 36 or 40 miles from any equally lofty summits to the south, in which direction alone do other high mountains lie. It lies well in the centre of the "dry" zone of north Ceylon, and it is fairly evident from the general configuration and climatology of Ceylon that these 40 miles, or at any rate the more northern 25 of them, must always have been "dry" country, *i.e.*, that they must always have had their rain mainly in the north-east monsoon from September to December, and have remained almost rainless for the rest of the year. The mountains to the south being very old, and the monsoons having blown as at present for a vast period, it is evident that this must be the case. There are damp spots round the tanks or great irrigation lakes that irrigate these regions, and under the bunds or dams that hold up their waters one finds occasional patches of a vegetation more resembling that of the low-country of south-west Ceylon, but nowhere does one find any trace of the plants of the mountain regions.

As there was of course the possibility that Ritigala might have comparatively recently risen, or have been lowered, I referred to Dr. A. K. Coomaraswamy, the Director of the

---

* The remainder of the paper is an enumeration of the plants found, which is incorporated below with the list in this paper.

Mineral Survey, who writes "the latest movements seem to have been downwards, which is shown by the occurrence of submerged littoral concrete. There are also *legends* of submergence. I think the existence of the islands and paars of Adam's bridge are the remains of a more continuous land surface, broken up by erosion and submergence. This would tend to show that the top of Ritigala might have been somewhat *higher* than it now is, a few thousand years ago.

"What happened before that? The evidence is scanty. Mr. Parsons' observation on p. 15 of my Administration Report for 1905, which I send, tends to show that a previous elevation amounted to as much as 60 feet. So that *previous* to that again the elevation of Ritigala must have been at least 60 feet *less* than it is now, and, indeed more, for the subsequent depression has to be added on. This is all there is to say—the evidence is scanty, but is not opposed to the theory that an elevation of more than 60 feet took place in Post Tertiary times. The effect of that elevation was subsequently reduced by the amount of the latest depression; not very much, perhaps."

The great bulk of the peculiar flora of Ritigala lies within 100 feet (vertically) at most of the summit; so that prior to the rise of 60 feet there was perhaps but little of it. But this amount of elevation is not sufficient to bring the mountain top within the limits of a wetter zone than it previously occupied, and I think that consequently we may leave the question of elevation and depression out of consideration.

It would therefore seem practically certain that the peculiar more or less montane "moist region" flora of the top of Ritigala must have got there entirely or almost entirely by leaping in one operation the 40 miles that separate it from the Matale hills to the south, or the 280 miles from the Palnis or other hills of Southern India. None of the other hills of the dry zone appear to be lofty enough for the survival of this flora, even if they lay in such positions—which they do not—as to shorten the gaps to be traversed.

That the peculiar flora found on Ritigala can survive there is due to the dampness of the spot. Isolated, lofty, and steep, Ritigala summit condenses a great deal of vapour, and is commonly cloud-capped at night even in dry weather, and during the south-west monsoon is often constantly bathed in mist and perhaps rain, though the country below is suffering from a rainless wind. My own visit, on March 22 and 24, 1905, illustrated this peculiarity of the spot. Though the rest of the country was very dry, Ritigala was cloud-capped nightly for many days, and on my second ascent I was caught in a heavy thunderstorm at 4.30 P.M., during which probably $\frac{1}{4}$ in. of rain fell over the eastern side and summit of the hill.

My ascents were made from Galpitigala, where by the courtesy of the Director of Public Works I occupied the Public Works Department bungalow. The first few miles are upon the level on the eastern side of the mountain, through old chena land and patches of jungle. Opposite the chief summit, the path turns westwards, and thenceforward there is a steep ascent to the top. Even at the base of the hill the effect of the moister climate is visible in the green appearance of the jungle and grass, and after passing the ruins which strew the lower slopes the jungle is very fine, containing large trees and a rich undergrowth, among which are a good many ferns—rare in the dry zone—and a lot of Geophila repens. Further up, in the cooler and moister air above 1,000 feet, the flora assumes a greener and more "up-country" look. Ardisia Missionis is very frequent all the way to the top, also Begonia malabarica, (both with green and with speckled leaves) and Ophiorrhiza Mungos, Calami, Caryota urens, Asplenium Nidus, and other things were also noticed. At about 2,000 feet the flora begins to show a more distinct montane element, Anoectochilus zeylanicus, Strobilanthes, and other hill forms, and many ferns, becoming common. Peperomia pseudo-rhombea var. tenuis is very common in rock crevices all the way up, and shows considerable variety of form, having particularly large leaves in very shady places and rich soil. Mosses abound all the way up, but I could not find any in fruit. Splendid large butterflies abound on the way up, and at the summit I noticed others, which may be forms only found in the moist region; I regret that having no net I could not capture any of them. Procris laevigata is common on rocks at 1,800 feet and Munronia pumila was abundant in flower. Acalypha lanceolata and orchids began to be numerous at about 2,000 feet. Carex leucantha is not uncommon in the grass near the top Piper sp. is abundant.

At the steps about 100 feet below the summit, one climbs a steep fairly open rock face, which in the shadier parts is covered with Dendrobiums and other orchids, and has fine cactus-like Euphorbias, a Heptapleurum, and other trees upon or overhanging it. Here, or near here, I found Cyanotis fasciculata, Exacum zeylanicum var. Ritigalense, Leucas biflora, Desmodium Wightii, Coleus elongatus, Hoya ovalifolia, Pouzolzia Walkeriana, Gynura lycopersicifolia, and other things. Above this the path runs gently southwards up to the summit, along the nearly flat narrow ridge, which is perhaps one-third of a mile long and all above 2,400 feet. There is an old bungalow site near the top on the east side with a few orange trees round it, but I could see nothing else that looked as if it might have been introduced at the period when this station was a sanitarium for the North-Central Province.

At the summit one might quite well be "up-country," it being covered with gnarled stunted trees, not over about 15 feet high, with small xerophytic leaves, and heavily draped in hanging mosses and lichens, while their branches were covered with orchids. Such a wealth of these plants I have never seen elsewhere. The trees are more blown from the south-west than from the north-east, and the slope on the western side seems to be drier than that on the eastern, but I did not go far down, as it is very precipitous, and it is difficult to get through the trees. The commonest tree is Eugenia spicata; Cleistanthus pallidus is very common, also Erythroxylon obtusifolium, Salacia reticulata, &c. The trees and rocks at the summit and for some way down are covered with orchids and with a fair number of ferns, and the latter are abundant in the undergrowth, especially on the damper and shadier eastern side. Lycopodium Phlegmaria is epiphytic in places.

The great abundance of wind-carried forms strikes one at once in the orchids and ferns, and several bird-carried trees are also very common. Going down the hill one finds fewer and fewer of them, until they disappear at the foot, where it is obviously warmer and drier. Trimen is wrong in stating that the peculiar flora of Ritigala all occurs close to the summit, and this being so, I hope at some future time to investigate at any rate the flora of Friar's Hood, which is almost as lofty as Ritigala, and even further from the main mountain chain.

A list of the plants observed follows, arranged and named in the order followed in Trimen's Flora of Ceylon, but though this list is as complete as I can make it, it must not be assumed that it is an absolutely complete flora. The area to be explored is considerable, especially as soon as it became evident that the peculiar flora of Ritigala was to be found to some extent lower down than the summit, and the summit area itself requires more careful search. From Galpitigala one cannot reach it before 9.30 and has to leave at 3. Much of the vegetation, too, occurs in places somewhat difficult of access. A careful search just after the rains, say in early February, would probably be rewarded with the discovery of other things. My own intention had been to visit the mountain at that time, but I was delayed, and must consider myself fortunate to have seen it when I did. Unfortunately the very serious accident that befell me within a few days has somewhat destroyed the vividness of my recollections, but I had already entered everything that had occurred to me in my note books.

List of the Flora of Ritigala, described in the order adopted in Trimen's Flora of Ceylon.

1. *Polyalthia Korinti* Benth. and Hook. f. The carpels are fleshy, and the plant is probably bird-carried, but it is common in the low moist zone, and perhaps in the dry.

2. *Cyclea Burmannii* Miers. Common in the low moist country ; bunches of fruit like small grapes, bird-carried. The specimens from Ritigala are slightly different from any already in the Peradeniya herbarium. Their leaves are pilose hispid with scattered longish hairs on the upper surface, especially at the cup above the insertion of the stalk, and markedly ciliate at the margins. Some specimens of C. P. 1,049 labelled by Thwaites " Peradeniya, &c., &c." have the margins rather ciliate, but not so well as in the Ritigala specimen. Some of the Peradeniya herbarium specimens have a few hairs in the cup over the insertion of the stalk, but none are so hairy as the Ritigala specimen.

3. *Capparis Moonii*, Wight. Fruit large, to 4 inches in diameter. Seeds big and pinkish. Bird-carried. Occurs in Uva at Welimada, &c., and may therefore occur in the dry region proper.

4. *Pittosporum zeylanicum*, Wight. Also found by Trimen. Seeds with a pulpy orange-red testa, bird-carried. Moist low country and to 6,000 feet.

5. *Erythroxylon obtusifolium*, Hook. f. Also found by Trimen. Abundant on the summit. Drupe ½ inch in diameter, scarlet, bird-carried. Common in the lower montane wet zone; the nearest recorded locality is Hunasgiriya, near Matale.

6. *Glycosmis pentaphylla*, Corr. A small form, with leaflets to 2½ inches alternate, shortly stalked. Flowers in small axillary racemes, or (in one case) panicles, one inch long. Fruit a berry, bird-carried ; forms much of the undergrowth in the dry region.

7. *Gomphia angustifolia*, Vahl. Common at the summit. Ripe carpel purple black and fairly large. Occurs in the dry zone.

8. *Munronia pumila*, Wight. On the side of Ritigala. Capsule with narrowly winged seeds, perhaps wind-carried, though extremely improbably. Occurs in the dry zone, though rarely.

9. *Walsura Gardneri*, Thw. Summit. Fruit dull orange and seeds with a white aril, bird-carried. Only recorded from Hantane and Alagalla, both of them mountains near the northern end of the moist zone, and from 2,000 to 3,000 feet.

10. *Olax zeylanica*, L. Summit. Fruit drupaceous, scarlet, half covered by the enlarged calyx, bird-carried. Common in the moist low country.

11. *Salacia reticulata*, Wight. Summit. Fruit a scarlet berry, bird-carried; rather common in moist low country to 3,000 feet.

12. *Vitis pedata*, Vahl. Summit. Fruit a berry, bird-carried. Common in the dry zone.

13. *Desmodium Wightii*, Grah. Summit. No arrangements for transport, so far as can be seen. Common in the low country, and also occurs in South India, but as it occurs about Badulla, is not altogether unlikely to occur in the dry zone, and may progress by way of tank bunds.

14. *Dalbergia Championii*. Thw. Summit. Rather rare in the moist region 2,000–4,000 feet. Pod very large and compresssed, with one flat seed inside, about 2¾ by ¾ inch, flat and thin. It *may* have been carried by wind, but this is extremely improbable, for in Ceylon the wind is as a rule very gentle. The other countries recorded for this species are South India and Penang to Borneo, so that it must be able to travel in some way, but it remains doubtful how it reached the summit of Ritigala.

15. *Weihea zeylanica*, Baill. Summit. Fruit a fleshy capsule, perhaps bird-carried. Common in the dry zone.

16. *Eugenia spicata*, Lam. The commonest tree at the summit. Fruit fleshy, bird-carried. Very common in the dry country.

17. *Eugenia rotundata*, Trim. Abundant at the summit (and *fide* Trimen). Fruit a scarlet berry, bird-carried. Common in the low country on rocky hills especially in the " intermediate " zone, between the wet and dry zones. Nearest recorded locality Lagalla, about forty miles to the south.

18. *Osbeckia aspera* Bl. var. *Kleinii*, Arn. Summit (and *fide* Trimen) Seeds very small, perhaps carried in lumps of mud, but the plant is common in the dry zone.

19. *Memecylon umbellatum*, Burm. f. (?) The twigs of this specimen are without flowers, so that the determination cannot be guaranteed. Summit. Very common in the dry zone.

20. *M. capitellatum* L. (?) Identification not to be guaranteed, as the specimen is very small. Summit. Common in the dry zone.

21. *Cephalandra indica*, Naud. Summit. Fruit a scarlet cylindrical " berry," bird-carried. Common in the dry zone.

22. *Begonia malabarica*, Lam. Summit and slopes (and *fide* Trimen). Seeds very small, *possibly*, but very improbably, wind-carried ; much more probably carried in lumps of mud attached to the feet of birds, and this the more probably, as this species mainly grows upon wet rocks, where birds are quite likely to walk about, and where mud would be very likely to stick to them. Common on wet rocks in the moist hills. This specimen is slightly different from any in the Peradeniya herbarium, but as practically no two are alike, no stress can be laid upon this. The plant may possibly occur in wet places in the dry zone.

23. *Rhipsalis Cassytha*, Gaertn. Summit. Fruit a fleshy berry, bird-carried. Common on tree trunks, rocks, &c., in the moist region, to 4,000 feet.

24. *Heptapleurum stellatum*, Gaertn (?) Summit. A young plant only, but almost certainly this species, as it has the leaf of the genus, and agrees much more closely with this than with any of the other species. Fruit a berry, bird-carried. Common in the moist low country, and to 3,000 feet.

25. *Hedyotis fruticosa*, L. Summit. Fruit dehiscing and giving many small seeds, perhaps carried attached to the feet of birds. Common to 3,000 feet in the mountain zone.

26. *Anotis nummulariformis*, Trim. (?) Specimen not in flower, so the indentification cannot be guaranteed. The specimen differs somewhat from all the existing herbarium specimens both of this species and of *A. nummularia*, Hk. f., but seems to come nearer to the former. Summit. Capsule about ⅛ inch, indehiscent, so its mode of reaching Ritigala must remain doubtful. Common in the wet mountain zone.

27. *Canthium didymum*, Gaertn. f. Ascent (*fide* Trimen). Drupe, bird-carried. Common in moist zone to 4,000 feet.

28. *Ixora coccinea*, L. Summit. Fruit fleshy, bird-carried. Common in the low moist country to 2,000 feet.

29. *Pavetta indica*, L. Summit. Fruit fleshy, bird-carried. Common in the low country and in the dry zone. There do not appear to be any of the usual bacterial warts upon the specimen gathered, a fact, if it apply to all the plants on the mountain top, which would indicate that the plants came as seeds.

30. *Morinda umbellata*, L. Summit. Fruit-head scarlet, fleshy, bird-carried. Common in the moist region to 4,000 feet.

31. *Psychotria Thwaitesii*, Hk. f. (?) Specimen only in bud, so identification uncertain. Summit. Fruit a berry, bird-carried. Common in the moist zone from 1,000 to 6,000 feet.

32. *Chasalia curviflora*, Thw. Summit. Fruit a berry, bird-carried. Common in the moist zone to 5,000 feet.

33. *Geophila reniformis*, D. Don. Very abundant on the slopes of Ritigala. Fruit a red berry, bird-carried. Rather common in the moist region to 3,000 feet.

34. *Lasianthus strigosus*, Wight. Forms the chief undergrowth on the ascent (*fide* Trimen ; it was not in flower when I was there). Fruit a berry, bird-carried, but it also occurs in the dry zone, and is common in the moist and intermediate zones from 1,000 to 5,000 feet.

35. *Vernonia Hookeriana*, Arn. Summit. Fruit pappose, wind-carried. Common in the moist region from 1,000 to 6,000 feet.

36. *Adenostemma viscosum*, Forst. Summit. Pappus viscid, probably bird- or animal-carried. Common throughout the island.

37. *Gynura lycopersicifolia*, DC. Summit. Fruit pappose, wind-carried. Common in the moist region to 6,000 feet.

38. *Ardisia Missionis*, Wall. Summit. Fruit a red berry, ¼ inch in diameter, bird-carried. Common in the lower montane zone of the moist region.

39. *Jasminum flexile*, Vahl. Summit. Fruit fleshy, bird-carried. Common in the lower montane zone of the moist and intermediate regions. The Ritigala specimens are most like those from Nitre Cave, which is one of the nearest points of the southern mountain mass.

40. *Anodendron rhinosporum*, Thw. Summit. Seed with long tuft of hairs, wind-carried. Rather rare in moist lower montane zone.

41. *Gymnema lactiferum*, Br. Summit (*fide* Trimen). Seed with long tuft of hairs, wind-carried. Low country to 3,000 feet, common in the moist zone, rarer, but occurring, in the dry.

42. *Tylophora cordifolia*, Thw. Summit (and *fide* Trimen). Seeds with long tufts of hairs, wind-carried. Common in the moist region from 2,000 to 4,000 feet.

43. *Hoya ovalifolia*, W. & A. Summit. Seed with long tuft of hairs, wind-carried. Rare in forests of moist lower montane zone (only recorded from Ambagamuwa).

44. *Fagraea obovata*, Wall. Summit. Fruit fleshy, bird-carried. Common in lower montane zone.

45. *Exacum zeylanicum*, Roxb., var. *Ritigalense*, Willis. Summit. This specimen has rather acuminate acute petals like *E. macranthum*, but in other respects is nearer to *E. zeylanicum* and has a very marked quadrangular stem almost winged at angles, and very thin (when dry; they were fleshy alive) and

rather large leaves. Seeds very small and probably accidentally carried. Common in the moist lower montane zone.

46. *Ehretia buxifolia*, Roxb. (*fide* Trimen). Summit. Fruit drupe, bird-carried, but common in dry zone.

47. *Didymocarpus Humboldtianus*. Gardn. (*fide* Trimen; I did not see it). Summit. Seeds very small, but occurs on rocks at Sigiri and other places in the dry zone.

48. *Wrightia angustifolia*, Thw. Summit. Seeds with a bunch of hairs, wind-carried. Occurs in the dry zone, at Dambulla, Anuradhapura, &c.

49. *Thunbergia fragrans*, Roxb. var. *parviflora*, Trim. (Journ. Bot. XXVII., p. 165) Summit. Transport probably accidental. None was noticed on the way up, but the type occurs in the dry zone. The variety is endemic to Ritigala.

50. *Daedalacanthus montanus*, And. Summit. Transport method doubtful, but common in the dry zone.

51. *Stenosiphonium Russellianum*, Nees. Summit, &c. Common. Transport method doubtful. Common in the dry zone. These specimens are thickly clothed with glandular hairs, and thus differ considerably from all in the Peradeniya herbarium excepting one sent in by Mr. Vincent, who reported on the Ceylon forests many years ago; this specimen is labelled by Trimen, Northern Province.

52. *Strobilanthes viscosus*, And. (?) No flowers, so the identification must remain uncertain. Captain Gage of Calcutta also thinks it is this species. Summit. Means of transport doubtful. Common in the montane moist zone from 3,000 to 7,000 feet.

53. *S. stenodon*, Clarke. Summit. Transport method doubtful. Very rare in the intermediate district. Only recorded for Lagalla, and below Lakkaigala both in Matale East. The specimens from Ritigala probably represent a local variety, the leaves being densely hairy below while the Matale specimens are glabrous. But there is a solitary specimen in the Peradeniya herbarium, from Lagalla in 1884,

labelled by Trimen, though it is not in flower, with the name of this species and this is hairy, but with white, not with golden-sulphury hairs. I therefore refrain from giving the Ritigala specimens a varietal name.

54. *S. Walkeri*, Arn. var. *stenocarpa*, Clarke (?) No flowers, so identification uncertain. Means of transport doubtful, but occurs in the dry zone.

55. *Eranthemum malabaricum*, Clarke. Summit. Means of transport doubtful, but is common to 3,000 feet, and occurs at Sigiri, Dambulla, &c., in the dry zone.

56. *Rungia parviflora* Nees. Summit. Transport method doubtful. Common in the moist region to 7,000 feet, and as one of Thwaites' specimens is labelled Topawe, probably occurs in dry zone also.

57. *Coleus barbatus*, Benth. Summit. Distribution method doubtful, but also occurs at Dambulla and elsewhere in the dry zone.

58. *C. elongatus*, Trim. Summit. Distribution method doubtful. An endemic species to Ritigala.

59. *Anisochilus velutinus*, Trim. Summit. Distribution method doubtful, but occurs on dry rocks in the dry zone, as at Gunner's Quoin, &c.,

60. *Leucas biflora*, Br. From 1,800 feet to the summit. Distribution method doubtful, but is common in the dry zone.

61. *Piper sylvestre*, Lam. (?) No flowers or fruits, so the identification must remain quite uncertain. Distribution method doubtful, perhaps by birds. Occurs in the dry zone, and to 3,000 feet elevation.

62. *Peperomia pseudo-rhombea*, Cas. DC. var. *tenuis*, Trimen. Summit. Distribution method doubtful, but perhaps by birds, the fruits being a trifle clinging. The variety is confined to the summit of Ritigala, the type is rather rare in the montane zone from 3,000 to 5,000 feet.

63. *P. Wightiana*, Miq. var. *Ritigalensis*, Willis. Stems to 10 or 12 inches long, leaves opposite, to 1¼ inches long, usually rotundate, sometimes ovate (on same plant), tapering

to base, very obtuse, five-nerved, with membranous margin, absolutely glabrous. Spikes not seen. Summit. Distribution method doubtful. Very rare in the higher montane zone. Only once found, in Bopatalawa at 6,000 feet.

64. *P. confusa.* Hk. f. Summit. Distribution method doubtful. Rather common in montane zone from 3,000 to 5,000 feet.

65. *P. dindigulensis*, Miq. Summit. Fruit viscous, probably bird-carried. Rather common in montane zone to 3,000 feet.

66. *Alseodaphne semecarpifolia*, Nees (*fide* Trimen). Summit. Bird-carried (?) Common in the dry region.

67. *Litsea zeylanica*, Nees (?) Not in flower, but the leaves resemble those of this species, but are a good deal longer and usually falcate. Summit. Bird-carried. Very common in the moist region to 4,000 feet.

68. *Viscum orientale*, Willd. Summit. Fruit a berry, bird-carried. Common in the dry zone.

69. *Cleistanthus pallidus*, Muell. Arg. Abundant at the summit (and *fide* Trimen). Distribution method doubtful, but is common in the dry zone, *e.g.*, at Dambulla.

70. *C. patulus*, Muell. Arg. (?) A very doubtful specimen, not in flower. Distribution method doubtful. Rather rare in the low moist country.

71. *Phyllanthus cinereus*, Muell. Arg. (? var.) Very abundant on the uppermost 1,000 feet of Ritigala. Not in flower. The stems are rather too pubescent for true cinereus, in fact are almost hairy, but the leaves dry green, and not black, above. It may therefore perhaps be regarded as an endemic slight variety of P. cinereus. Distribution method doubtful. The type rare, in Maturata and on Wattekelle hill.

72. *P. polyphyllus*, Willd. Summit. Distribution method doubtful, but common in the dry zone.

73. *Glochidion, sp. nov.* Summit. This specimen I sent to Calcutta, and Captain Gage and Mr. Burkill report that it is

"exactly like an undescribed sheet in the Calcutta herbarium, bearing the ticket

Herb. Ind. Or. Hook. fil. et Thomson. 58.
Bradleia (33)
Hab. Malabar, Concan, &c. Regio trop.
Alt.— Coll. Stocks, Law, &.

I have myself subsequently compared it with this plant, of which I found a sheet in our herbarium, and find this to be so. It is a quite distinct species, not perhaps distant from *G. rigidum*, Muell. Arg., but with the lobing of the fruit much better marked.

Distribution method doubtful. It would appear that this species, unless it occurs elsewhere in Ceylon, from which it has not previously been recorded, must have been carried from India, a distance of 200–300 miles, but in all likelihood it also occurs in some of the intermediate districts. I refrain from naming it ; this should in general be done only by monographers in difficult genera like this.

74. *Croton caudatus*, Geisel. (?) Summit. Distribution method doubtful, but occurs, though rarely, in the dry zone. The specimens are rather small, and may be of *C. aromaticus*, which also occurs in the dry zone.

75. *Acalypha lanceolata*, Willd. Summit. Distribution method doubtful, but a weed in the dry country.

76. *Mallotus philippinensis*, Muell. Arg. Summit (and *fide* Trimen). Distribution method doubtful, but common in the dry zone.

77. *Excoecaria crenulata*, Wight. Summit and sides (and *fide* Trimen). Distribution method doubtful. Common in the moist zone from 4,000 to 6,000 feet.

78. *Phyllochlamys spinosa*, Bureau. Summit. Fleshy achene, probably bird-carried, but common in the dry zone.

79. *Ficus infectoria*, Roxb. Lower slopes (*fide* Trimen). Bird-carried. Low moist country, rare.

80. *Dorstenia indica*, Wall. Summit. The specimen has not, in the one inflorescence available, long pubescent arms from

the margin. Distribution method doubtful, but occurs at Dambulla in the dry zone.

81. *Procris laevigata*, Bl. Summit. Distribution method doubtful. Common in the moist zone from 3,000 to 6,000 feet.

82. *Pouzolzia Walkeriana*, Wight. Summit. Distribution method doubtful, the wings being hardly good enough to carry the fruit such a long distance. Common in the moist zone to 2,000 feet.

83. *Liparis obscura*, Hook. f. Summit. Seeds very light, wind-carried. Rather rare in the moist region from 2,000 to 5,000 feet.

84. *Dendrobium Macraei*, Lindl. Summit (and *fide* Trimen), abundant. Wind-carried. Rare in rocky places in moist zone.

85. *Bulbophyllum sp. nov.* (?). Specimen not in flower, and may be a new species. I only got one flower, and roughly examined that and put it into alcohol. From my rough notes I feel pretty sure that this is a new species, but my alcohol material was lost in the confusion caused by my accident. Summit. Wind-carried. Genus rare in moist low country and mountain zone.

86. *B. purpureum*, Thw. (?). Specimens not in flower, but very like this species. Summit. Wind-carried. Very rare in the lower montane zone.

87. *B. elegans*, Gardn. Summit. Wind-carried. Rather rare, 3,000—6,000 feet.

88. *Cirrhopetalum Macraei*, Lindl. Summit. Wind-carried. Rather common in the lower montane zone. According to Trimen the flowers on Ritigala are almost white, thus constituting a slight variety.

89. *Pholidota imbricata*, Lindl. Summit. Wind-carried. Common in the moist zone to 3,000 feet.

90. *Eria muscicola*, Lindl. (and *fide* Trimen). Summit. Wind-carried. Common in the montane zone.

91. *E. Lindleyi*, Thw. Not in flower. Summit. Wind-carried. Rather common in the montane zone to 7,000 feet.

92. *Polystachya zeylanica*, Lindl. (?) No flowers or leaves on the specimens collected. Summit. Wind-carried. Common in the moist zone to 4,000 feet.

93. *Sarcochilus complanatus*, Hk. f. (*fide* Trimen). Summit. Wind-carried. Rare in moist zone to 3,000 feet.

94. *Luisia teretifolia*, Gaud. Summit. Wind-carried. Rather common in the moist zone to 4,000 feet.

95. *Saccolabium niveum*, Lindl. Summit. Wind-carried. Common in the moist zone from 3,000 to 6,000 feet.

96. *Cleisostoma maculosum*, Lindl. (?) Not in flower. Summit. Wind-carried. Rare in moist zone from 1,000 to 3,000 feet.

97. *Mystacidium zeylanicum*, Trim. Summit. Wind-carried. Rather rare in moist zone below 1,000 feet.

98. *Cottonia macrostachya*, Wight. (?) Not in flower. Summit. Wind-carried. Rather rare in the moist region to 3,000 feet.

99. *Taeniophyllum Alwisii*, Lindl. Summit. Wind-carried. Rare in moist region to 6,000 feet.

100. *Podochilus saxatilis*, Lindl. Summit. Wind-carried. Rather rare in moist and intermediate regions to 3,000 feet.

101. *Anœctochilus regalis*, Bl. Summit and slopes. Wind-carried. Rather common in moist region to 4,000 feet.

102. *Disperis zeylanica*, Trim. (*fide* Trimen). Summit. Wind-carried. Common in moist zone from 3,000 to 5,000 feet.

103. *Curculigo Finlaysoniana*, Wall. Summit. Distribution method doubtful. Rather common in moist zone to 3,000 feet.

104. *Asparagus gonoclados*, Baker. Summit. Fruit a berry, bird-carried. Not uncommon in the lower moist zone.

105. *A. falcatus*, L. (?). Some specimens collected seem to agree with this, though their cladodes are rather short, and some similar ones collected on Ritigala by Trimen are labelled with this name, somewhat doubtfully. Summit. Bird-carried. Common to 4,000 feet in the moist and intermediate zones.

106. *Cyanotis fasciculata*, Schultes f. (?). Not in flower. Summit, on the open rocks. Distribution method doubtful, but common in the dry zone.

107. *Floscopa scandens*, Lour. Summit. Distribution method doubtful. Rather common in shady places in the moist low country.

108. *Caryota urens*, L. Sides of Ritigala. Fruit bird-carried (?). Occurs in the dry zone.

109. *Calamus Thwaitesii*, Becc. (?). Sides of Ritigala. Distribution method doubtful. Rather rare below 2,000 feet in moist country. Kurunegala.

110. *Cyperus, sp. nov.* This specimen was examined by Capt. Gage and Mr. Burkill, who report that it is unlike anything in the Calcutta herbarium. It also differs very markedly from all the Ceylon species, but as it has no flowers, only the central rachis of the spikelets, I shall not attempt to describe it. Summit. Distribution method doubtful.

111. *Fimbristylis asperrima*, Boeck. Summit. Distribution method doubtful. Very common in the low country, moist, and perhaps dry.

112. *Carex leucantha*, Arn. Summit. Distribution method doubtful. Rather rare in moist zone from 1,000 to 3,000 feet.

113. *Panicum ovalifolium*, Poir. Summit. Distribution method doubtful. Common in the warmer parts of the Island.

114. *P. pilipes*, Nees & Arn. Summit. Distribution method doubtful. Central Province.

115. *P. patens*, L. Summit. Distribution method doubtful. Central Province.

116. *Oplismenus compositus*, Beauv. Summit. Distribution method doubtful. Common in the dry zone.

117. *Andropogon squarrosus*, Linn. f. Summit. May have been introduced at the bungalow that formerly stood on the summit. Common in the dry zone. Distribution method doubtful.

118. *Dichætaria Wightii*, Nees (*fide* Trimen) Slopes. Distribution method doubtful. Dry zone.

119. *Lophatherum gracile*, Brongn. Summit. Distribution method doubtful. Common in the moist zone to 4,000 feet. Occurs at Matale, only 45 miles away.

120. *Centotheca lappacea*, Desv. Summit. Distribution method doubtful. Common in the wet (and ? dry) region.

121. *Hymenophyllum polyanthos*, Sw. Summit. Spores light, wind-carried.

122. *H. Neesii*, Hook. (*fide* Trimen). In large sheets at summit. Spores wind-carried.

123. *Trichomanes, sp. nov.?* I have only one lanceolate leaf, about 1½ inch long, non-sporiferous, of this plant. It is different from any known Ceylon species, but in the absence of spores I shall not describe it. Spores wind-carried.

124. *Humata pedata*, J. Sm. Summit. Spores wind-carried.

125. *Prosaptia Emersoni*, Presl. Summit. Spores wind-carried.

126. *Adiantum caudatum*, L. Summit. Spores wind-carried.

127. *Pteris quadriaurita*, Retz. Summit. Spores wind-carried.

128. *Thamnopteris Nidus*, L. Summit. Spores wind-carried.

129. *Asplenium Wightianum*, Wall. Summit. Spores wind-carried.

130. *A. tenerum*, Forst. Summit. Spores wind-carried.

131. *A. falcatum*, Lam. Summit. Spores wind-carried.

132. *Aspidium subtriphyllum*, Hk. Summit. Spores wind-carried.

133. *Lastrea recedens*, J. Sm. Summit. Spores wind-carried.

134. *L. Blumei*. (*fide* Trimen). Summit. Spores wind-carried.

135. *Nephrolepis cordifolia*, Presl. Summit. Spores wind-carried.

136. *N. exaltata*, Schott. Summit. Spores wind-carried.

137. *Niphobolus Gardneri*, Kunze. Summit. Spores wind-carried.

138. *N. adnascens*, Sw. (?) Summit. Spores wind-carried.

139. *Pleopeltis nigrescens*, Bl. Summit. Spores wind-carried.

140. *Antrophyum plantagineum*, Kaulf. Summit. Spores wind-carried.

141. *Vittaria scolopendrina*, Schk. Summit. Spores wind-carried.

142. *Hemionitis arifolia*, Burm. Summit. Spores wind-carried.

143. *Gymnopteris quercifolia*, Benth. Summit. Spores wind-carried.

144. *Lycopodium Phlegmaria*, L. Summit. Spores wind-carried.

Having enumerated the flora, we may proceed to deal with its methods of distribution in more detail. In the first place, let us exclude those plants which occur in the dry zone* of Ceylon as recorded in Trimen's Flora, since these have not to travel 40 miles to reach the summit. These plants are :—

Glycosmis pentaphylla
Gomphia angustifolia
Munronia pumila
Vitis pedata
Weihea zeylanica
Eugenia spicata
Osbeckia aspera
Memecylon umbellatum
M. capitellatum
Cephalandra indica
Pavetta indica
Lasianthus strigosus
Adenostemma viscosum
Gymnema lactiferum
Ehretia buxifolia
Didymocarpus Humboldtianus
Wrightia angustifolia
Thunbergia fragrans var
Dædalacanthus montanus
Stenosiphonium Russellianum
Strobilanthes Walkeri
Eranthemum malabaricum
Rungia parviflora

---

* These are of course only the dry zone plants which occur at or near the summit, and there are many others on the slopes.

Coleus barbatus
Anisochilus velutinus
Leucas biflora
Piper sylvestre
Alseodaphne semecarpifolia
Viscum orientale
Cleistanthus pallidus
Phyllanthus polyphyllus
Croton caudatus
Acalypha lanceolata
Mallotus philippinensis
Phyllochlamys spinosa
Dorstenia indica
Cyanotis fasciculata
Caryota urens
Oplismenus compositus
Andropogon squarrosus
Dichætaria Wightii

Among these there is one form (Thunbergia) endemic to the summit of Ritigala, and we may notice here that it belongs to a genus whose seeds are, so far as we can tell, extremely ill adapted to transport over long distances, so that it was probably only with difficulty, so to speak, that it reached the summit at all.

The exclusion of these 41 species leaves us with a flora of 103 species, all, so far as we are aware, only found elsewhere in the moist region of Ceylon, *i.e.*, at least 40 miles away, and with the few exceptions to be pointed out below, all species which must have travelled in one journey over the whole of that distance, they being species, not of the low country, but of the lower slopes of the mountains.

We may next exclude the species which, by reason of their fleshy fruits, have obviously been carried by birds. These are—

Polyalthia Korinti
Cyclea Burmanni, var
Capparis Moonii
Pittosporum zeylanicum
Erythroxylon obtusifolium
Walsura Gardneri
Olax zeylanica
Salacia reticulata
Eugenia rotundata
Rhipsalis Cassytha
Heptapleurum stellatum
Canthium didymum
Ixora coccinea
Morinda umbellata

Psychotria Thwaitesii
Chasalia curviflora
Geophila reniformis
Ardisia Missionis
Jasminum flexile
Fagraea obovata
Litsea zeylanica
Ficus infectoria
Asparagus gonoclados
A. falcatus

Excluding these 24, our flora is reduced to 79 species.

It is worthy of note that these are all fairly common species, and that of them 8 are scarlet-fruited, 5 purple, 1 orange red, 1 orange and white, 4 green or greenish white, 3 white. It would thus seem to be evident that conspicuousness of the fruit has something to do with its chance of being carried away by a fruit-eating bird.

Here again the endemic form, if it can be regarded as a distinct form, viz., the slight variety of Cyclea Burmanni, is probably one of the least conspicuous and least likely to be carried by birds. As it is only hitherto recorded from the low country of Ceylon, it is also living in a markedly different climate on the summit of Ritigala.

We may now exclude those evidently carried by the wind. Here we are practically limited to the orchids and ferns, with a few Compositae, Apocynaceae, and Asclepiadaceae, because though adaptations for wind carriage are very widespread, they as a rule are not efficient enough to carry the seeds more than a few yards in a climate like that of Ceylon, where the wind is very light. The island is too near to the equator to come within the zone of cyclones, and there is no reason to suppose that there can have been strong winds here for a vast length of time. These wind-carried species are :—

Vernonia Hookeriana
Gynura lycopersicifolia
Anodendron rhinosporum
Tylophora cordifolia
Hoya ovalifolia
Liparis obscura
Dendrobium Macraei
Bulbophyllum, *sp. nov.*
B. purpureum
B. elegans
Cirrhopetalum Macraei, var.
Pholidota imbricata
Eria muscicola
E. Lindleyi

Polystachya zeylanica
Sarcochilus complanatus
Luisia teretifolia
Saccolabium niveum
Cleisostoma maculosum
Mystacidium zeylanicum
Cottonia macrostachya
Taeniophyllum Alwisii
Podochilus saxatilis
Anaectochilus regalis
Disperis zeylanica
Hymenophyllum polyanthos
H. Neesii
Trichomanes, sp nov.
Humata pedata
Prosaptia Emersoni
Adiantum caudatum
Pteris quadriaurita
Thamnopteris Nidus
Asplenium Wightianum
A. tenerum
A. falcatum
Aspidium subtriphyllum
Lastrea recedens
L. Blumei
Nephrolepis cordifolia
N. exaltata
Niphobolus Gardneri
N. adnascens
Pleopeltis nigrescens
Antrophyum plantagineum
Vittaria scolopendrina
Hemionitis arifolia
Gymnopteris quercifolia
Lycopodium Phlegmaria

Here again we get an indication of the great predominance that ferns and other spore-bearing plants obtain in oceanic islands and in other far distant spots, provided the conditions are suitable to their growth. The summit of Ritigala is almost the only spot thus suitable in the north country, and they have reached it, and established themselves there, in large numbers, 24 out of 49 wind-carried plants, and those mostly common on the summit, being ferns or Lycopodiums.

Here again, the endemic species among the ferns belongs to Trichomanes, the genus which obviously lives in the most sheltered spots, where the wind can hardly be imagined to penetrate. Its spores consequently will be but little liable to be carried off, and will very rarely indeed reach the summit of Ritigala, if more than once. The endemic orchids belong, the species to Bulbophyllum, the variety to the rarest species of Cirrhopetalum. It may seem strange that orchids, whose seeds are so very transportable, should readily give rise to new forms, but two important points must be remembered. (1)

that they live in general in the jungle, where the wind rarely gets to them, and (2) that they live comparatively isolated on trees, &c., and are probably little cross-fertilized.

It is noteworthy that the wind seems to carry a greater proportion of *species* than any other mode of distribution. The wind-carried forms on the top of Ritigala represent about 1 in 10 of those of Ceylon, while the bird-carried are only 1 in 28, and those with doubtful mechanisms 1 in 60 (approximately for all).

We are thus left with only 30 species, whose distribution methods may be called *doubtful* and it will repay us to examine these in more detail.

Desmodium Wightii.—The pod breaks up into joints which are slightly rough with minute bristles, and might conceivably cling to a bird or a flying fox. This is a low country species, and so may very probably have come in stages by way of the damp spots under the tank bunds.

Dalbergia Championii.—The seeds are oblong, very large, and flat, and were the distance only a mile or so, might conceivably be carried by wind, but over a distance of 40 miles or more it is extremely hard to see how they can have been carried, even accidentally, they being too large to be attached to birds' feet.

Begonia malabarica.—The seeds are very small, and might possibly (but very improbably) have been carried by the wind, but as the plant rather affects spots near streams they may quite easily, one would imagine, be attached to birds' feet at times, in lumps of mud.

Hedyotis fruticosa.—Possibly carried attached to birds' feet, the seeds being very small.

Anotis nummulariformis, var.—This specimen differs a trifle from any others in the herbarium, but one can hardly distinguish it as a variety without more material.

Exacum zeylanicum, var. *Ritigalense.*—Seeds very small, probably carried in mud attached to birds' feet. The variety appears to be endemic to Ritigala.

Strobilanthes viscosus (?).—Seeds probably carried by jungle fowl or other birds, which eat them greedily.

S. stenodon, var.—This species is extremely rare in the main mountain mass, and is represented on Ritigala by a distinct variety, having probably only been carried there on one occasion.

Coleus elongatus.—A very distinct species, so distinct that it is quite uncertain from which Ceylon species it can have been derived, or from what common ancestor with which species. It may even possibly be descended from a Plectranthus, and would thus make the genus Coleus polyphyletic.

Peperomia pseudorhombea, var. *tenuis.*—Seeds or rather fruits very small and probably carried attached to birds' feet. The type of the species is rare in the montane zone, and the Ritigala form is endemic.

P. Wightiana, var. *Ritigalense.*—Seeds as in the last. The type form is extremely rare, and is only known from the far south of the montane zone, and the Ritigala form is endemic.

P. confusa.—Seeds as before. Common in the mountains, and occurs on Hantane, which is far north. The Ritigala form does not differ appreciably from the type.

P. dindigulensis.—Seeds as before, but sticky, and so perhaps carried attached to the feathers of birds. Common in the mountains, and found on Hantane. The Ritigala form agrees with the type.

Cleistanthus patulus. Capsule over ¼ inch in diameter, with large seeds. How this was carried must remain doubtful, but it is worth noting that it is a low country species only, and so probably arrived by easy stages, using the damp ground under the tank bunds as intermediate resting places, *Phyllanthus cinereus*, var.—The Ritigala specimens differ from the type in as many points as it itself differs from P. affinis, Muell. Arg., but not having found it in flower I hesitate to give it a name. The type form is rare, recorded onlv from two spots.

Glochidion sp. nov.—The Ritigala specimens represent an entirely new species of this genus, but agree very closely with some unnamed specimens from South India. There are several explanations possible of this remarkable fact. The seeds are so large that it is difficult to see how they can have been transported, but probably they were accidentally carried in mud or otherwise. They may have been carried the whole way from the nearest locality in Southern India, say 200 to 300 miles. The plant may however occur in the intermediate districts, and not have hitherto been noticed, or again the same species may have arisen quite independently in two different spots. It is quite possible that this may be the true explanation.

Excoecaria crenulata.—Large capsule and seeds, distribution method extremely doubtful. Common in the mountain zone.

Procris laevigata.—Achenes minute, probably carried in mud on the feet of birds. Common in the mountains.

Pouzolzia Walkeriana.—The fruit, being winged, might conceivably be carried by wind were the distance shorter, but over so long a distance it is impossible to imagine this to be the case. It is common in rocky places in the intermediate region, and so has not so far to come as some of the purely wet zone things. It may perhaps travel in mud on birds' feet.

Curculigo Finlaysoniana.—Seeds small, perhaps carried in mud. Common in the mountains.

Floscopa scandens.—Perhaps like the last. Common in the moist low country, and so perhaps arrived by easy stages, like Desmodium Wightii.

Calamus Thwaitesii (?). How this plant with its large scaly fruit is carried must remain doubtful. Being a low country plant, it may also have travelled in easy stages, for I am certain that there are species of Calamus, though whether the same I know not, under some of the tank bunds.

Cyperus sp. nov.—Only three members of this large family have reached the top of Ritigala, and one of these has given rise to an endemic species—or it may be that this species has arisen from one of the other two. The fruits probably travel in mud.

Fimbristylis asperrima.—This may possibly occur in the dry zone also, and in any case is a low country plant which might come by easy stages.

Carex leucantha.—The seeds probably travel in mud.

Panicum ovalifolium, *P. pilipes*, and *P. patens.* It is rather curious that out of the eight species which represent this enormous family, no less than three should belong to this one genus. Someone showed that the shoots of species of Panicum could be eaten by animals and the nodes voided in a state fit to grow, and perhaps this is the explanation in the present case. P. ovalifolium probably occurs in the dry zone also, and probably should not be included here.

Lophatherum gracile.—Probably carried in mud.

Centotheca lappacea.—Probably carried in mud. Perhaps occurs in the dry zone, and any how is a low country species which could travel in easy stages.

When we go over this list with care, we are thus confronted with some very striking facts. There are only 30 of these species in any case, and if we exclude the low country species as being capable of travelling in easy stages, there are only 24. Yet out of these there are no fewer than nine which are endemic—either as species (3) or as varieties (6) to the little area of a few acres on the summit of Ritigala. One of the species (Glochidion) is not perhaps strictly endemic, as it seems also to occur in South India, but leaving this out of account we still have 8 out of 24, or 1 in 3, a higher proportion than occurs among the general Ceylon flora.

In the plants of the dry zone we had 1 endemic variety in 41 or more species; in the bird-carried things 1 very slightly marked form among 24 species; in the wind-carried things 2 endemic species and 1 variety among 49.

These facts at once suggest that endemism, other things being equal, goes in general with difficulty of distribution, and with rare arrival in one spot, as has already been hinted at in another paper*. On the top of Ritigala, it being the only high land for a long distance in every direction, birds will naturally settle; the bird-carried things will in consequence tend to arrive more regularly than others. The wind will carry perhaps more species (though if one leave out the ferns, the numbers are approximately the same), but there is no reason why a wind-carried seed or spore should settle on the summit of Ritigala rather than on the plain a few miles away. The average result will thus on the whole perhaps tend to be that except the ferns and the commoner orchids, the wind-carried things will arrive but rarely on the summit of Ritigala. Still more rarely will the plants whose methods of distribution we have classed as doubtful be able to reach the summit. We might thus expect that in families which are reasonably prolific in giving rise to new species, we should find most of these among the doubtful mechanisms, the next among the wind-carried, and the least among the bird-carried, and this is in fact what we do find, the proportions being 1 to 3, 3 to 49, and 1 to 24, the last named being only a very slight variety.

If this be a fair explanation of the facts, we shall expect to find endemism commoner among those things which are rare elsewhere, and in fact we do find this. Note for instance that the two rare species of Peperomia have both endemic varieties on the top of Ritigala, while the two common ones

---

* Willis and Gardiner. The Botany of the Maldive Islands. Ann. Perad. I, 1901, p. 45.

have not Strobilanthes stenodon and Phyllanthus cinereus, both rare species, are represented by varieties. Cyperus and Coleus are represented by endemic species, but we do not know the ancestry of these, whether dry zone or moist, rare or common. The only common forms represented by endemic varieties are Anotis nummulariformis and Exacum zeylanicum.

Not only do these facts stand out, but the endemic forms are on the whole among the families which show the greatest number of endemics elsewhere in Ceylon ; thus—

Anotis	Rubiaceae	73	endemics out of	138
Exacum	Gentianaceae	5	do.	91
Strobilanthes	Acanthaceae	38	do.	93
Coleus	Labiatae	10	do.	42
Peperomia	Piperaceae	5	do.	14
Phyllanthus	Euphorbiaceae	45	do.	127
Cyperus	Cyperaceae	9	do.	159

and to add to these the endemic forms among the bird and wind-carried species, we have—

Cyclea	Menispermaceae	0	endemics out of	13
Trichomanes	Filices	23	do.	239
Bulbophyllum	Orchidaceae	79	do.	161
Cirrhopetalum	do.	79	do.	161

and the one form among the dry zone plants—

Thunbergia	Acanthaceae	38	endemics out of	93.

Adding up these figures we find that the endemics of Ritigala are in all among families which possess in Ceylon 325 endemic species among a total of 1,098 species. While if we take the other members of the Ritigala flora we find that the other 15 species with doubtful mechanisms belong to families which have only 200 endemics among 975 species, and this proportion is largely brought up by the fact that there are non-endemic Rubiaceae and Euphorbiaceae among them.

We may put the facts in another way, thus :

In the Ceylon flora there are carried (approximately)—

			On Ritigala.	Proportion.
By wind,	234	phanerogams ..	25 ..	1 in 9
	264	ferns, &c. ..	24 ..	1 in 11
By birds,	689	phanerogams ..	24 ..	1 in 28
Doubtfully	1,803	do. ..	30 or 24 ..	1 in 60 or 1 in 75
Total	2,990		103	1 in 29

We ought however, probably to halve the figures of the Ceylon flora, as it is hardly likely that more than half of it can survive at 2,500 feet on Ritigala in any case. And perhaps we should nearly halve it again, as only seeds ripened in the first half of the year will be carried by the south-west monsoon, or, probably, by migrating birds.

When we come to compare the flora of Ritigala with the Ceylon phanerogamic flora as a whole, we find the proportions of endemics different :

		Endemics.	Proportion.	Pro. on Riti.
Wind-carried .	234 ..	105 ..	1 in 2¼ ..	1 in 16
Bird ..	689 ..	252 ..	1 in 2¾ ..	1 in 24
Doubtful ..	1,803 ..	446 ..	1 in 4 ..	1 in 3

The greater proportion of endemics in the Ceylon flora as a whole may be set down to the greater distance from any congeners, and goes to prove the point that endemism goes with difficulty of arrival in any given place. The very large proportion of "doubtfuls" goes to show that such plants may travel more easily than we are usually inclined to suppose, though not perhaps so easily as bird and wind-carried things. It would at any rate indicate that if this be not the case, then Ceylon must in former times have had more nearly approaching land masses than at present. The relative proportions of doubtful, and of bird and wind mechanism rather tends to show that at such a distance the latter are less useful than at shorter ranges.

The Ceylon flora being derived from at least three sources, Malayan, Indian, and African types being all present in it, forms a much more complex problem than the flora of the summit of Ritigala, which is pretty evidently, with the exception of the Glochidion, derived from that of the hills only forty miles to the south, and I hope to deal with it, and with the floras of other oceanic islands, in more careful statistical detail in a subsequent paper.

On the Application of the Theory of Limiting Factors to Measurements and Observations of Growth in Ceylon.

BY

A. M. SMITH

(late Frank Smart Student of Cambridge University and Research Student of Emmanuel College).

With Plates XXII.—XXV.

CONTENTS.

[Annals of the Royal Botanic Gardens, Peradeniya, Vol. III., Pt. II., November, 1906.]

Application of Theory of Limiting Factors—
    Two Limiting Factors in turn.
    Humidity only indirectly a Limiting Factor.
    Summary of General Explanation of Facts for Dendrocalamus.

Further tests of the Theory—
    (1) Night Growth at Hakgala.
    (2) Day Growth with Rain at Hakgala.
    (3) Minimum Temperatures and Night Growth
    (4) Maximum Growth at the three places.
    (5) Day and Night Growth at the three places.
Another Theory. Periods of Rest necessary.

3. Comparison of Agave and Dendrocalamus.

4. Other Cases.
    Capparis Roxburghii and Stifftia Chrysantha—
        Methods of Measurement.
        Results.
        The Light Factor
    Vitis Lindeni.

III.—Consideration of previous work.

IV.—General application of the Theory to cases of Growth from Reserve:

The Factors—
    Temperature.
    Water supply.
    Light.
    Atmospheric Pressure and Velocity of Wind.
    Summary.
Extent of application of Theory:
    Sharp bursts of Growth of Tropical trees.
    Cauliflory.

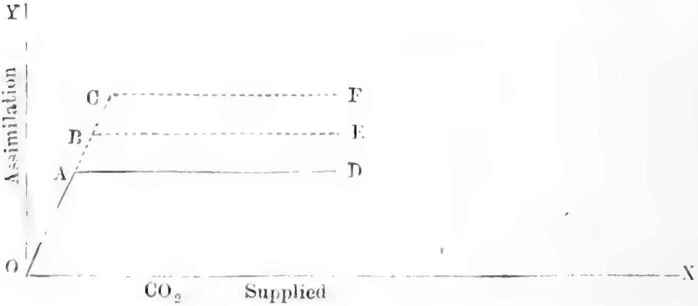
I.—OBJECT OF THE RESEARCH.

The measurements and observations recorded in this paper were carried out in Ceylon from January to July, 1906.

The object of the research was to test the applicability to facts of growth of the Theory of Limiting Factors outlined by F. F. Blackman in his paper on "Optima and Limiting Factors" (2).

Theory of Limiting Factors.

In this paper Blackman suggests that out of the physical factors conditioning any of the physiological processes of plant life, there is as a rule one which at any one time limits the speed of the process. In assimilation he has shown that, given a sufficient supply of light, the rate of the process is limited by the supply of CO_2 available. If the CO_2 supply is also in excess, the rate of assimilation is limited by the temperature.



The above is a diagram typical of the results usually obtained in assimilation. The curve OAD represents the relation between assimilation and CO_2 supply at a given temperature. The part OA represents increase of assimilation in proportion to increase of CO_2 supply. After the point A is reached no further increase of assimilation is obtained. This is due to the insufficiency of light energy for greater assimilation. The line OA represents a stage in which the light is in excess and the assimilation is limited by and increases with the supply of CO_2. The line AD, on the other hand, represents a stage in which the CO_2 supply is in excess andthe assimilation is limited by the light. If the light is increased a curve OBE is obtained in which BE is the portion where light is limiting, but allowing a higher assimilation than before. A further increase of light gives the curve OCF consisting, as before, of two parts. OC where CO_2 is limiting, and CF where light is limiting.

In this connection Blackman gives the following axiom: "When a process is conditioned as to its rapidity by a number of separate factors the rate of the process is limited by the "slowest factor."

In the case of growth the number of factors is large, and some of them are obscure, but the principal effective conditions of whose action we know something are temperature and supply of water. The most complete sets of measurements of the growth of Bamboos yet taken, those of Lock (12) on Dendrocalamus giganteus, in which the growth showed a close relation to the humidity of the atmosphere, and of Shibata (20) on Phyllostachys mitis, in which the growth was closely related to the temperature, are taken to be examples of the theory of limiting factors.

At Peradeniya Blackman supposes that, the temperature being high was favourable to growth and would permit more growth than actually took place, the amount of water available being the limiting factor in the growth of the bamboo stems. The temperature in Shibata's experiments was considerably lower, and this kept the growth-rate down. The moisture being in excess showed no influence on the growth-rate.

The three Climates of Ceylon.

Dendrocalamus giganteus grows in Ceylon in the Botanic Gardens at Peradeniya, at Hakgala, and at Anuradhapura. These three places are situated respectively in the three different climatal regions of Ceylon. *Peradeniya* is at an elevation of 1,500 feet above sea level and has a warm moist climatewith only a short dry season in the months of February and March. It gets rain in both the North-East and South-West monsoons, so that the total yearly rainfall of about 80 inches is well distributed. The temperature in 1906 reached a lower limit of about 14° C. on a few nights in January and an upper limit of about 33° C. on some days in March. In general, however—and this is especially true of the months of June and July during the South-West monsoon—the temperature varies very much less than this. In these months the range is usually from 20° to 26° C. during the twenty-four hours.

Hakgala is at an elevation of 5,600 feet and has a slightly greater rainfall than Peradeniya. The average rainfall for the last twenty-one years is 91·70 inches. This rainfall is well distributed throughout the year, though it receives more rain in the North-East monsoon and less in the South-West than Peradeniya. It differs from Peradeniya chiefly in the temperature. The lowest recorded temperature is 2·9° C, and in February the temperature not infrequently approaches within 4° or 5° C. of freezing point. From March to May an upper limit of about 22° C. is sometimes reached, but in the South-West monsoon the temperature varies very little, the range being usually from 13° to 17° C. during the 24 hours. The temperature during my observations on July 9—11 varied within these limits. It also differs from Peradeniya in the much greater prevalence of mist.

Anuradhapura, elevation about 300 feet, has an average annual rainfall of 54·2 inches. This falls chiefly in the months of October, November, and December in the North-East monsoon. These three months have an average rainfall of 8·5, 10·6, and 9·3 inches respectively. 7·3 inches fall in April, so that the remaining eight months have a very small rainfall. June and July in the South-West monsoon are the driest months of the year, having respectively an average rainfall of 1·4 inch and 1·1 inch. The lowest recorded temperature is 13·4° C. and the highest 39·4° C., but of course the temperature very rarely varies as much as this. For the months of June and July the mean maximum temperature is 32·8° C. and 33·3° C. respectively and the mean minimum temperature is 24·4 and 24·3° C.

The average humidity for both months is 77 per cent. Thus, speaking broadly, Peradeniya may be said to have a warm, moist climate, Hakgala a cool, moist climate, and Anuradhapura a hot and rather dry climate.

Kandy, where some of the measurements of Furcrœa were taken, is four miles from Peradeniya, and resembles it closely in climate. It is subject to slightly greater extremes of temperature.

There seemed therefore to be a good opportunity to take measurements of the growth of Dendrocalamus through a large range of temperature and under widely different conditions of water supply, and under these conditions it seemed possible that a decisive test of the Theory of Limiting Factors could be obtained.

Since the climate of Ceylon is so favourable to growth, other examples of very rapid growth are to be obtained, and it has been possible in the case of some other species, notably in the case of the inflorescence axis of Agave and Furcrœa, to obtain evidence which further tests the theory.

The present paper is mainly concerned with cases of growth from a large store of reserve food material, not only because it is usually in these cases that the fastest growth takes place, but also because here the problem of growth is theoretically much simpler. Such growth once started only implies the transference of a certain amount of highly-organized material from one part of the plant to another, and the elaboration of this material to a higher stage of complexity. All the supplies both of organic and mineral food, and often of water too, are contained within the plant. In other cases the growth depends on material which has to be worked up from the simple form of oxygen and carbon-dioxide, and the provision of a sufficient supply of food to the growing organ involves conditions favourable not merely to the elaboration and transference of such a highly-organized material as starch, but also to the processes of assimilation and transpiration.

The methods of measurement were simple. They varied with the plant measured and will be given with the description of the results in each case.

II.—OBSERVATIONS.

1. *FLOWERING SHOOT OF AGAVE AND FURCRŒA.*

As is well known, these plants grow for a number of years without flowering, storing up in the thick leaves a large reserve of food.

At the end of this period of vegetative activity a flowering shoot is produced, which grows out to form a large terminal inflorescence. The production of the inflorescence exhausts the supply of reserve material, and when the flowers (and afterwards the fruits) have appeared and matured, the whole plant dies.

Several opportunities presented themselves of measuring the rate of growth of the flowering shoot of species of Agave and Furcroea and the results of the more instructive cases are given in Plate 1.

In these cases the measurements were made in the following way :—A bamboo pole was placed firmly in the ground as near as possible to the growing shoot. A scaffolding having been erected so that the top of the shoot could be easily reached, a ½-metre scale was placed so as to rest on the tip of the growing shoot. The scale was placed horizontal by means of a spirit-level resting on it, and the height thus marked off on the pole by means of a penknife or a sharp-pointed lead pencil.

The tips of the large sheathing bracts which terminate the shoot were scarcely or not at all injured by this process, and successive measurements of the same height never varied by more than ·05 cms. In the case of the plant measured at Kandy, which was difficult of access, this error may have been exceeded. Measurements were made at intervals of two hours and the shade reading of the dry and wet bulb thermometers was taken at the same time.

Observations were made in this way on the following occasions and at the following places :—

(1) On Agave Morrissii in the Hakgala Botanic Gardens from March 9 at 6 A.M. to March 10 at 6 P.M. Elevation 5,600′; highest temperature reached 21·2° C. (70·2° F.).

(2) On Agave Americana at Hakgala from June 1 at 8 A.M. to June 2 at 6.30 P.M. Elevation 5,600′; highest temperature reached 21·8° C. (71·2° F).

(3) On Furcraea gigantea at Kandy from June 11 at 8 A.M. to June 12 at 6 P.M. Elevation 1,700′; highest temperature 27·8° C. (82·0° F.).

The curves of growth and shade temperature observations are given in Plate 22.

Growth limited by Temperature.

It is obvious from these curves that the growth throughout shows a remarkable agreement with the temperature of the surrounding air. In every case the rate of growth increases toward the middle of the day, slackens in the evening, and then gradually decreases through the night. Perhaps the most instructive example is the case of Agave Morrissii at Hakgala. The first day was bright and fine with hot sun, and the air temperature reached 21·2° C. (70·2° F.). The second day was dull and cloudy with rain, and the temperature did not rise above 17·2° C. (62·9° F.). The difference in the rate of growth was most marked. On the first day the greatest growth, that between 12 noon and 2 P.M., was 1·95 cms. On the second day it was only ·95 cms. between 2 P.M. and 4 P.M.

The lowest temperature ever recorded in this set of experiments, 9·6° C. (49·2° F.), occurred at 6 A.M. on March 9, and though the temperature rose by 8 A.M. to 16·3° C. (61·3° F.). the resulting growth in the two hours from 6–8 A.M. was only ·15 cms. Throughout the three curves shown on Plate 22 a close correspondence between growth and the temperature of the surrounding air is obvious. Other observations taken in addition to those shown fully confirm this general conclusion.

In a set of readings at Peradeniya on September 1 to 2 the air temperature reached 29·0° C. (84·2° F.), and through the kindness of Mr. H. M. Leake, Government Botanist, Saharanpur, India, I obtained some readings in which the air temperature reached 31·1° C. (88° F.). In both these sets of observations the close relation between growth and temperature was obvious, so that the total observations show that throughout a range of from 9·6° C to 31·1° C. (49·2° to 88° F.) the growth of the flowering shoot of different species of Agave and Furcraea corresponds with the temperature of the surrounding atmosphere. Readings taken at Anuradhapura in the dry region of Ceylon, where the temperature reached 30·7° C. (87·3° F.), were unfortunately spoilt by the splitting of the shoot lengthwise early in the course of the experiments, and I omit them.

Leaving a fuller discussion till a later part of the paper, it may here be pointed out that the influence of light or the humidity of the atmosphere cannot be traced in any of the results obtained. Some of the records were taken on days of bright sun when the humidity of the atmosphere was quite low, but no diminution of growth from either cause was ever observed, in fact it was just at the periods of brightest sunshine that the most rapid growth was recorded.

Except for the readings of June 10 to 11 at Kandy I have full records of the temperature recorded by dry and wet bulb thermometers from which the humidity can be calculated, but in the absence of any correspondence between humidity and growth these records have not been included in this paper. The water supply seems to have been in excess throughout.

Internal Temperature of the Growing Organ.

The rapidity of growth when the shoot was exposed to bright sun was often greater than would be expected from the temperature readings. The curves for March 9th at Hakgala and for June 11th at Kandy show that when the shoot is exposed to bright sunlight the growth increases very rapidly and the curve rises more sharply than the curve of temperature.

At Hakgala, on March 9th, the sun shone full on the plant from sunrise at 6.5 A.M. to about 1.30 P.M. It will be noticed what a rapid increase of growth takes place at this period. The fact that between 2 and 4 P.M. the growth curve falls more rapidly than the temperature may perhaps be correlated with the fact that after 1.30 P.M. the greater part of the flowering shoot was in the shade.

The difference between the growth of Furcraea at Kandy on June 11th, a day when the shoot was exposed to bright sunlight, and on June 12th, when the sun was obscured till about 3.30 P.M., is very striking and is greater than we should expect on the assumption that the temperature of the surrounding atmosphere is the governing factor in the growth of the plant.

These facts point to the idea that the factor which really regulates the growth of the shoot is the internal temperature of the growing region of which the temperature of the surrounding air is only a more or less rough measure. It becomes therefore of importance to find out the temperature of the growing region. Owing to the difficulty of obtaining shoots at the right stage it was thought advisable to use all the available plants for growth measurements so as to have a large number of observations on which to base deductions. The insertion of a thermometer into the growing region would possibly have injured the plant and rendered the growth measurements unreliable, so that no records of internal temperature for Agave or Furcraea flowering shoots were obtained.

Failing this a number of observations of internal temperature were made in the case of the Giant Bamboo (Dendrocalamus giganteus), of which species a large number of growing culms was available at Peradeniya, Kandy, and Anuradhapura. A small hole was cut into the growing region and a thermometer bulb inserted. A continuous set of readings every two hours was taken with several culms, of the temperature shown by the thermometer in the culm and at the same time the temperature of the surrounding air in the shade. As the culm grew fresh holes had to be made, and in some cases this treatment, continued for some time, had an obvious effect in retarding the growth of the plant. However, other readings taken in culms which were only used once or twice quite agree with the general result of the observations, so that this may be taken as sound. Of course in any plant of ordinary size such drastic treatment as the above would no doubt injure the growing part so much as to render all results useless, but the growing region of the culms of Dendrocalamus is so large that the growth was not perceptibly affected unless repeated incisions were made. The following tables are typical of the general results obtained:—

TABLE I.

June 11, 1906, at Kandy.

Time.	Temp. in Bamboo.	Shade Temp. of Air.	Weather.
8·25 A.M	23·0° C.	24·1° C.	Sunny, but young culm in shade
9·28 ,,	23·6	25·0	—
11·20 ,,	26·4	26·7	In sun occasionally since 9.28 A.M.
2·10 P.M.	29·0	27·1	In sun
3·30 ,,	31·0	27·7	In full sun
5·45 ,,	30·0	25·0	Sun gone down
8·20 ,,	27·0	24·0	—
10·20 ,,	25·2	22·5	—
June 12.			
1· 5 A.M.	24·0	22·0	—
5· 0 ,,	23·0	21·6	—
7·10 ,,	22·8	22·2	Much duller day till after noon
9·10 ,,	23·7	24·0	—
11·15 ,,	25·3	26·0	—
1·50 P.M.	27·9	26·4	—
3·45 ,,	31·0	26·2	Full sun
5·20 ,,	31·0	25·0	—

This culm was about 18 in. high and growing very slowly.

TABLE II.

June 19, at Anuradhapura.

Time.	Temp. in Bamboo.	Shade Temp. of Air.	Weather.
8·20 A.M.	25·3°C.	25·6°C.	Slight shower about 9.30 A.M.
10·15 ,,	26·9	27·4	—
12·15 P.M.	28·7	28·0	Very slight shower about 11.50 A.M.
2·25 ,,	29·0	28·1	Showers 1 to 1.30 P.M.
4·15 ,,	29·0	27·8	In sun
6·15 ,,	28·2	26·9	—
8·20 ,,	27·6	26·2	—
10·35 ,,	26·4	24·7	—
12·30 A.M.	26·1	25·4	—
2·35 ,,	26·0	25·0	—
4·30 ,,	25·8	25·0	—
6·25 ,,	25·6	24·7	—
8·25 ,,	26·7	26·8	—

June 21.

Time.	Temp. in Bamboo.	Shade Temp. of Air.	Weather.
5·30 P.M.	30·3	28·4	After a hot sunny day
7·30 ,,	28·3	27·0	—
11·40 ,,	25·4	24·4	—
1·30 A.M.	24·5	24·0	—
3·40 ,,	24·4	24·4	—
5·35 ,,	24·5	24·5	—
7·30 ,,	24·7	24·5	—

Taking these tables and other observations made at Peradeniya together we find that unless exposed to sunlight the bamboo culms tend to heat up and cool down more slowly than the air. If the bamboos are in the shade the air rises in temperature at daybreak faster than the bamboo, and we get as a rule at about 8 or 8.30 A.M. the air temperature higher than the bamboo temperature. If the morning is dull, as occurred on June 13th and 14th at Peradeniya, the temperature of the bamboo remains lower than the temperature of the air until noon. Should rain occur, accompanied as it usually is by a rather sudden lowering of air temperature, we find that the bamboo temperature falls much more slowly, so that after rain the internal temperature of the bamboo is higher than the surrounding air temperature. Again, when the air cools rather rapidly towards evening, say 4–6 P.M., the bamboo lags behind and is invariably higher than the air temperature at this period. If this were the only effect however we should find the bamboo on the average with the same temperature as the surrounding air, but exhibiting a lag all through the observations. This simple result is usually complicated by the effect of bright sunlight or very bright diffuse light. If a culm is exposed to sunlight its internal temperature rises rapidly and often, as in the case of the one at Kandy (Table I.), reaches a temperature higher than the maximum reached by the surrounding air. Having been thus heated up the culm takes a long time to cool down, and in these cases is higher in temperature than the surrounding air all through the night. This is very well seen in the case of the culm at Kandy (Table I.), which shows a higher temperature on the average than the surrounding air, and is only in fact lower for a short period in early morning before it receives the rays of the sun. The culm at Anuradhapura (Table II.) was not exposed so freely to the direct sun, and here we do not get an internal temperature very much exceeding the temperature of the air. The effect of the very bright diffuse light however seems to be seen in the fact that the temperature for the greater part of the 24 hours is slightly (from 1° to 2° C) above the temperature of the surrounding air.

Observations taken morning and evening on different culms showed that at the morning reading the internal temperature was usually lower than that of the surrounding air by a small amount.

Table III.

At Peradeniya.

Date.	Time.	Air Temp.	Culm 1.	Culm 2.	Culm 3.
Aug. 7	8.35 A.M.	24·0° C	23·5	23·0	22·9
Aug. 8	8.45 A.M.	24·7	23·3	22·8	23·3
Aug. 9	8.40 A.M.	23·5	23·9	23·5	23·7
Aug. 10	8.30 A.M.	23·2	23·7	23·3	23·2
Aug. 7	5.45 P.M.	25·0	27·8	27·0	26·3
Aug. 8	4.54 P.M.	26·1	28·2	27·8	26·7
June 9	5.40 P.M.	24·8	28·9		
June 13	5.25 P.M.	22·3	24·6	23·7	
June 15	5.35 P.M.	22·5	25·5	25·7	

This, however, was not invariably the case (see Table III., August 9 and 10). In the evening the temperature of the culms was invariably higher than that of the air, often by a considerable amount (see Table III., June 9th, 5.40 P.M.).

These figures agree with the continuous observations every two hours and show (1) the slower heating and cooling of the culm so that the internal temperature lags behind the temperature of the air; and (2) the effect of exposure to sunlight, which raises the general average of internal temperature, in some cases producing a temperature higher than the maximum experienced in the air. This general effect is seen in the invariably higher temperature of the bamboo towards evening—a difference which is often considerable if the day has been sunny.

Some such heating up must take place, and probably to a more marked degree in Agave and Furcraea. These are usually fully exposed to the sun, while the young bamboos are often partly or wholly shaded by the adult members of the clump. A rise of internal temperature when in full sun would probably account for the rapid rate at which these grow under such conditions.

It being so clear that temperature is the factor which regulates the rate of growth of these flowering shoots, we may examine the curves more closely to give us an idea of the accuracy which the methods used are capable of. The temperature both at Hakgala and Peradeniya was taken in the thermometer shed some 150 yards or so away from the plant measured. It was difficult to obtain the shade temperature out in the open near the plant, but on one occasion a thermometer reading 62·6° F. in the thermometer shed was taken immediately to the plant and there registered 61·7° F., a difference of ·9° F. It appears, therefore, that the record of temperature may vary by a small amount either way from the actual air temperature near the plant. Then, as has been pointed out, the temperature of the surrounding air may differ somewhat from the internal temperature of the growing shoot. That notwithstanding this, the correspondence between the two curves should be so striking is an indication of the accuracy attainable in a continuous series of measurements, where the error of any one measurement does not seriously affect the general form of the curve.

It will be useful to notice that though the general correspondence is clear there are deviations from it of small magnitude. Thus, on June 12th at Kandy the rate of growth of Furcraea increases between 2 and 6 A.M. somewhat considerably, though the temperature is almost stationary.

Influence of Grand Period.

The general result does not seem to be affected by the stage at which the shoot is measured.

Agave Morrissii at Hakgala was measured during the earlier stages of growth when the shoot was about 6 feet high. Furcraea gigantea at Kandy was in its later stages, and had already begun to branch. It was about 25 feet high. Agave americana at Hakgala was about 18 feet high and branches were just appearing, while the same species at Peradeniya was about 15 feet high and measured before any side branches had appeared.

Comparison of Absolute Rate of Growth at the different places.

As the temperature is the controlling factor in the growth of the shoot, it would perhaps be expected that, setting aside individual peculiarities of the plants measured, there would be faster growth in the low country where higher temperatures are the rule. Taking the total results of all the species, this does not come out clearly, for, although the greatest growth in two hours recorded in the whole series of experiments was at Kandy, where the shade temperature reached 28° C, yet a rate of 2 cms. per 2 hours was recorded at Hakgala with a temperature of only 21·1° C, and this is considerably greater than the growth at Peradeniya of 1·6 cms. per 2 hours with a temperature of 29° C and the 1·4 cms. per 2 hours at Saharanpur with a temperature of 30° C. It is in fact scarcely to be expected that with different species and even genera at different stages of growth any such uniformity should exist. It is sufficiently remarkable that all show the same relationship to one of the factors of the environment. It may be pointed out, without much stress being laid on the fact, that in the only case where the same species was measured both up-country at Hakgala and at Peradeniya, the average rate of growth as well as the maximum growth recorded was considerably greater at Peradeniya, where the temperature was higher throughout. The maximum growth measured for Agave americana at Hakgala was 1·1 cms. per 2 hours with a temperature of 20·6° C, while the maximum growth of a plant of the same species at Peradeniya was 1·6 cms. per 2 hours with a temperature of 29° C.

Summary for the genera Agave and Furcroea.

It will be seen that the Theory of Limiting Factors is easily applicable to the results for the cases so far considered. The temperature of the growing shoot is the Limiting Factor throughout, and we must suppose that both water and food are available in excess of the requirements for any of these temperatures.

2.—DENDROCALAMUS GIGANTEUS (THE GIANT BAMBOO).

Methods and Conditions of Measurements.

The measurements of the growth of young culms of this species were made in a similar manner to that used for Agave and Furcroea. The growth was marked off on one of the older adult culms of the clump, and instead of placing the ½-meter scale on the extreme tips of the sheathing bracts, it was placed on a level with the neck of the culm.

This continued throughout a fairly definite and well-marked point, while the tip of the longest bract was continually changing and being replaced by the next.

As the growth at Peradeniya had been so fully and clearly described by R. H. Lock (12), attention was directed to the growth of the same species at Hakgala in the Cold Moist Region and at Anuradhapura in the Dry Region. Measurements were taken later at Peradeniya also, but these only confirmed those taken by Lock (12).

The curves given in Plate 23 show the rate of growth per two hours of Dendrocalamus giganteus on two occasions at Hakgala, March 31st to April 2nd and July 10th to July 12th, with the temperature and humidity for the same period. These are the curves of the growth of single culms, the one measured on the later occasion being in a different clump from the one measured on March 31.

Plate 24 shows the growth of the same species at Peradeniya from July 6 to July 7. This curve represents the total growth of five culms measured. The scale is reduced so as to compare accurately with the growth at Hakgala.

Plate 24 also gives the growth of the same species at Anuradhapura, June 19 to June 20. This curve represents the total growth of six culms and the scale is reduced so as to be accurately comparable with the others.

The culm represented in Plate 23, measured on March 31 to April 2, was the subject of continued observations from March

14th to May 5th. During the greater part of this period its growth was measured twicea day, in the morning about 7 A.M. and in the evening about 6 P.M. A series of two-hourly measurements was made through the night, April 9th to 10th, which are not represented on the plate, and on several occasions other measurements were made at special times when the weather conditions were in any way unusual. When these observations resulted in striking evidence as to the growth under different conditions they will be quoted in discussing the results.

The culm of which the growth is represented in the upper part of Plate 23 measured on July 10th to 12th was the subject of observations from July 9th at 5 P.M. to July 12th at 6 A.M., and of no others.

Results.

The following facts seem to me to stand out clearly on a comparative examination of the curves of growth given for the three places.

1. *Growth and Rainfall.*

The rate of growth is in no way directly dependent on the rainfall. This is most clearly brought out by the measurements made at Anuradhapura in the dry country. The culms begin their growth here as a rule in June in the dry season, and throughout their growth, which is completed or nearly so by the end of September, there is as a rule little rain.

A clump with young culms in different stages of growth was under observation from June 15th to 25th, and during this time the total rainfall was ·03 inch falling on two days, ·02 being the highest amount per day. The average rainfall for the month of June is 1·4 inch and for July 1·0 inch as has before been stated.

Notwithstanding this the highest rate of growth per 2 hours ever recorded in the whole of my observations was observed here, and the average rate of growth during the night was higher than at either of the other places.

That the supply of water necessary for such rapid growth can be maintained during an almost rainless period is no doubt due to the fact that the clump was on low-lying, rather swampy ground in the vicinity of several large tanks where abundant water is always found close under the surface of the soil.

The correspondence between growth during the day and rainfall which is observed at Peradeniya and Hakgala is no doubt due to the fact that a rainy day is one in which the humidity is high and transpiration from the adult culms very small, but the observations at Anuradhapura show that the true controlling factor in the growth of the culms is the humidity of the atmosphere and not, except indirectly, the rainfall.

2. *Growth and Temperature.*

Taking the records of 2-hourly growth at the three places there is a clear general correspondence between the rate of growth and the shade temperature recorded.

The maximum growth at Hakgala in 2 hours was 2·55 cms. Average temperature 18·4° C.

Another case of rapid growth at Hakgala in 2 hours was 2·27 cms. Average temperature 17·4° C.

Maximum (average of 5) at Peradeniya in 2 hours was 2·8 cms. Average temperature 22·0° C.

Maximum (a single culm) at Peradeniya in 2 hours was 3·8 cms. Average temperature 22·0° C.

Maximum (average of 6) at Anuradhapura in 2 hours was 3·4 cms. Average temperature 25·0° C.

Maximum (a single culm) at Anuradhapura in 2 hours was 4·5 cms. Average temperature 25·0° C.

All these culms were at that stage of the Grand Period when the growth fluctuates about a steady value.

That this rapid growth is not continued throughout the 24 hours at Anuradhapura, so that the growth per day is in most cases smaller at Anuradhapura than at Peradeniya, is due to the greater number of the hours during which humidity is high at Peradeniya, so that rapid growth takes place for a greater number of hours out of the 24 there. This gives us a hint which will be developed later of the possibility of two factors in the environment in turn controlling the growth of the culms. What I wish to insist on now is the general fact that, *confining ourselves to growth for the short period of 2 hours*, the maximum rate of growth observed at the three places as well as the general average of growth during the night, is proportional to the temperature recorded, the lowest at Hakgala, the highest at Anuradhapura.

3. *Comparison between Day and Night Growth at the three places.*

Hakgala is the only place where the rate of growth per 12 hours of daylight exceeds the rate of growth per 12 hours of darkness. I have not myself observed either at Peradeniya or Anuradhapura any case of the growth during the day being greater than the growth during the night. Lock (12) during a series of observations extending from June 19th to July 18th on culms of Dendrocalamus only once recorded a greater growth by day than by night at Peradeniya, 12·4 mm. per hour and 12·2 mm. per hour respectively, the day in question being one of continuous rain. At Hakgala, however, the daily growth exceeded the night growth on nine occasions between March 14th and May 5th, viz., on March 15th, 19th, 20th, April 6th, 27th, 29th, 30th, May 1st, and 4th.

4. *Steady Fall of Growth Rate at Hakgala.*

The records of growth during the night at Hakgala show in the majority of cases a steady falling off in rate. The curves for the nights March 31st to April 1st and April 1st to 2nd, are in this respect typical of a considerable number of observations made during the north-east monsoon. This decrease in growth rate usually goes on steadily through the night, so that either the 6 P.M. or more usually the 8 P.M. reading gives the maximum rate for that night, all the later readings showing a slower rate of growth.

Though not so obvious an effect as the one due to changes of humidity (Lock) it is to be noted that the rate of growth at the 6 A.M. reading on the nights in question was only about two-thirds of the rate recorded at the 6 or 8 P.M. readings of the previous evening, so that the falling off amounts to about one-third of the fastest rate. It is so constant and so marked as to be certainly outside the limits of error of the observations. No similar falling off in rate was observed either at Peradeniya or Anuradhapura as is seen, not only by the curves in Plate 24, but by those for each culm.

5. *Day Growth and Humidity at Hakgala.*

The growth during the day at Hakgala is certainly controlled by the humidity, as will be at once seen by the marked change in growth from day to night and *vice versa*, and by a comparison of the curves for humidity and growth during the day.

Application of Theory of Limiting Factors.

Such being the main results of the observations, it remains to apply the theory of Limiting Factors and see if it furnishes a general explanation of all the facts.

Two Limiting Factors.

Taking first the case of the bamboo at Hakgala, it will be seen that unlike the case of Agave or Furcraea no single factor of the physical environment controls throughout the 24 hours. Obviously the humidity of the air is the governing factor during the day. It will be noticed, however, that at night the humidity stands practically constant at saturation 100% and thus there is nothing in this factor to account for the marked and steady falling off observed on so many occasions. The light is practically constant during the night, so that even if the growth of the bamboo culms were affected by light, which Lock (12) denies, this would not account for the steady fall of growth rate. The factor which does decrease in intensity during the night is the temperature, and it will be observed that the curves of temperature between 6 P.M. and 6 A.M. are markedly parallel with the curves of growth for the same period. We seem here, therefore, to have a case in which one physical factor, humidity of air, regulates the growth during the day, and another, temperature, at night. I think the theory of Limiting Factors is fairly applicable to this case. If we suppose that during the day the transpiration of the adult culms is so great as to draw off the supply of water from the growing culms, we get the reason why in the daytime the growth shows a correlation with the humidity of the atmosphere. After 6.30 P.M. darkness and the saturation of the atmosphere produce a set of conditions in which transpiration from the adult culms is practically nil. The supply of water to the growing culms may then be supposed to be in excess, so that the temperature, which is considerably lower than this species ever naturally experiences, becomes the limiting factor and continues so until with the next morning the light and the decrease of humidity again bring about conditions in which the water supply is the limiting factor.

Humidity only indirectly a Limiting Factor.

If we are to apply this theory to our observations of Dendrocalamus at Hakgala we must at once recognise that the Humidity of the Atmosphere is only indirectly the controlling factor in the growth at Peradeniya or Anuradhapura or in the daytime at Hakgala. The young culms are on the same rhizome as a number of adult leaf-bearing culms, and the supply of water to the young ones depends almost entirely on the amount of water drawn off by the transpiration of the adult culms. If transpiration is vigorous the water supply to the growing culms is small, and *vice versa.* Now the transpiration of the adult culms, depending as it does upon the opening or closing of the stomata, is not regulated merely by the one factor of the humidity of the atmosphere, but by the light also. Light is generally held to cause an opening of the stomata and therefore an increase of transpiration.

Francis Darwin in his paper "Observations on Stomata" (4) comes to the general conclusions—

(1) That the nocturnal closure of stomata is not so complete as to prevent transpiration, but that it does greatly diminish it.

(2) That this degree of closure is extremely common in unspecialised terrestrial plants.

Leitgeb (11) and Stahl (21) both found many plants with open stomata at night and Leitgeb (11) went so far as to say that as many plants have open as shut stomata at night, but the very extensive researches of Darwin (4) led him to the conclusion that in non-specialised plants there is a great preponderance of nocturnal closure. Darwin is supported in this conclusion by Schellenberger (17).

It also seems clear from Darwin's work that in the daytime different degrees of illumination have a marked effect in producing different degrees of opening of the stomata.

Measurements taken on the night of April 9th to 10th become intelligible when the light factor is taken into account. On this night the humidity of the air was considerably below 100 per cent. throughout the night, an unusual condition at Hakgala. At 8 P.M. the humidity was 88 per cent. and decreased steadily to 75 per cent. at 2 A.M., when it increased up to 90 per cent. at 6 A.M. The growth, however, showed a steady decrease from 1·2 cms. per two hours to ·65 cms. per two hours, and thus showed a close relationship to the steadily falling temperature curve and not to the curve of humidity. A humidity of 75 per cent. is lower than that recorded on some sunny days when the growth fell off owing obviously to lack of sufficient water. Yet if our theory is to apply we must suppose that the water supply is in excess for the growth at this temperature (14°C. to 9° C.), even though the same humidity on other occasions in the daytime obviously causes an insufficient supply of water. That this might occur seems probable when we consider that in the absence of light the stomata are closed, or nearly so, and the comparatively low humidity is probably only acting through the epidermis of the leaf.

Close examination of the curve for Anuradhapura seems to me to lend support to this view. One of the striking features of this curve is that there is a very marked change in rate of growth between 4 P.M. and 8 P.M., which does not seem to be at all adequately accounted for by the change in humidity. A corresponding rapid change in the opposite direction the following morning after 6 A.M. is also greater than the general correspondence between the curves of growth and humidity would lead us to expect. It seems to me reasonable to suppose that there we can trace the influence of the change from light to darkness and the reverse.

In this case the day was almost uniformly sunny and the light intense, so that the change of light intensity at sunset and sunrise was very marked. That this marked and (as always in the tropics) fairly rapid change in the intensity of light caused a considerable change in the transpiration of the adult culms and thus indirectly affected the growth of the young culms seems to supply an explanation for the very considerable changes which would otherwise be inadequately accounted for.

It is also easier to see on this view why the daily growth of Dendrocalamus at Peradeniya should only once in the total series of measurements made by Lock (12) and myself have exceeded the growth at night. When the day (as happens fairly frequently) is one of continuous high humidity with continuous or intermittent rain, there seems no reason to expect on any hypothesis that the day growth should not equal or exceed the growth at night. If, however, we consider that even when the humidity is high during the day, the light is always far more intense than at night, we see that the transpiration is likely to be greater in the day even when the humidity during day and night are almost equal. Thus, even on days of high humidity we should not expect the growth during the day to equal that during the night. It seems therefore that it is only during the night that we can look for such conditions as will allow of an adequate supply of water to the young culms. Only then are we likely to get the supply of water in excess so as to bring in the temperature as the limiting factor.

The growing bamboo culms usually exude drops of water (often copiously) from the tips and axils of the sheathing bracts during the night, and it may be safely supposed that when this occurs the supply of moisture is in excess of the requirements for growth at that temperature. This exudation usually begins at Hakgala as soon as darkness sets in and continues through the night, so that for about eleven hours of darkness we have conditions in which the temperature may be supposed to be the limiting factor, and a falling curve of growth is usually observed.

At Peradeniya the atmosphere is not by any means so usually at or near saturation during the night, and the exudation of drops of water varies considerably with the state of the atmosphere. Sometimes the exudation of water begins early in the night, sometimes it is postponed till later. The time when the exudation begins also varies with the height of the culms, the taller culms always being later than the short ones.

On the night of July 6th to 7th, represented in the curve on Plate 24, the exudation was not taking place in all 5 culms until 11 P.M. The important point to notice here is that after this time we should expect on our theory that the growth would be limited by the temperature. It will be seen however that the temperature after this time varied so little that it could scarcely be reflected in the curve of growth.

The growth curve after this time presents at least as much resemblance to the curve of temperature as to the curve of humidity, but the circumstances are not such as to present a decisive case as to which is the controlling factor during the short time that we have clear evidence of the supply of water being in excess.

The same reasoning would apply to the observations at Anuradhapura, except that here the exudation of water usually occurs later still as the humidity is as a rule lower than at Peradeniya. At Anuradhapura the average humidity for June and July is 77 per cent., while at Peradeniya for the same months it is 81 per cent. and 82 per cent. respectively.

We do not get therefore suitable conditions for a sufficient length of time to exhibit the limiting effect of temperature when water supply is in excess of requirement.

Summary of General Explanation of Facts.

To sum up, the general explanation which I offer of the observations on Dendrocalamus at the three places is, that two factors of the physical environment chiefly affected the rate of growth of the young culms: (1) the temperature; (2) the supply of water to the growing culms. This second factor being intimately connected with the amount of water drawn off by transpiration by the adult culms which are on the same rhizome, depends in its turn on two factors: (1) the humidity of the atmosphere; (2) the intensity of the light.

During the day at Hakgala, and during the day and also a varying part of the night at Peradeniya and Anuradhapura, the conditions are such that the supply of water is the limiting factor in the growth of the culms, the temperature being high enough to allow of greater growth than actually takes place.

During the whole night at Hakgala, and during a varying part of the night at Peradeniya and Anuradhapura, the moisture supply is in excess, and temperature is the limiting factor.

Further Tests of the Theory.

1. *Night Growth at Hakgala.*

If this is the true explanation of the facts, we should expect that the falling off of growth at Hakgala during the night would vary in amount according as the fall of temperature through the night was greater or smaller, *i.e.*, the curve of night growth at Hakgala should on the whole be parallel with the temperature curve. The following observations bear on this point.

On fourteen nights at Hakgala the rate of growth for the first four hours of the night, *i.e.*, from about 6.30 P.M. to 10.30 P.M., was measured and compared with the rate of growth for the next eight hours, *i.e.* 10.30 P.M. to 6.30 A.M.

During these fourteen nights varying weather conditions prevailed, and the curves of air temperature through the night varied from a considerable fall as night went on to a practically uniform temperature through the night.

If the temperature is the limiting factor in growth we should expect to get a falling curve of growth on the nights when the temperature falls and a steady curve on the nights when the temperature is uniform. The average temperature for the first four hours of the night was obtained by taking the mean of the temperature readings at the beginning and at the end of that period, and so also for the next eight hours. The temperature at 6.30 A.M. is as a rule either the minimum temperature for the night or very little removed from it.

The mean temperature for the 8-hour period was subtracted from the mean temperature for the 4-hour period. The difference is a number which enables us to compare the different nights as regards the fall of temperature. Similarly the rate of growth per two hours for the 8-hour period was subtracted from the rate of growth for the 4-hour period and the difference gives a measure of the fall of growth rate during the night. The results are given in Plate 24 (below, on left) and constitute, it seems to me, striking evidence for the truth of our hypothesis; that the two factors measured in this way should come so near to proportionality as the curve shows by mere coincidence is unthinkable, and the general form of the curve must, it seems to me, reflect a real connection between the two factors.

Only three of the points on the curve are seriously out of the straight line of direct proportionality, and the general conclusion that when the temperature falls considerably the rate of growth also shows a considerable falling off, and when the temperature is nearly uniform the growth curve is also nearly uniform, seems to me to be fully established. It may be pointed out here, as in the case of the Agaves, that the temperature observations are liable to an error of 1° F. and that the mean for the periods is obtained in a way which can only give, in the absence of intermediate readings, roughly approximate figures. Further, if we suppose (as we did for Agave) that the true controlling factor is the internal temperature of the growing culm itself and not the temperature of the surrounding air the two or three seemingly aberrant results may be to some extent accounted for.

Thus, the general correlation between the fall of air temperature and the fall of growth rate through the night is unmistakable and fully supports our hypothesis.

The above observations were made on two different culms, the figures for the three nights, July 9, 10, and 11, referring to one culm and those for the other eleven nights referring to another culm in a different clump. The curve for July 10-12 on Plate 23 is typical of the nights of nearly uniform temperature accompanied by nearly uniform growth.

2. *Day Growth with rain at Hakgala.*

Since the temperature is as a rule considerably higher during the day than the night, we should expect if the supply of water could be maintained in excess that faster growth would be observed in the daytime. Conditions under which this could be tested rarely occurred, as in wet weather the difference between day and night temperature is usually very small, while the weather which shows a considerable contrast between day and night temperature is dry and the days usually without rain. It is significant in this connection to notice that when two hours of more or less continuous rain did occur during the day after sunny weather, with fairly high temperatures, the growth recorded was more rapid than occurred at any time during the night with lower temperatures. The highest growth rates per two hours recorded for Hakgala were in fact observed during the day and not during the night. The maximum record for two hours of darkness at Hakgala is 1·4 cm. on April 1st, 6–8 P.M., the temperature for the beginning of the period being 16·6° C. (62·0 F.). This was exceeded by the following records for two hours of light, rain in each case falling continuously or nearly so during the period.

On April 1st, 4 to 6 P.M., 1·65 cms. Temperature at 4 P.M. 19·3° C. (66·7° F.).

April 25th, 1.40 P.M. to 3.40 P.M., 2·55 cms. Temperature at 1.40 P.M. 21·1° C. (70·0° F.).

April 5th, 11.30 A.M. to 1.30 P.M., 2·27 cms. Temperature at 11.30 A.M. 18·8° C. (66·0° F.).

No exact proportion is to be expected in these figures, since it is probable, as has been pointed out previously, that the internal temperature of the culm is the true controlling factor, and this, as my observations show, was often considerably removed from the shade temperature of the air during the day, especially if the weather had been sunny, while during the night the two temperatures were as a rule not far apart. They do show that given a sufficient supply of moisture the highest rate of growth occurs at the highest temperatures.

3. *Minimum Temperature and Night Growth.*

The minimum temperatures were included in all the observations taken between March 31st and May 14th. These minimum temperatures are a guide, somewhat rough of course, to the average temperature of the different nights. It may happen that the minimum temperature is a sudden fall from a considerably higher temperature, and thus would not be a sound indication of the average temperature of the whole night. On the whole, however, the minimum temperature may be used as a rough guide to the average temperature during the night. This being so, we should expect if the temperature is limiting during the night that for the same culm the minimum temperature would show some relation to the amount of growth during the twelve hours of darkness. Plate 24 (below, on right) gives the growth in cms. per 12 hours during the night of Dendrocalamus at Hakgala from April 2nd to 3rd to April 14th to 15th, together with the minimum temperatures for the same period in F.° This period falls within that portion of the Grand Period when the growth fluctuates about a steady average value.

The correspondence between these two curves is again fairly close, though the measurements can only be roughly approximate. It must also be stated that at a later period in the growth of the same culm no correspondence between these two curves could be traced, so that little stress must be laid upon this particular point.

Consideration of all the facts of the Hakgala case seems to make clear that here, where the temperature is much lower than any the species is exposed to in its natural habitat, the temperature becomes the limiting factor of the growth whenever the supply of water to the growing culm is sufficient. This is usually the case during the night, and may perhaps occasionally be so during the day. As a rule, however, so much water is drawn off to supply the transpiration of the adult culms that the water supply during the day is not sufficient even for the growth which would be permitted by the comparatively low temperatures recorded at Hakgala.

4. *Maximum Growth at the three places.*

Taking a general view of the growth at the three places it has been noticed that the maximum growth recorded at the three places for short periods of two hours is in proportion to the temperatures recorded. These maximum growths are in every case measured at a time when the water supply is either sufficient or in excess (usually towards morning at Peradeniya and Anuradhapura), and therefore according to our view the maximum amount of growth allowed by that temperature is taking place, or, in other words, the temperature is limiting. There may be some risk in comparing the results with even the same species at places so wide apart and under conditions so different : I have, however, compared the growth of culms which are in the same or nearly the same stage, and I think the broad general fact that the growth at the three places is proportional to the temperature when moisture is in excess is too important to be ignored in considering the applicability of our theory.

5. *Day and Night Growth at the three places.*

It will be seen, too, that our theory provides an explanation for another of our general conclusions, namely, that at Hakgala the growth during the day not infrequently exceeds the growth during the night.

The uniformly high temperature at Peradeniya and Anuradhapura allows of growth at a very rapid rate during the night, and it is improbable that any day should be found in which the conditions of water supply are so favourable as to allow of an equal or greater growth by day, since days of continuous high humidity are rare and, as has been remarked previously, the light effect on the stomata is always present.

If now, however, the growth during the night were limited by the temperature to a much slower rate than occurs at Peradeniya it would obviously be more probable that days should be found on which the conditions would allow of the night growth-rate being exceeded.

At Peradeniya a day of continuous rain would be the only occasion on which the growth per day would be likely to exceed the rapid growth at night, and even then we could not expect much excess because in the rainy weather of the south-west monsoon the temperature is little, if any, higher during the day than during the night. At Hakgala, however, where the growth during the night is kept quite low by the low temperature, a day of intermittent rain and sunshine might cause a growth exceeding that of the following or previous night. The growth during the hours of rain at the high day temperature might in fact be equal to the growth during a larger number of hours favourable (as regards water supply) at night when the temperature is low.

It is to be noted that at Anuradhapura, where the high temperature allowed of very rapid growth at night and where the day was as a rule dry and sunny, there is no approach to equality between the growth-rates by night and by day.

Another Theory : Periods of rest necessary.

Our theory, it will be seen, provides an explanation which covers the facts of the case fairly completely. Another supposition which would account for some of the facts, is that which is sometimes held that a growing organ is not capable of continuous rapid growth, but must have intermittent periods of rest.

In this connection a paper by W. E. Kellicott (8) is of some importance. He shows that in the root of Allium the periods of slowest growth are the periods of most active cell division. Thus it seems that there are two operations going on in the growing organ: (1) cell-division, which takes place when growth is slow; (2) increase in size of the cells thus formed causing the more rapid elongation of the organ. If slow growth or cessation of growth is necessary for active cell-division, we get the idea that periods of rest are necessary for subsequent rapid growth.

On this theory we should expect that growth would be more rapid if favourable conditions occurred immediately after a period of rest than if similarly favourable conditions occurred after a period of activity. The very rapid growth during 2-hourly periods of rain during the day, when such periods follow bright sunshine (a time of rest for the growing culm), would fall in with this idea. It would also account for the rapidity of growth at the beginning of the night at Hakgala. The return of favourable conditions after the resting or almost resting period during the day causes a greater growth than the continuance of those conditions later in the night is able to sustain coming after a period of great activity. It would furnish also some clue to the cases in which the day growth exceeds that of the following night. If the culm is actively growing during the day owing to favourable conditions then a continuance of those conditions during the night would not result in continued rapid growth. Taking two days, one rainy the other dry and sunny, we should expect that the following nights being equally favourable to growth, the growth during the night following the dry day would be greater than the growth following the wet day.

Cases of this sort may perhaps be found in the record of the measurements at Hakgala, but a careful examination, both of Lock's figures and my own, shows a large number of cases in opposition to this theory, *i.e.*, there is often as rapid a growth at night after a day of rapid growth as after a day of slow growth. Further, the 2-hourly measurements at Peradeniya show that provided the humidity keeps high the falling off of growth to be expected on this theory by a continuance of favourable conditions does not as a matter of fact occur. In fact neither is the theory itself capable of such accurate statement, nor is it so fully applicable to our results as the theory of limiting factors outlined above.

3. *COMPARISON OF AGAVE AND DENDROCALAMUS.*

Let us now broadly compare the two cases of Agave and Dendrocalamus. Both on our theory come under one general rule, namely, that water supply being sufficient or in excess, the growth is limited by the temperature of the growing shoot. In the case of Agave the supply of water seems always to be sufficient, so that the temperature effect is observable throughout. None of our cases has shown any falling off of growth even in the hottest part of the day. On the other hand, the water supply to the young bamboo culms is constantly in defect during the day, and at Peradeniya and Anuradhapura is so during part of the night also, so that the time during which the temperature effect can be observed is curtailed to the hours of the night or to part of the night. This difference between the two plants seems to receive an explanation when we contrast their general organization and habit of growth. In the case of Agave each growing shoot is on a separate plant and completely independent of every other. All the supply of moisture obtained, whether from the soil by the roots or from stores in the leaves, is available for the one growing shoot. Again, with such thick and fleshy leaves with thick cuticle the loss of water from the leaves must be quite small even in conditions of intense light and low humidity. It does not seem surprising, therefore, that the supply of water to the growing axis should be sufficient even in the hotter and drier parts of the day.

The case of Dendrocalamus, on the other hand, is quite different. The culms grow in clumps from a complicated network of underground rhizomes. The supply of water available is drawn upon, not only by the growing culm, but also by a number of adult culms on the same rhizome. Each adult culm has a large area of thin leaves spread out to the atmosphere. Changes of light, intensity and of humidity of atmosphere must have a great effect upon such a system of thin well-spread leaves, and the amount of water transpired by the adult culms no doubt varies very largely with changes in these conditions. Thus the amount available for the growing culms, which have themselves no leaf-system which would draw up their own supply of water, must be largely a matter of the amount left over when the adult culms have been satisfied.

Thus we have two cases in which the actual rate of growth of the shoots depends upon the same factors, but on each in different degree according to the specific organization and habit of the plant.

4. *OTHER CASES.*

We now turn to cases of the growth of plants of very different character and habit. The gardens at Peradeniya offer several cases of shrubby plants which put out long shoots whose growth is rapid and whose leaves do not function until the growth of the shoot is finished or nearly so. Many of these are straggling prickly plants, whose long shoots thus reach to a considerable distance from the stem towards the light before the leaves begin to do the work of assimilation. In the growing stage the leaves on these shoots are as a rule closely pressed to the stem, often covered with a mealy tomentosity, very rarely presenting any considerable area of chlorophyllous tissue to the light. When the growth of the shoot is complete, or nearly so, the leaves become spread out to the light, become green by loss of their tomentosity or red colouring, as the case may be, attain their full development in size, and fully take on the function of assimilation.

The growth of these long shoots is often very rapid, and usually takes place from a copious reserve food supply in the thicker stems.

Capparis and Stifftia.

Two such cases were the subject of series of measurements at Peradeniya, namely, Capparis Roxburghii, DC., and Stifftia chrysantha.

One of the thicker stems of Capparis Roxburghii, which was just putting out two of these long runner-shoots, was examined for starch and found to be crowded with it all through the tissues, so that here again we have a case of the translocation and elaboration of supplies of food already stored. Stifftia chrysantha was not found to contain much starch under similar conditions, but the food supply may have been in a different form.

Methods of Measurement.

Here the methods were extremely simple. A narrow mark was made on the growing stem well below the region of growth, usually by means of white paint. The distance from this mark to the tip of the shoot (and these plants were chosen partly because the tip is quite well-defined) was measured by a half-metre scale at the successive observations. Successive measurements of the same shoot at the same time did not differ by more than ·05 cms., which may be taken as the limit of error for the method. This error is much more considerable than in the previous cases, because, although the growth is rapid for this class of plant, yet it is by no means so rapid as the growth of Agave or Dendrocalamus, and thus the error of the method becomes of greater importance. The curves represent however the growth of more shoots than one, and thus the errors will probably average out, and also when a continuous series of measurements is taken at fairly close intervals the general curve may be taken as more accurate than any one of the readings.

Results.

Plate 25 shows the curve of the growth in mm. per two hours of two shoots of Capparis Roxburghii from January 9th, 9 A.M., to January 11th, 7 A.M. It will be seen that during the day the growth is slow so that either the lowered humidity or the light checks the growth. It is to be observed that there is a contraction of considerable amount in the hotter part of the day when the sun is fully on the plants followed by rapid growth as darkness sets in. It is clear that the water supply is the limiting factor during the day. Does it continue so during the night? The night, January 10th to 11th, is an interesting reply to this question. The humidity curve rises steadily through the night, while the curve of temperature as steadily falls. The light factor being absent, the case would appear to be a decisive test as to which is the limiting factor through the night. The curve of growth, it will be seen, goes on the whole steadily downward parallel to the curve of temperature and shows no tendency whatever to rise in response to the increase of humidity as night advances. A similar curve was obtained for Stifftia chrysantha on the same nights. Rapid growth was observed as darkness set in, and this although no actual shortening of the shoots took place in the hotter part of the day. This rapid growth was followed by a gradual falling off during the night, the lowest reading for the night being recorded early in the following morning when the minimum temperature for the night was also recorded. The temperatures of 15° C. recorded on the morning of January 10th and 16·1° C. recorded on the morning of January 11th, are much lower than the usual minimum temperature at Peradeniya. It is only on a few nights in December and January that such temperatures as these are reached, so that the range of temperature through the night is considerably lower than that to which these plants usually are exposed, and it is under such circumstances of course that the temperature would be expected to be the limiting factor in growth.

The same plants were measured again on July 6th to 7th in the south-west monsoon, when the range of temperature was much more uniform, being considerably higher at night and lower in the day.

Plate 24 (middle, on right) shows the curve for Capparis Roxburghii from July 6th at 11 A.M. to July 7th at 9 A.M.

The day was dull on the whole with high humidity throughout, and we do not get any record of actual contraction during the day. Growth was fairly steady throughout the night and contrasts strongly with the steady fall in growth-rate recorded for January 9th to 10th and 10th to 11th. It is not easy to say whether the temperature, being now about 5° C. higher throughout, is in excess, and thus brings in the humidity as limiting factor through the night as well as through the day, or whether here again the water supply being in excess during the night brings in the temperature as the limiting factor.

The temperature curve shows such a slight fall during the night that it would be difficult to detect its effect on the growth. On the whole, perhaps, the growth shows a tendency to respond to the increased humidity of the later part of the night, but this cannot be stated with certainty, the result chiefly important being the contrast with the steadily falling night curve of January 9th to 11th when the temperature was considerably lower throughout. The curve for Stifftia chrysantha, July 6th to 7th, was generally similar.

The Light Factor.

The cases of these shrubby plants are important as bringing in to the question a factor which in considering the previous cases of growth we have been able largely to ignore, namely, light. In the case of Agave no retarding influence of light could be at any time detected, for it was just when the shoot was exposed to the hottest sun that the most rapid growth took place. In Dendrocalamus, though it cannot be decisively proved that the direct effect of light on the young shoots is not in the direction of retarding growth, since the factors of low humidity and intense light always occur together and their effects cannot easily be separated, yet what evidence there is on the question seems to show, as Lock (12) has pointed out, that such an effect is not probable, and in any case must be very small. The indirect effect of light acting through the transpiration of the adult culms is, as we have seen, considerable, but of course in a quite different category from the direct effect of which we are now speaking. It may be that the absence of response to light in Agave, Furcraea, and Dendrocalamus is due to the thick armour of bracts or leaf-sheaths in which the young shoot is enveloped, though in this respect the flowering shoot of Agave, in which the absence of light effect is most certain, is not so well off as Dendrocalamus. The bracts which surround the growing inflorescence axis of Agave do not form such a close and impenetrable armour as do the leafsheaths of Dendrocalamus. The cases of Stifftia, Capparis, and other similar shrubs are in this respect quite different. In these the growing region is exposed to the light with very little protection. The extreme tip of the bud is indeed surrounded by a number of developing leaves, but the growing region extends considerably below this and is exposed for the greater portion of its length with very little protection. It might be expected therefore that here the effect of light would show itself. It must be stated at once that under natural conditions the two factors of intense light and low humidity are so constantly associated that no very decisive evidence is to be obtained on this point. Neither is it easy to arrange experiments in which a plant of considerable size shall be subject to different degrees of humidity with constant light, or to constant humidity with varying light. Some little evidence has however been obtainable on this point in the following way :—

Eranthemum cinnabarinum is a shrubby plant whose shoots grow sufficiently rapidly for reliable measurements to be taken at intervals of two hours. The curves of growth for the day-time always show markedly the effect of lower humidity by either very slow growth or cessation of growth altogether. The shoots were measured on several fine days and always showed this effect, that while the curve of growth rapidly fell during the morning along with the curve of humidity, yet after about 1 P.M. the growth always began to increase. The curve of growth in fact after 1 P.M. rises previous to the rise of the curve of humidity and rises much more sharply.

This increase of length which clearly preceded the increase of humidity showed that some other factor was assisting to cause the slow growth of the period before 1 P.M. It was noticed that at about 1 P.M. the bush which had hitherto being exposed to the full sun came into the shade of an avenue of talipot palms close by. There is no doubt that the change from full sun to the less intense though still very bright diffuse light in the shade had an effect on the growth of the shoots and allowed growth to commence though the humidity did not increase but rather diminished. This effect was also noticeable in Capparis Roxburghii. The shoots measured were on two different bushes which received direct sunlight at different times of the day. It was observed that though the humidity of the air would be practically the same for each, since they were only about ten yards distant from each other, yet the period of actual contraction of the shoot varied and was usually coincident with the time of exposure to full sun.

This exposure to full sun was in fact often accompanied in Eranthemum by a patent wilting of the leaves and shoot, which showed under such circumstances a contraction in length. Turgidity was restored when the plant became shaded. This seems to point to the idea that the effect of the intense full sunlight was to increase considerably transpiration and loss of water from the leaves and shoot, and that the shortening of the shoot was due to this loss.

Experiments carried out with the aid of thermo-electric junctions on the growing region of shoots of Capparis Roxburghii show that in full sun at about 3 P.M. the internal temperature of the growing region rises 3° C. above the shade temperature of the surrounding air. Radiation of sufficient intensity to cause such a rise inside the shoot cannot be without a considerable effect in the direction of loss of water from the growing tissues. If this explanation of the facts be the true one there is still no evidence in these cases for the direct retarding effect of light upon growth as usually understood. Changes in intensity of light, apart from exposure to full sun, have not in these experiments ever been unaccompanied by changes of humidity, whose effect would act in the same direction, and the effect of each of the two factors has therefore never been distinguishable in the results.

Hanging roots of Vitis Lindeni.

We now turn to a case of considerable interest, that of the hanging roots of Vitis Lindeni. The plant is a straggling climber whose thin stems sprawl over other vegetation often to a considerable height and send down large numbers of long thin roots which, on reaching the ground, take root and then begin to increase in thickness, no doubt taking up the function of conduction of water to the stems above. These roots are positively geotropic and are quite sensitive to contact, but exhibit no trace of heliotropism. If unimpeded their course is in a straight line from the point of origin to the earth. Their growth is surprisingly rapid, 7 mm. per hour having been recorded.

Plate 25 shows the curve of growth in mm. per two hours (three added) from July 6th, 10 A.M., to July 7th, 5 P.M., with the curve of humidity, and below two growth curves for two separate roots from January 9th, 6 A.M., to January 11th, 7 A.M., with the curve of temperature for the same period. Taking the curves of earlier date first there is no doubt of the general correspondence between the curve of growth and the curve of temperature. The most rapid growth is always during the day, though these were days of continuous sun and low humidity, and the slowest growth coincides with the minimum temperature, which it must again be pointed out was on these dates much lower than is experienced at Peradeniya during the greater part of the year.

The curve for the same roots on July 6th to 7th shows a striking contrast to that on January 9th to 11th. Here the occurence of low humidity and sunshine during the day is always followed by either slow growth, total cessation of growth, or even in some cases a decrease in length. During the night or during heavy rain in the daytime the growth is rapid. There is no trace, even during the night when water supply might be expected to be in excess, of any correspondence between growth and temperature. Throughout the whole period there is visible a close correspondence between growth and humidity, and whether by night or by day an increase of humidity is followed by an increase of growth.

This contrast between the curves of growth for two different times of the year is puzzling, for it will be noted that one set of temperatures is not uniformly either higher or lower than the other. If the January curve had been lower throughout the case would have been easily explained on our theory, for at the low temperature we should expect the temperature to be limiting, while when the temperature rose the supply of water would probably fall short of that required for the more rapid growth permitted by the higher temperature. Such is however not the case, for the temperature rises on January 9th to 27·3° C. and on January 10th to 26·1° during the day, while on July 6th it rises only to 25·1° C. and on July 7th to 25·0° C.

That a temperature of 27° C. in January on a day of low humidity should result in increased growth, while a lower temperature 25°C. in July on a day of much higher humidity should be followed by a very marked decrease in growth-rate is inexplicable on our theory, nor do I see any suggestion or theory which can account for the facts and help us out of the difficulty. The records of soil temperature at one foot below the surface at the Experiment Station, about a mile away, were obtained and showed a difference of 0·5° F. between the two periods at 9.30 A.M. and 3.30 P.M., the temperature being higher by this small amount for the July period. This if it were sufficient to have any visible effect, would act in the direction of increasing the water supply and therefore would make it still more inexplicable that at this period the water supply should be insufficient during the day. The number of rapidly growing roots from this plant was greater in July than in January, so that it is possible that the water supply which was always in excess of requirement for the few roots growing in January, would be found to be inadequate for the larger number of roots growing in July. Another possible loophole of explanation would be furnished if it should be noted that the leaf-area of the plant was greater in July than January, for then the much larger transpiration from the greater leaf-area would presumably allow of a smaller water supply for the growing roots. Though at the time sufficient attention was not directed to this point, yet there is no reason to suppose that a marked leaf-fall took place previous to the January readings, or it would not have escaped attention. Further observations on this point may serve to clear up the difficulty. It remains now to notice that whatever the explanation, the facts support our theory so far as this, that only one factor of the physical environment regulates the growth at one time. It is of the essence of the theory of limiting factors to suppose that given any physical factor in excess of requirement, it will not, however much it fluctuates, affect the growth which is all the time limited by another factor. Thus, if a temperature fluctuating round, say 15° C., on a dry day is low enough to limit the growth, then if the same temperature prevails on a wet day we do not expect any increase of growth, for the growth being still limited by the low temperature the large amount of water available on the wet day is merely superfluous and does not affect the growth. Similarly if on a day of given humidity and temperature the growth is limited by the supply of moisture. then as long as the humidity remains the same an increase of temperature would not increase the growth, since this would be still limited by the low humidity. The extra temperature would in this case be merely superfluous.

Thus, though the physical factors of the environment may change sufficiently during 24 hours to bring in first one and then another as limiting factors, yet at any one time (*i.e.*, any sufficiently short period) the growth is not the product of two or more of the physical factors, but is regulated by one alone, the other being in excess of requirements to a greater or smaller degree. It seems probable therefore, since the curves for Vitis Lindeni show in each case the effect of only one factor throughout, in January temperature, in July humidity, that whatever the ultimate explanation of the facts may be, it will be one which can be brought under our theory or under some slight modification of it.

III.—CONSIDERATION OF PREVIOUS WORK.

The theory of limiting factors being on the whole so clearly applicable to the results given above, it remains to consider how far previous results can be co-ordinated by its application. Unfortunately it is seldom that such observations have been taken with sufficient accuracy or under such conditions as to furnish any clear evidence for or against our point of view.

Take for instance the observations of Shibata (20) on the growth of Phyllostachys mitis in Japan. Here the general conclusion is that the daily growth is in close agreement with the fluctuations of average daily temperature and has no relation to changes of moisture. Lock's results with Dendrocalamus and Gigantochloa show, on the other hand, a close agreement between humidity and growth and none between temperature and growth. Blackman (2) suggests that, since the temperature range at Peradeniya is from 19° C. to 30° C. and that in Japan from 11·6° C. to 20·7° C., we have a clear case of the low temperature being the limiting factor in Japan, while at Peradeniya the higher temperature would admit of more growth than actually takes place, the moisture being the limiting factor.

The case can, however, scarcely be so simple as this, since my own measurements of Dendrocalamus giganteus at Hakgala show an extreme temperature range of 9·1° C. to 21·1° C., *i.e.*, almost the same as that in Japan, and yet the growth is found to be in close agreement with the fluctuations of humidity during the day and only to show a relation to temperature during the night. Thus taking the total growth for 24 hours there is no recognisable agreement between the growth and the mean temperature for the period. A day of low humidity will cause quite a slow total growth for the 24 hours compared with a day of rain, even though the average temperatures for the two periods are about the same. Shibata's figures show no such result. The 29th April, for example, was a day of very low humidity, the mean being 43·5 per cent., yet the growth shows a distinct increase in response to the higher temperature, and this is the case on other days also.

It is quite possible that if more frequent observations had been made by Shibata, reconciliation of the two sets of figures might be supplied. In the absence however of any figures to show the difference between day and night growth in Japan no comparison of the cases can be attempted and the figures must remain outside our generalisation.

The observations of Lock on Dendrocalamus are, as has been shown generally in the preceding part of the paper, explicable on our theory, but the following point also deserves notice. As has been previously stated, under conditions of high humidity the growing culms of Dendrocalamus exude drops of water from the tips and axils of the sheathing leaves. If several culms of different lengths have been exposed to an atmosphere of low humidity and the humidity then increases, the shorter culms always begin the exudation previous to the taller ones. Thus at Anuradhapura on June 19th, at 10.30 P.M., culm 1 about 3 feet high and culm 4 about 13 feet high were both exuding drops of moisture. Culms 6 and 7 which were about 22 feet high were dry at the top, but had drops of water on the lower sheaths. It was not until 12 midnight that these tall ones were exuding moisture right to the top.

Now since the most rapid growth permitted by the temperature does not take place until water is in copious supply, of which the exudation of water is a sign, it follows that under the usual conditions the shorter culms have a greater number of hours during which their full growth is possible. It also seems to follow that the higher the culms go the more dependent their growth is upon rainfall which brings high humidity, for though a short culm may reach its most rapid growth while the humidity is still below saturation, a very tall one will not have sufficient water supply until saturation is reached. This supplies an explanation for certain facts noted by Lock (12) with regard to Dendrocalamus. He says "The variations in rate of growth become more marked in the late part of the Grand Period than in the earlier, and they appear also in the late portion to show a more marked agreement with the curve of rainfall."

W. H. de Vries measured a flowering shoot of Agave americana and his general results are quoted by Sachs (15). These are not accompanied by any actual figures either of temperature or of the humidity of the air so that little can be gained by discussing them.

It may be worth while however to note shortly their bearing on the observations and theory of the present paper.

The interest of the record for us is that our theory indicates that for species of Agave cases might be found when the growth would be so great that the necessary water supply would be lacking and would become the limiting factor. This would be expected at the highest temperatures. No such case has come under my own direct observation. De Vries' measurements of Agave, while showing at first some relation to temperature, afterwards showed a decided relation to the humidity as shown by a cessation of growth on fine mornings while some growth was recorded on dull or rainy mornings.

It is probable that this occurred at a lower temperature than those recorded in Ceylon, since the measurements were made in Holland (though as the time was summer, it is not certain) and this lack of water supply did probably not occur at a time of very high temperature. It is noted however that the experimental plant had no roots and the absorption of water took place by the porous dead mass covering the living root-stock. It is quite probable that under such circumstances the water supply might be limiting at a much lower temperature than occurred in Ceylon. Again it is quite possible that the absorptive power of the roots may have been checked by the comparatively low temperature of the soil which may have been considerably lower than in the cases measured by me in Ceylon. All this however is conjectural in the absence of figures. There is some difficulty in giving any explanation for the whole 24 hours in this case, for it is recorded that while growth ceased or almost ceased during the period 9 A.M. to 12 noon, yet the period 12 noon to 3 P.M., although probably hotter and with lower humidity, yet always showed considerable growth. Sachs explains the cessation of growth in the morning as due partly to the retarding effect of light, but in view of my own results this scarcely seems possible.

A result which would be easily explained on our theory is that before August 10 when the shoot was in its earlier stages the growth was greater in the day than in the night and Sachs observes that this is no doubt due to temperature. Later, at the time of greatest growth, the night growth is occasionally greater than the day. This is presumably due to lack of sufficient water supply during the day. It will be seen that it is just when the shoot is growing the fastest that the necessary water for so quick a rate of growth would be lacking. and therefore the water supply would be the limiting factor at any rate during the day. During the earlier stages of slower growth the point when water is lacking is presumably not reached, and it is likely that the temperature is limiting throughout, as in all my observations.

Sachs (15) also quotes the measurements made by A. Weiss on Agave Jacquiniana Schult (A. lurida Jacq.) at Lemberg. Weiss says that the growth rises and falls with temperature which would bring his results into line with mine, but Sachs states that the figures given do not support this general result. and that the results are really very similar to those of de Vries discussed above.

Sachs (15) gives as a typical example of his own results the case of Dahlia variabilis. In this case the stem showed a maximum growth in the morning usually between 7 A.M. and 8 A.M., and a minimum in the afternoon between 3 and 5 P.M.

The temperature curve which varies from 15° to 21·2° C. is usually in an opposite direction to the growth curve and thus temperature is not the effective factor in controlling the growth. Sachs himself attributes the afternoon minimum partly at any rate to the continued and stored up effect of the strong light and the morning maximum to the absence of light during the previous night.

It is however by no means clearly shown that the humidity of the atmosphere is not the controlling factor, for the growth in the hotter parts of the day is always slower, while there is an increase through the night when the humidity may be supposed to be increasing. No figures of the humidity are given for the night periods but it is to be noticed that of those given for the day, the highest humidity is usually found either late in the evening or early in the morning, thus pointing to the supposition that the humidity in the night was higher than in the day.

This being the case a full curve of humidity would probably show a fairly close relationship to the curve of growth and the possibility of humidity being the limiting factor throughout is by no means excluded. The Psychrometer figures* during the day do not fully account for the exact position of the maxima and minima of growth, yet the general explanation relating to humidity here suggested seems preferable to the supposition of Sachs that the retarding light effect of the day is stored up in such a way that its influence is not removed when night comes on, but persists until early the following morning.

The results of F. Darwin's measurements on the growth of the fruit of Cucurbita (5) show very clearly the relation between growth and the water supply, the latter depending largely on the amount transpired by the leaves. The very complete set of tables of results and curves of growth led me to search here for a similar case to my measurements of Dendrocalamus at Hakgala, that is to say, a case in which moisture being the limiting factor as a rule, the temperature became limiting whenever the moisture was in good supply. I looked therefore for continuous periods of high humidity to see if during these the growth curve resembled the curve of temperature and not the curve of humidity.

No decisive case was found, though in some periods such an explanation would do no violence to the figures given.

It was impossible to find a period of sufficient length during which one could be certain that the humidity was high enough to leave temperature as the limiting factor. The possibility of demonstrating that temperature was limiting at night in the case of Dendrocalamus at Hakgala depends, it must be remembered, upon the fact that for 12 continuous hours of darkness

---

* As Lock points out Sachs' Psychrometer figures are not very reliable.

the air was saturated or almost so with moisture, and also the secretion of drops of water from the growing culms was a certain sign of superfluity of water supply. Such conditions are quite exceptional. They are nowhere approached in Darwin's observations and probably will be seldom possible in any series of measurements.

Reinke (14) deals with the question of irregularities of growth and their dependence on internal or external conditions. He is able by more refined methods to attribute some of the "Stossweise Aenderungen" of Sachs to small changes in the external conditions, but finds others which are really spontaneous changes independent of external conditions. He has one case of great regularity however in which the moisture of the air is the limiting factor throughout. This is the case of the growth in thickness of the stem of Datura Stramonium. His conclusion presents one very interesting point for our theory, namely,that his plants became acclimatised to a smaller supply of moisture which at first caused a strong decrease in growth rate. This fact cannot be reconciled with the idea of limiting factors at all, for if the first effect, *i.e.*, decrease of growth is due to the water supply being insufficient for the faster growth, then we cannot expect any increase until the water supply is increased. It is possible however that changes of turgidity without any growth change would have considerable effect on the thickness of the stem and, as Lock (12) has pointed out, the researches of Kraus (9) have shown a periodic interchange of water between the wood and the cortex of certain stems which is accompanied by a change of size of the stem. The whole change may not therefore be due to growth alone.

It does not seem unlikely therefore taking all the results into consideration that the idea of limiting factors may supply a general basis of explanation for a considerable number of cases of growth, among which there hitherto appears to have been little agreement. It is desirable that numerous measurements should be taken of the growth of the different parts of plants with careful records of temperature and humidity of atmosphere, notes on light conditions, and, if possible, records of soil temperature (especially where this varies considerably). It is possible that with complete records available some general principles of the relation of growth to the environmental factors may be traced, where now results seem contradictory and even chaotic.

IV.—GENERAL APPLICATION OF THE THEORY OF LIMITING FACTORS TO CASES OF GROWTH FROM RESERVE.

THE FACTORS.

It seems justifiable from the results given in this paper to look for a general explanation on the lines of the theory of limiting factors at any rate in the case of rapid growth from large stores of reserve food. It may be useful to outline the general conditions in these cases. The food supply is already present in a quite highly organized condition and in such quantities that the supply is not likely to run short. The following is an analysis made by Shibata (20) of the reserve food supply in the rhizome of Phyllostachys mitis.

	Per cent. composition of the dried material.
Starch	24·01
Reducing sugar	0·95
Non-reducing sugar	4·31
Crude nitrogenous matter	5·41
Fat	0·61
Fibre	47·32
Ash	8·74
Undetermined (difference)	8·65
	100·00

Since the ash contains Phosphorus, Magnesium, Potassium, and small quantities of Calcium and Sulphur, it will be seen that the plant contains available within itself all the necessary materials for the building up of living protoplasm. This being the case no cessation of growth owing to lack of food supply will occur, and we may confine ourselves to the consideration of the physical factors necessary for the translocation and working up of these materials.

Temperature.

Of these temperature is of course very important. All the chemical changes which take place in the synthesis of protoplasm from the above substances are not at present known, but it is quite probable that as far as regards their relation to temperature they do not differ essentially from those simpler syntheses which take place during assimilation.

F. F. Blackman (2) has pointed out that the relation of the assimilation of certain leaves to temperature when light and CO_2 supply are in excess follows a definite rule. This is that an increase of temperature of 10° C. roughly doubles the amount of assimilation. He notes that certain numbers obtained for respiration and other widely different metabolic changes agree in following this numerical rule, and points out that this rule also applies to certain slow organic changes taking place *in vitro*, such as the saponification of esters and other processes which resemble the changes in the plant. He then suggests that this law is primarily applicable to changes in the cell as well as in the test-tube and goes on to show how this application may be made to the process of assimilation, of respiration, and with certain qualifications to that of growth also. It is quite probable therefore that if all the synthetic processes which are involved in growth were known, and that if they could be isolated and carried on *in vitro*, each one of them would follow the same rule. It follows that if all the food materials and the water are in good supply we should expect growth as a whole to exhibit this general relation to temperature and to increase with the temperature up to the death-point of protoplasm.

That growth shows on the other hand a true temperature optimum after which further increase of temperature causes slower growth is, he supposes, due to secondary causes which work in the opposite direction to this primary temperature-relation. For the causes suggested as well as for certain other qualifications in the application of this rule, the whole of the admirable discussion of the question in the original paper should be consulted. It appears to me that this idea gives a closer insight into the relation of growth to temperature than we have hitherto been able to get. We may I think provisionally look upon the process of growth as the product of many different chemical changes and syntheses each of which has the above-named primary relation to temperature and that this primary relation exhibits itself when other factors such as water supply are not limiting the growth. This at any rate gives a reason for such a case as the Agave inflorescence of this paper, where growth was limited by temperature throughout the whole range of conditions prevailing during the different experiments. It may be taken as the primary reason also for the general relation of growth to temperature which has been established by so many observers.

Temperature is no doubt also important in facilitating the translocation of materials. This we know involves certain organic chemical changes, starch for instance changing to sugar in translocation, and such changes will go on more rapidly at higher temperatures. Sachs (16) has shown that low temperatures prevent the translocation of starch. He says that on August 8, after a cool night, when the temperature at sunrise was 9° C., the leaves of Phaseolus, Ampelopsis, and Aristolochia were not completely cleared of starch. On the morning of August 3 (temperature at 5 A.M., 8° C.) the leaves of Dioscorea Batatas, Catalpa, and Morus were quite full of starch. In October (morning temperature 6° C.) there was no translocation in Nicotiana and very imperfect destarching in Datura and Atropa.

We see therefore why the temperature of the growing shoot itself and not, except indirectly, the temperature of the surrounding air should be the controlling factor in growth, for of course the internal temperature is the one at which all the organic chemical changes of the growing shoot take place.

Water supply.

It is no less obvious that the supply of water to the growing shoot is an important factor. When we consider how high a percentage of the weight of such a shoot is water we at once realise how necessary it is for water to be in good supply. This factor is by no means so simple as the last in its action. It often depends, as in the case of Dendrocalamus, on two or more other factors and varies in many cases with the organisation and habit of the plant as a whole.

In the case of such plants as Agave where the growing shoot is the only one on the plant the case of water supply is simple. The amount available for the growing shoot is evidently the amount taken up by the roots, minus the amount lost by evaporation or transpiration from the shoot and leaves. The leaves themselves no doubt supply water to the shoot since the reserve substances conveyed from them to it are in solution, but we may confine ourselves to the root supply, minus the loss by transpiration. The supply of water taken up by the roots depends evidently on the extent and vigour of the root system, and any defect in this respect may cause a limiting water supply. This was probably the case with De Vries' Agave which, he says, had no roots but absorbed water by a porous dead mass covering the living root stock. Given however a vigorous root system the absorption chiefly depends, as long as the water content of the soil is sufficiently high, on the soil temperature. We know that a cold soil containing plenty of water may yet be physiologically dry, the absorption of water being limited by the low temperature. It is this fact which makes it necessary in obtaining measurements to which our theory can be applied, to take the soil temperature whenever possible. The records for soil temperatures in Ceylon show that these are remarkably uniform. Where the air temperature varies so little as in June or July in Ceylon the soil temperature varies less still and the readings of soil temperature at a depth of one foot taken at 9.30 a.m. and 3.30 p.m. very rarely show a difference of more than 3° F at Peradeniya. None of the phenomena of growth observed in my work could with certainty be ascribed to so uniform a factor. Where however the soil temperature varies considerably it should certainly be taken when possible. The loss of water from leaves and stem depends on the humidity of the atmosphere and upon the intensity of the sun's radiation.

Other cases such as Dendrocalamus are by no means so simple as that of Agave, for since the supply of water to the growing organ depends on the amount required by the other organs of the plant, conditions become very important which do not directly affect the growing organ itself. Another instance of this is the case of Cucurbita fruit in which the supply of water to the fruit is conditioned by the amount required by the leaves for transpiration so that the growth of the fruit is affected by every change which alters the transpiration of the leaves.

Again the case of Vitis Lindeni shows us another possibility, for here we have a case of which one possible explanation is that the number of the growing organs decides whether the water supply shall be limiting or not. If with a given number of *absorbing* roots the supply of water is sufficient for a small number of *growing* roots, it may be insufficient for a larger number. This is on the assumption that the number and activity of the absorbing roots are not adjusted to the number of growing organs. It seems quite probable however, and investigations on this point are being carried on here, that the total water absorbing power of the roots of a given plant is adjusted to the demand made by the growing organs. If this is so the above explanation of V. Lindeni does not hold good, but whether it is so or not, we may still keep in mind the above explanation as one of the possibilities with which we have to deal in the application of our theory. The supply of water to the growing organ is thus a much more complex factor than the temperature.

Light.

The other factor which must always be kept in mind is the light intensity. There is a very general belief that light has a distinct retarding effect on the growth of stems and roots. This conclusion is based mainly upon the work of Sachs, Baranetzky, Godlewski, and Wiesner. Sachs (15), upon whose work, more than any other perhaps, the general conclusion rests, certainly, as we have seen, did not distinguish between the effects of darkness and increased humidity. The difficulty of distinguishing between the effects of changes of light and changes of humidity is very great in the open air and even in the laboratory experiments must be contrived with this object fully in view before reliable results can be obtained. It is therefore somewhat remarkable to find workers ascribing changes of growth to alterations in light intensity alone, when no records of changes of humidity were taken.

Thus Baranetzky (1) ascribes all his daily changes of growth to alterations of light and darkness, although he makes no records of alterations of atmospheric humidity. It is quite true that in the laboratory changes of humidity are not likely to be so great as outside, but in the absence of records we cannot tell how great or how small they may have been.

Godlewski (6) using the epicotyl of Phaseolus multiflorus compares his results with those of Sachs (15) on the daily periodicity of stem growth. Sachs finds, as we have seen in discussing the case of Dahlia variabilis, a maximum growth in the early morning and a minimum growth in late afternoon to be usual for a certain number of plants, and on this fact bases his explanation with regard to the stored up retarding effect of light. Godlewski, however, finds no regularity in the daily periodicity. He has some cases in which the maximum is in the afternoon and the minimum after midnight and others which show 2 maxima and 2 minima per day. If the daily periodicity therefore is not generally as Sachs described it, his explanation of the facts as due to light effect, even if true, must be of limited application. Godlewski himself actually performed experiments in which the light intensity changed, while he states distinctly the humidity was not altered. In these the retarding effect of light was marked. It is to be noticed however that he is himself unable to connect the daily periodicity with the alterations of light intensity, *e.g.*, he finds in June, 1888, a maximum growth in the afternoon and a minimum after midnight a state of things which is directly opposed to the supposition that light has a retarding effect. He also finds that the daily periodicity is very irregular at different times and in different individuals so that not much value can be attached to his conclusion that the daily periodicity depends on light conditions.

Wiesner (22) comes to the general conclusion that light retards stem growth and up to a certain limit favours leaf growth. He remarks however that there are cases of stem growth resembling leaf growth in this respect, and therefore the retarding effect of light is by no means generally established even granting the validity of those cases in which he supposes the retarding effect of light is shown.

It seems to me quite probable therefore that the retarding effect of light has been somewhat over-estimated. The most satisfactory experiments on this question have been done on seedlings, and it is doubtful whether a generalisation drawn from these, which grow as a rule in more or less shady situations, should be applied to parts of plants normally growing in full sunlight, such as the runner shoots of Capparis Roxburghii described in this paper.

Whatever our judgment may be upon the experiments which are supposed to have established the retarding effect of light on growth as a generalisation applicable to all growing organs, it is undoubtedly true that the light effect is comparatively small compared with those of temperature and moisture. The measurements of Shibata (20) on Phyllostachys, of Lock (12) and myself on Dendrocalamus and my own observations on various other plants have not yet shown a clear instance of unmistakable light effect, while effects of temperature and moisture have in different cases been very marked. There has in fact been nothing in our results which needed the introduction of any other factor besides water supply and temperature. The case of Agave inflorescence axis shows that very rapid growth may take place even while the growing organ is exposed to the full intensity of a tropical mid-day sun. It may be of course that even here the growth would be somewhat greater but for the retarding influence of light, but this, considering the rapidity of the growth, is improbable. It certainly seems that compared with the other environmental factors the effect of light is negligible in some cases and may be generally so. The mechanism of the retarding light effect is of course entirely unknown to us, but whatever it may be there seems to be some difficulty in regarding light as a " limiting factor " in growth. Suppose for instance a growing organ was subjected to constantly increasing water supply in a light of given intensity, the temperature being throughout high enough for much greater growth than is taking place. The growth being in this case limited by water supply would increase with that factor. If the light is of the nature of a limiting factor the growth will increase with the humidity up to a certain point when this increase will no longer be observed. At this point the intensity of the light may be supposed to limit the more rapid growth while it did not affect the slower growth. In other words there is not sufficient ' absence of light ' or ' darkness ' for the rapid growth while there had been sufficient ' darkness ' for the slower growth. Such a conception is highly artificial, and we must suppose that the retarding effect of light, however large or small it may be, acts equally on both slowly and quickly growing organs.

Atmospheric Pressure and Velocity of Wind.

Other factors which may influence growth are (1) Pressure of the Atmosphere and (2) Velocity of the Wind.

Jaccard (7) has shown that a diminution of pressure has the effect of greatly increasing the rate of growth. It is also well known that wind of high velocity checks the growth of trees. This is partly from the direct breaking effect of very high winds and also, as Schimper (18) has pointed out, from the increase of transpiration caused by the wind. Neither of these factors however is of much importance with regard to the present or similar investigations.

The variations of atmospheric pressure in the course of a series of growth measurements are not likely to be large enough to have any appreciable effect on growth. Under ordinary conditions also the wind will not be strong enough to affect the growth very much except in the way of increasing transpiration.

Summary of this Section.

To sum up, the three effective factors of the environment in cases of undoubted reserve food supply are Light, Temperature, and Water supply. Of these, the action of light is doubtful, in many cases absent or negligible, and when present cannot be conceived of as a limiting factor as that term is used by Blackman (2) and in this paper. The other two factors may either limit growth throughout or become in turn limiting factors according as their intensities vary.

It must be noted that the true temperature for the purposes of this theory is the temperature of the growing organ itself and not the temperature of the air. Temperature is therefore a complex factor in so far as it may depend not only on the temperature of the air, but also on the intensity of solar radiation incident upon the growing organ.

Water supply is a much more complex factor and depends upon (1) Absorption and (2) Transpiration both cuticular and stomatal. These factors in their turn depend (1) upon (*a*) Soil Temperature and (*b*) Water content of soil; (2) upon (*a*)

Humidity of Atmosphere and (*b*) Intensity of Light. This factor is also complex in that it varies with the general organisation and habit of the plant.

It must however be strongly insisted on, notwithstanding the complexity of these factors, that if careful records are taken of (1) Shade Temperature of Air, (2) Humidity of Air, (3) Intensity of Light, (4)Temperature of Soil, (5)Rainfall ; and if in addition the general organisation of the plant is carefully noted, there should as a rule in the case of plants with reserve food be no factor wanting for an elucidation of the problem of growth.

Rapidity of translocation of food supply might conceivably be a limiting factor even when all the others were in excess, but since rapidity of translocation depends to some extent upon temperature a temperature which limits this will limit growth generally and will come under the head of Temperature effect.

EXTENT OF APPLICATION OF THEORY.

If the above outline should furnish a basis for the explanation of all cases of growth from large supplies of reserve material it will clear up a very much wider field of facts than has been generally realized especially with regard to growth in the tropics.

Sharp Bursts of Growth in Tropical Trees.

The general fact of alternating periods of growth and rest in tropical trees has been often noticed. (See Schimper (19).) Botanists in the tropics have been struck with the fact that many species of trees put on new leaves, which are often conspicuous by their bright colours, in bursts and not continuously. The occurrence of large numbers of trees with new leaves of different bright colours may in fact alter the appearance of the whole forest and has not failed to attract attention. It does not however seem to have been so clearly noticed what this implies with regard to the growth of the shoots in general. Investigations are being carried out on this point now and will form the subject of a future paper. It may be stated here that in all these cases, growth in length of shoots takes place in restricted periods which may occur once, twice, or oftener annually, but always with periods of rest intervening. As far as can be seen the climate in Ceylon is favourable to growth almost all the year round and one would perhaps expect that the shoots of a tree would increase in length continuously, since there is only a very short period, the dry season of February and March, when we can see obvious cause for cessation of activity. Instead of this we find a very large number of species which choose a restricted period of 3 or 4 weeks in which to complete all their growth either for the year or for some shorter period, and during the remainder of the time are at rest as far as growth in length is concerned. During the period of rest assimilation is of course going on and the tree stores up reserve materials in its stem, branches, and twigs, and from this supply of reserve the rapid growth of the shorter periods takes place. The reserve is as a rule exhausted by this growth. This growth though rapid in comparison with that of temperate trees is not sufficiently rapid to make possible observations (at any rate unless instruments for magnifying the growth are devised) to show the relation between the growth and the environmental factors. It may however be justifiable to suppose that our general theory of limiting factors is applicable to these cases, and if this is so the theory will be adequate to explain a very large number of growth phenomena.

Cauliflory.

Another phenomenon which probably has some relation to our theory is that of Cauliflory, so common and so often noted in the tropics. It is well known that stores of reserve food are usually found in trees in the stems and larger branches. Fruits which grow from the main stem or from the larger branches may be expected to grow from these stores of reserve food. It is in fact not unlikely that the biological advantage of cauliflory lies in this very proximity to large stores of reserve. A tree which has its fruits very near to stores of reserve food will probably produce larger fruits than one where the fruits are at the ends of long branches. In the latter case it is quite conceivable that growth might be checked by difficulties of translocation of food to the growing fruit and thus even when temperature and water supply were favourable the growth might not be at all rapid. On the other hand a fruit which is in close proximity to reserve will presumably be able to take advantage of all periods when the environment is favourable to growth, since lack of food supply or difficulty of translocation will rarely or never occur.

It seems significant in this connection that of three species of Artocarpus in Ceylon, A. integrifolia, A. incisa, and A. nobilis, by far the largest fruits are produced by A. integrifolia, which is cauliflorous while the other two are not. This fact is of course no proof of the suggested biological advantage of cauliflory but is at any rate in harmony with it.

The following measurements of the fruit of Artocarpus integrifolia were taken morning and evening by passing a piece of thin copper wire round a fixed axis. The fruit is roughly ellipsoidal and the circumference was measured round both the longest and shortest axes. The results are given in cms. of growth per twelve hours.

TABLE IV.

Artocarpus integrifolia fruit at Peradeniya.

Longest circumference.			Shortest circumference	
Date.	Day.	Night.	Day.	Night.
	per 12 hours, cms.	per 12 hours, cms.	per 12 hours, cms.	per 12 hours, cms.
July 24 ..	+ ·35	+ ·75	+ ·21	+ ·59
.. 25 ..	— ·20	+ ·74	— ·10	+ ·66
.. 26 ..	+ ·23	+1·17	— ·30	+ ·96
.. 27 ..	+ ·00	+ ·85	+ ·00	+1·01
.. 28 ..	+ ·10	—	— ·10	—
.. 29 ..	—	—	—	—
.. 30 ..	+ ·05	+1·16	+ ·25	+ ·72
.. 31 ..	— ·15	+1·16	+ ·62?	+ ·62?
August 1 ..	+ ·05	+ ·72	+ ·20	+ ·72

The measurements were taken about 8 A.M. and 5 P.M. Thus the day's growth was wholly in the light while the night growth included about 3 hours of light as well as 12 of darkness. The case is clearly one in which water supply is the limiting factor. The days were on the whole bright and sunny and transpiration was energetic. The very much greater growth at night is no doubt due to the fact that with transpiration almost in abeyance the fruit had a good supply of water. On some days there is actually a contraction in size while the nights show always a considerable increase.

The case is in fact very like that of Cucurbita measured by F. Darwin (5) and no doubt if sufficiently refined methods of measurement had been employed the smaller fluctuations with changes of humidity would have been marked.

Whenever there is a period of good water supply the fruit increases rapidly in size and does not show any signs of a check to growth due to insufficient food supply.

Contrasting with this a series of measurements was taken of several fruits of Artocarpus incisa, the breadfruit. These are borne on young shoots at the ends of the branches. Although they may ultimately reach a size of about $\frac{1}{3}$ to $\frac{1}{2}$ that of a typical fruit of A. integrifolia they do not approach at any time to the rate of growth during the night recorded for the latter species. The fastest rate observed on any night was ·48 cms. per 12 hours, and the average was very much less than this being about ·2 cms. per 12 hours. So small was the increase in size that errors of measurement became very large and no very great reliance can be placed on the results in consequence. They did show however that though as a rule growth was slightly greater by night, it was very irregular, and on some quite favourable nights the growth was very small or ceased altogether. This may be due to difficulties of translocation or supply of food material since in other respects the conditions were highly favourable to growth on the nights in question and the fruits of A. integrifolia were as a matter of fact making rapid growth.

The growth of the fruit in the case of cauliflorous trees therefore may be justifiably included among those cases which are covered by our general theory.

V.—APPLICATION OF THEORY TO CASES OF GROWTH WITHOUT RESERVE STORES.

It is now necessary to turn to the question how far the theory can account for growth in cases where large quantities of reserve food are not stored by the plant. There are undoubtedly a large number of cases, both in the Tropics and in Temperate Regions, of plants which live from hand to mouth as it were, or in other words the food assimilated during the day by the leaves is almost immediately conducted to the growing organs and is there elaborated into new tissue. The growth of a large number of herbaceous plants and of many shrubby plants is of this kind.

Now it will be seen in dealing with these cases how much more complicated the application of our theory becomes. To the factors which may become limiting in cases of growth from reserve, several new ones are added. The growth from reserve was presumably never limited by lack of the organic food-materials themselves, nor, since the reserve food material contains the mineral elements necessary for growth, does it slacken for lack of mineral food. Now it is conceivable that in cases of growth in which there is no food-store, both these causes may at any time check the growth. It may be that organic food material is lacking on account of conditions unfavourable to assimilation, or it may be that with sufficient organic food, the mineral food is not in good supply either from the small amount of transpiration, or from absence of sufficient quantities of mineral solutions in the soil.

In fact for this kind of growth to be rapid a larger number of external conditions must be jointly favourable than in the case of growth from reserve. Besides the conditions previously mentioned, viz.:—

Temperature of the Growing Organ,
Water supply to the Growing Organ,
Light (of subordinate importance),

we must also have conditions favourable to—

Assimilation and Transpiration.

Now as Blackman and Matthaei (3) (13) have shown, assimilation is itself a process which depends on 3 factors : Temperature, Light, and CO_2 supply, each of which may become limiting and check the whole process. In the same way transpiration may be limited by darkness, by saturation of the atmosphere, by low temperature of the soil, or by absence of water from the soil.

The case of the growth of Tea I take to be an example of the failure of one of these conditions, a failure which would probably not take place if the plant grew from reserve material. It is a well known fact in Ceylon that during a period of very wet and dull weather when the atmosphere is saturated with moisture or almost so both day and night, the growth of the young shoots of tea falls off very markedly, *i.e.*, there are very few young growing shoots to be found. The average temperature does not fall as a rule in these periods, for though the days are cooler the nights are warmer than in drier periods, so that the cessation of growth is not due to temperature. It is also obviously not due to lack of water supply, for the humidity is high and the rainfall great. It is often supposed that it is due to the lack of organic food since the dull days check assimilation. This explanation can scarcely be accepted since Blackman and Matthaei (3) have shown that the supply of CO_2 in the air is always so small that it limits the assimilation to a much slower rate than the light energy is capable of performing. It does not seem probable that even on dull days the intensity of the light is so low as to check an assimilation which is always limited to a very slow rate by the small amount of CO^2 available in the air.

When we consider that throughout the whole of these periods transpiration is either very slow or altogether in abeyance since humidity is at or near saturation the whole time and rain is almost continuous, it becomes at once probable that lack of mineral food is the important factor in this cessation of growth. If no salts are obtained by the leaf for a considerable period, the formation of new living tissues must cease through want of the necessary mineral elements which are normally brought into the leaf in sufficient quantities by the transpiration current. If now these necessary minerals were stored by the plant as reserve, the growth need not be checked for want of them. We see therefore that in the case of a plant with no reserve food a factor (the supply of mineral food) may become limiting which would not be so in the case of growth from reserve. The number of factors which must all be simultaneously favourable to promote rapid growth in plants which do not form stores of reserves is large. They have been indicated above and include the various factors upon which assimilation and transpiration depend as well as those which promote the translocation and elaboration of food supplies.

If now any one of these numerous factors may become the limiting factor in the final product, growth, and may after limiting growth for a shorter or longer period in its turn give place to some other factor which becomes limiting, it will be seen that the final growth curve may be very irregular. Notwithstanding this irregularity the whole curve may be quite in harmony with the theory of limiting factors, and if all the factors were known every change of growth might be accounted for. Now it is just in cases of growth without reserve stores that seemingly inexplicable irregularities occur. In my cases of growth from reserve some general regularity was a rule to be detected, but I have made observations of many cases of 'hand to mouth' growth in which the results were so irregular that an explanation seemed hopeless. Kraus (10) in his measurements of Dendrocalamus giganteus at Buitenzorg gets very large irregularities of growth which he supposes to be the "Stossweise Aenderungen" of Sachs on a large scale. It is however as a rule in the case of herbaceous plants such as the Dahlia variabilis of Sachs (15) and the Gesnera tubiflora of Baranetzky (1) that such irregular results are obtained. Growth from reserve usually shows some regularity.

The results of Baranetzky (1) and Sachs (15) on the growth of certain herbaceous stems show a large number of occurrences of irregularity of growth. These Sachs called "Stossweise Aenderungen" and attributed them to something inherent in the plant itself and independent of external conditions. They do indeed in some cases seem so large and so irregular as to preclude dependence upon the fairly constant conditions of the laboratory in which the experiments were carried on. It may be however that even these could be accounted for by the supposition that several different factors out of the many on which growth depends became limiting in turn for shorter or longer periods. In the case of plants under open air conditions when all the external factors concerned are liable to considerable variations and irregularities, it is even more probable that the irregularities of the growth curves could be explained on these lines.

It seems therefore probable that our theory will be adequate to account for cases of growth where no reserves have been stored as well as for cases of undoubted growth from reserve. The fact that there may possibly be no sharp dividing line between the cases of growth from reserve and of growth without reserve does not at all invalidate the above reasoning.

VI.—BIOLOGICAL ADVANTAGE OF RESERVE FOOD STORES.

The biological advantage of the formation of large stores of reserve does not seem clear in the case of climates like Ceylon where growth conditions are favourable nearly all the year round. It is to be remembered however that there is some difference, even if small, between the different parts of the year as far as their suitability to growth is concerned.

A plant therefore with large stores of reserve is able, so to speak, to choose the most favourable time of the year for its growth and to store materials during the remainder. This resting period, though not so favourable for growth, is favourable for assimilation and storage, and so, on the whole, the plant may gain by this division of function.

In conclusion, I wish to express my thanks to Dr. J. C. Willis for constant help and suggestions throughout the course of the research and to Mr. F. F. Blackman, upon whose work the whole paper is based and whose paper on Optima and limiting factors first suggested this work to me. I am also greatly indebted to Mr. H. M. Leake, Government Botanist, Saharanpur, who was kind enough to take for me some measurements of Agave Sisalana, to Lieut.-Col. Prain and Mr. J. R. Drummond of Kew who forwarded valuable information on the species and distribution of Agave and Furcræa, and to Mr. Francis Darwin who kindly supplied me with information regarding transpiration and stomata. I have been aided throughout by the help of the staff of Peradeniya and am especially grateful to Mr. H. F. Macmillan, Curator of the Botanic Gardens at Peradeniya, and to Mr. J. K. Nock, Curator of the Hakgala Gardens, for their help in carrying out the observations at these two places. Mr. W. T. Southorn, Assistant Government Agent at Anuradhapura, kindly placed the resources of the (late) Botanic Gardens there at my disposal.

SUMMARY.

1. The object of the research was to test the theory of Limiting Factors by application to growth measurements in Ceylon.

2. In the case of the inflorescence axis of Agave and Furcræa the growth was controlled by the temperature throughout. Observations of the internal temperature of growing organs make it probable that the internal temperature is the true limiting factor.

3. In the case of the culms of Dendrocalamus the following explanation on the lines of the theory of Limiting Factors seems to fit all the facts :—

Two factors of the physical environment in turn limited the rate of growth of the culms, (1) the temperature of the culm, (2) the supply of water to the culm. The second factor being intimately connected with the amount of water drawn off by the transpiration of the adult culms on the same rhizome, depends in its turn on 2 factors, (1) the humidity of the atmosphere, (2) the intensity of the light.

4. The supposition that a growing organ is not capable of continuous growth, but must have intermittent periods of rest, though in harmony with some of my results, is inadequate to explain others.

5. A comparison of the cases of Agave and Dendrocalamus shows that the correspondence between the rate of growth and one or other of the factors of the environment depends largely on the organisation and habit of the plant.

6. The cases of the runner shoots of Capparis and Stifftia are explicable on the hypothesis that the supply of water is the limiting factor by day and the temperature by night. No decisive case of retarding light effect was obtained.

7. The growth of the hanging roots of Vitis Lindeni is limited in January by the temperature, in July by the water supply. This case is at present not to be fully explained by our theory.

8. Consideration of previous work shows some cases which can be explained by our theory, others in which the data are insufficient for its application.

9. A general application of the theory to cases of growth from reserve material shows that the effective factors of the environment are—

(1) Temperature.
(2) Water Supply.
(3) Light.
(4) Atmospheric Pressure.
(5) Velocity of Wind.

Of these, reasons are given for regarding the Light factor to be of somewhat minor importance. Atmospheric pressure and Velocity of Wind are also of small importance except in special cases.

The observations to be taken in measurements of growth from reserve are—

(1) Shade Temperature of Air.
(2) Humidity of Air.
(3) Intensity of Light.
(4) Temperature of Soil.
(5) Rainfall.
(6) General Organisation and Habit of the Plant.

10. The theory is possibly applicable to the common phenomenon in the tropics of sharp bursts of growth of the shoots of trees. This growth takes place from reserve stores.

11. The theory is applicable to the growth of the fruits of the Cauliflorous tree, Artocarpus integrifolia. A suggestion is made that the biological advantage of Cauliflory is that the proximity of the fruit to stores of reserve food allows of more rapid growth and the attainment of a greater size.

12. If further factors, namely, those on which Assimilation and Transpiration depend, are added, the theory may be applied to cases of growth in which there is no reserve store. There is a possibility of the explanation of cases of growth of great irregularity on this theory by supposing that several different factors in turn limit the growth for varying periods.

13. The Biological advantage of Reserve Food Stores may probably consist in the ability of the plant to grow in the most favourable time of the year and to carry on the processes of assimilation and storage in those periods which are not so favourable to growth.

LIST OF LITERATURE.

1. *Baranetzky, J.*—Die Tägliche Periodicität im Langenwachsthum der Stengel. Mem. Acad. Imp. des Sciences de St. Petersbourg. VII^{e} Serie. 1879.

2. *Blackman, F. F.*—Optima and Limiting Factors. Ann-Bot. Vol. XIX., No. LXXIV., April, 1905.

3. *Blackman, F. F.*, and *Matthaei, G. L.C.*—A Quantitative Study of Carbon-dioxide Assimilation and Leaf-temperature in Natural Illumination. Proc. Roy. Soc., Vol. B 76. 1905.

4. *Darwin, F.*—Observations on Stomata. Phil. Trans. Series B, Vol. 190 (1898), pp. 531–621.

5. *Darwin, F*—On the growth of the Fruit of Cucurbita. Ann. Bot., Vol. VII. 1893.

6. *Godlewski, E.*—Studien über das Wachsthum der Pflanzen. Abh. d. Krakauer Akad. d. Wiss., Math-naturw. Cl., XXIII., p. 1–157.

7. *Jaccard, P.*—De l' influence des variations de la pression des gaz sur le développement des végétaux. Rév. gén. de bot. Tome V. 1893.

8. *Kellicott, W. E.*—The daily periodicity of cell-division and of elongation in the root of Allium. Bull. Torrey Bot. Club. Vol. XXXI. Oct. 1904.

9. *Kraus, G.*—Ueber die Wasservertheilung in der Pflanze. Festschrift der Naturforschenden Gesellschaft zu Halle. 1879.

10. *Kraus, G.*—Ann. Jard. Buitenzorg XII. 1895.

11. *Leitgeb, H.*—Beiträge zur Physiologie der Spaltöffnungsapparate. Mittheilungen aus dem Botanischen Institute zu Graz. 1886.

12. *Lock, R. H.*—On the Growth of Giant Bamboos. Ann. Peradeniya, Vol. II., Pt. II., Aug., 1904.

13. *Matthœi, G. L. C.*—Experimental Researches on Vegetable Assimilation. Phil. Trans. Series B, Vol. 197, pp. 47–105.

14. *Reinke, J.*—Untersuchungen über Wachsthum. Botanische Zeitung, 1876.

15. *Sachs*—Über den Einfluss der Lufttemperatur und des Tageslichtes auf die stündlichen und täglichen Aenderungen des Langenwachsthums der Internodien. Arb. d. Bot. Inst. in Würzburg., II., p. 101. 1872.

16. *Sachs*—Ein Beitrag zur Kenntniss der Ernährungsthätigkeit der Blätter. Arb. d. Bot. Inst. in Würzburg, vol. 3, Part I. 1884, p. 1.

17. *Schellenberger, H. C.*—Beiträge zur Kenntniss von Bau und Funktion der Spaltöffnungen. Bot. Zeitung, vol. 1., 1896, p. 169.

18. *Schimper*—Plant Geography, Eng. Transl., Pt. 1., Chap. IV., Sect. 3, p. 74.

19. *Schimper*—Plant Geography, Eng. Transl., Pt. III., Sect. I., Chap. II., p. 246.

20. *Shibata, K.*—Beiträge zur Wachsthumgeschichte der Bambusgewachse. Journ. Coll. Sci., Tokyo, Vol. XIII., Pt. III., 1900.

21. *Stahl, E.*—Ueber den Pflanzenschlaf und verwandte Erscheinungen. Bot. Zeitung, 1897, Pts. 5 and 6, p. 71.

22. *Wiesner, J.*—Photometrische Untersuchungen auf Pflanzen-physiologischem Gebiete. I. Abh. Orientirende Versuche über den Einfluss der sogenannten chemischen Lichtintensität auf den Gestaltungsprocess der Pflanzenorgane. S. Ak. Wien CII, I, 1893. Cf. Bot. Centralblatt 55, 1893, pp. 18–19.

EXPLANATION OF PLATES.

Plate 22—Growth in millimetres per two hours of Agave Morrissii at Hakgala from March 9th at 6 a.m. to March 10th at 6 p.m.

Growth in mm. per 2 hours of Furcræa gigantea at Kandy from June 11 at 8 a.m. to June 12th at 6 p.m.

Growth in mm. per 2 hours of Agave americana at Hakgala from June 1st at 8 a.m. to June 2nd at 6.30 p.m.

Temperature curves for each in F°.

Plate 23—(below) Growth in mm. per 2 hours of Dendrocalamus giganteus at Hakgala from March 31st at 7 a.m. to April 2nd 6 a.m. with curves for Humidity and Temperature in C°.

(Above) Growth in mm. per 2 hours of another culm of Dendrocalamus giganteus at Hakgala from July 10th at 7 a.m. to July 12th at 6 a.m. with curves of Humidity and Temperature in C°.

Plate 24.—(Above on right) growth in mm. per 2 hours of Dendrocalamus at Peradeniya (total of 5 culms) July 6th 10 a.m. to July 7th 11 a.m. with Humidity and Temperature.

(Above on left) growth in mm. per 2 hours of D. giganteus at Anuradhapura (total of 6 culms) June 19th 10 a.m. to June 20th 8 a.m. with Humidity and Temperature.

(Below on left) difference between the first 4 and the next 8 hours of the night at Hakgala in Temperature in F° and in growth of Dendrocalamus in mm. per 2 hours.

(Middle on right) Capparis Roxburghii (total of three culms) in mm. per 2 hours from July 6 at 11 a.m. to July 7 at 9 a.m. Humidity and Temperature are above with growth of Dendrocalamus on same date.

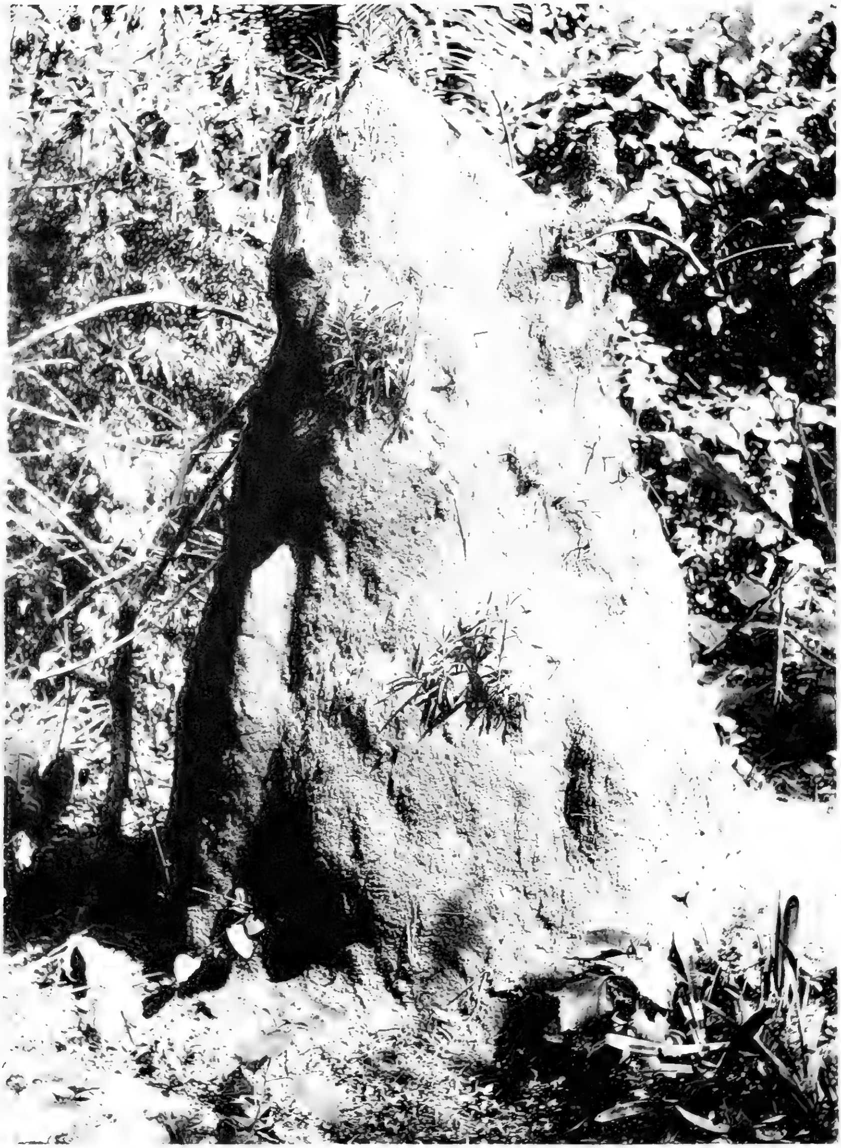
(Below on right) growth in cms. per 12 hours during the night of Dendrocalamus at Hakgala from April 2nd–3rd to April 14th–15th with minimum temperatures for the same period in F°

Plate 25.—(Above) growth of Capparis Roxburghii in mm. per 2 hours (2 shoots added) from January 9th at 9 a.m. to January 11th at 7 a.m. with curve of Humidity. Temperature is below with Vitis of same date.

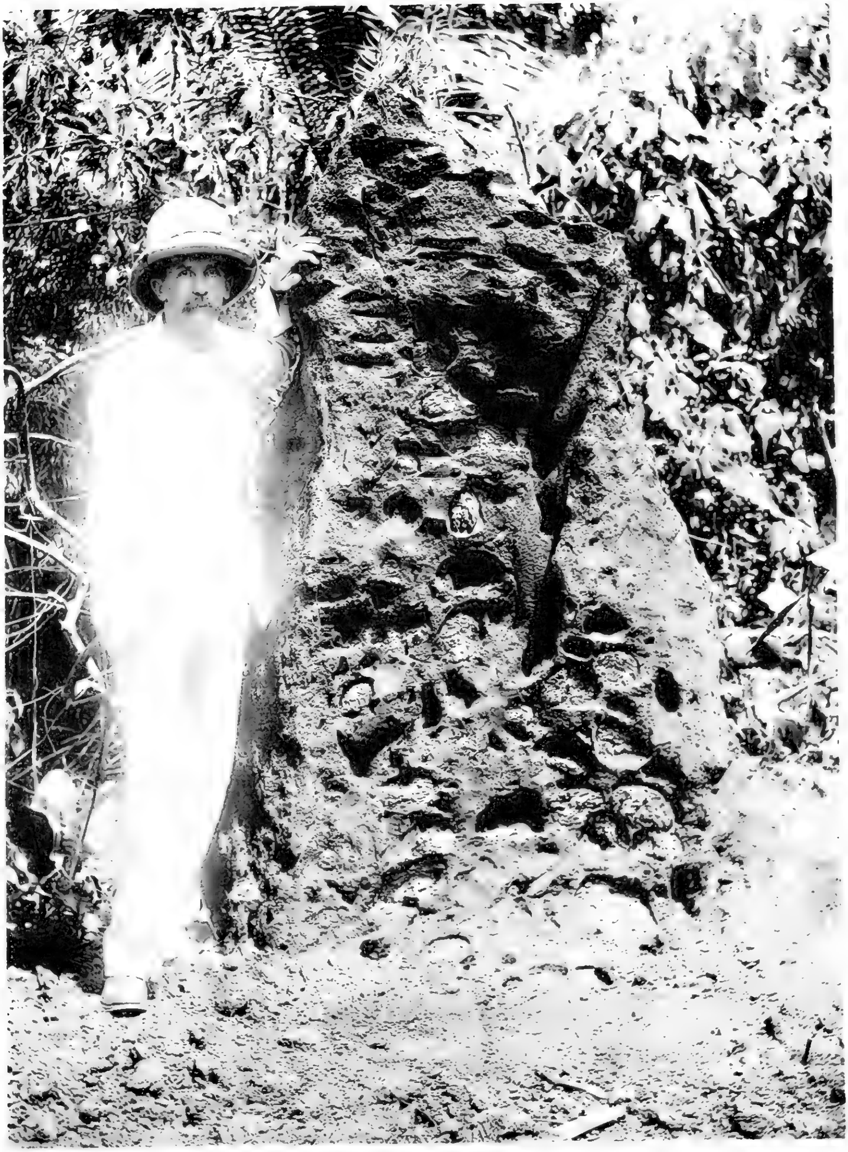
(Middle) growth of hanging roots of Vitis Lindeni in mm. per 2 hours (3 added) from July 6 10 a.m. to July 7 at 5 p.m. with curve of Humidity.

(Below) Vitis Lindeni 2 curves of growth of single roots in mm. per 2 hours from January 9th 6 a.m. to January 11th 7 a.m. with temperature in C°.

H. C. COTTLE, GOVERNMENT PRINTER, COLOMBO, CEYLON.



NEST OF TERMES REDEMANNI



NEST OF TERMES REDEMANNI

Pl. VII

COMBS OF TERMES REDEMANNI X 1/3

COMBS OF TERMES OBSCURICEPS X 1/2

AGARICS ON COMB OF TERMES REDEMANNI × 1/4

AGARICS ON COMB OF TERMES REDEMANNI × 1/2

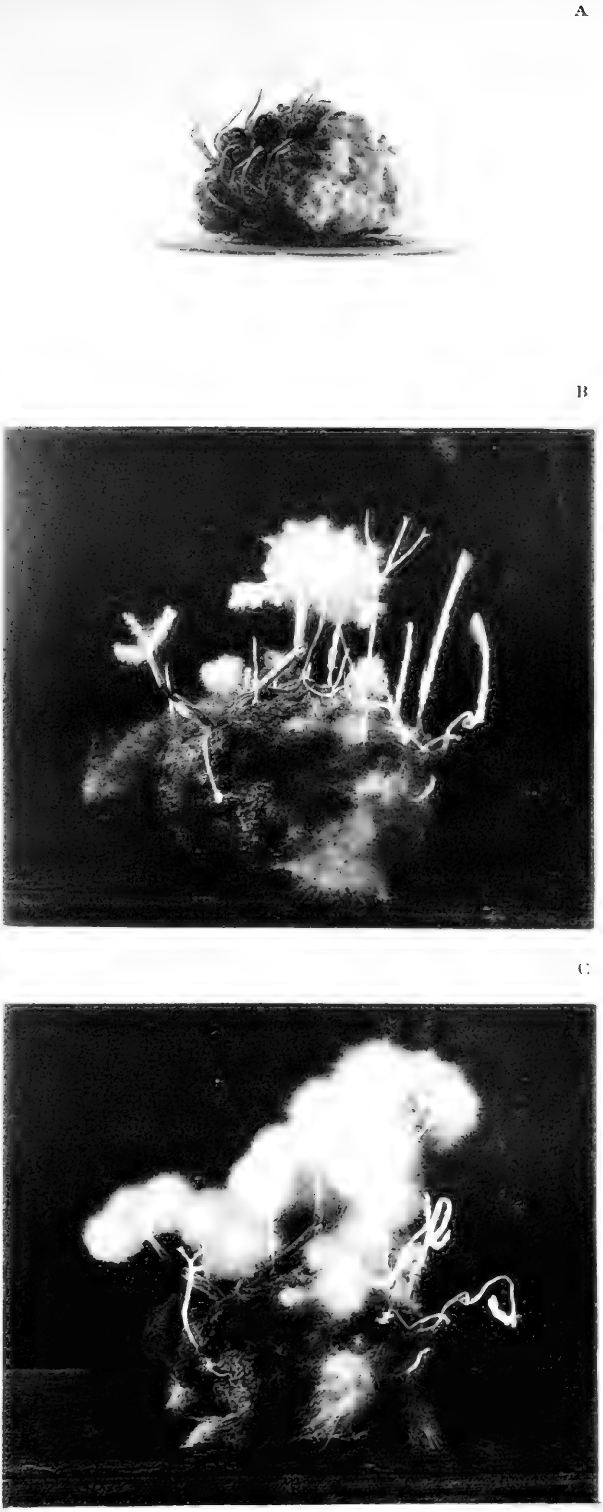
FUNGI OF TERMITE NESTS

THE AGARIC (PLUTEUS FORM) X 1/2

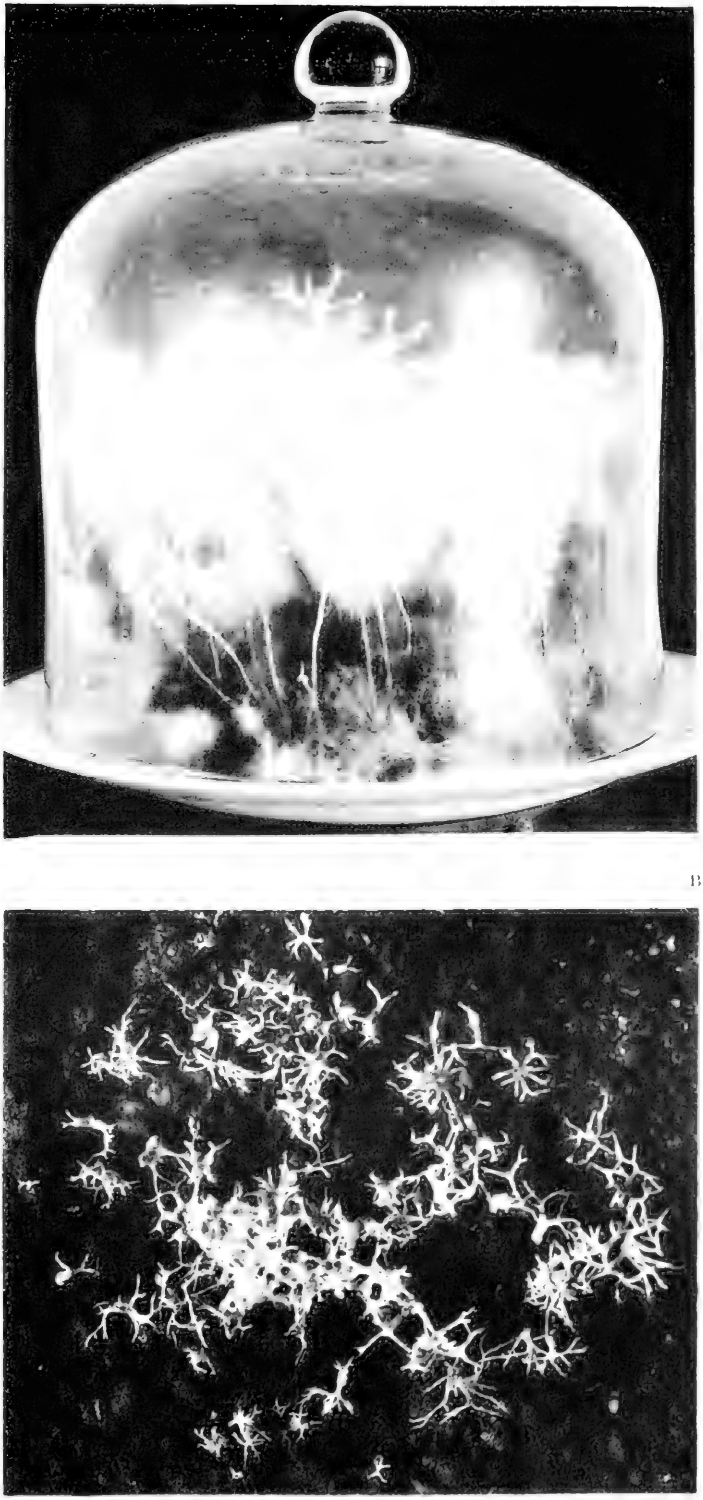
A

B

FUNGI OF TERMITE NESTS

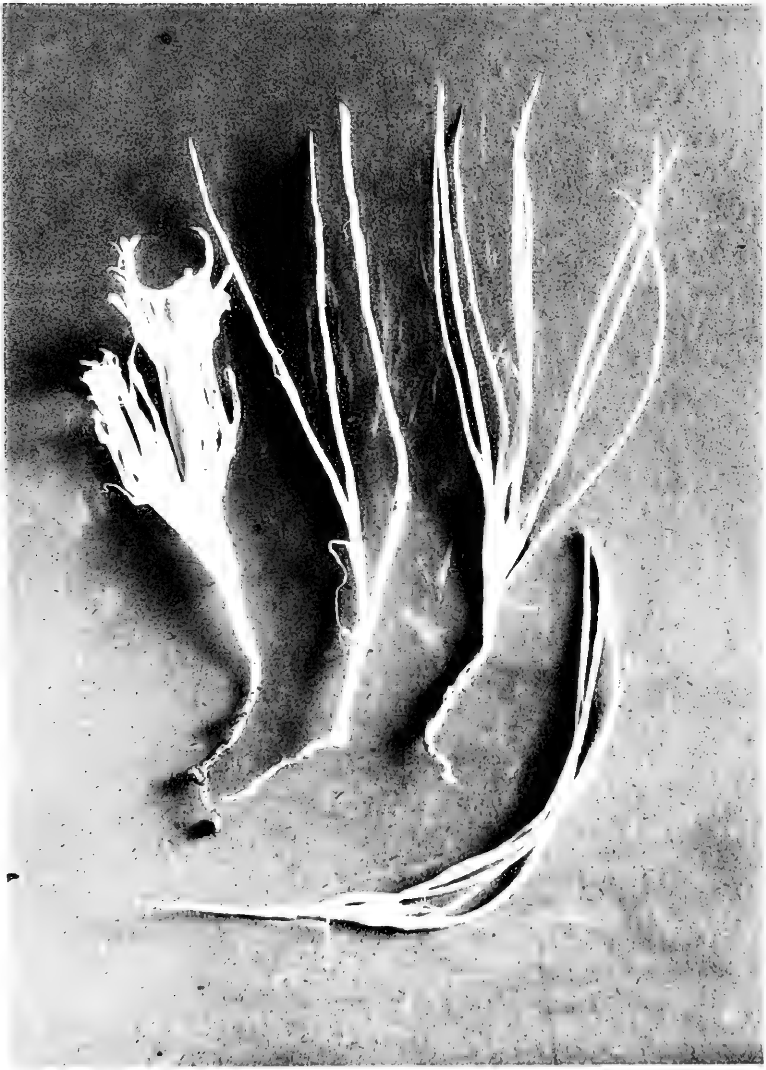


FUNGI OF TERMITE NESTS



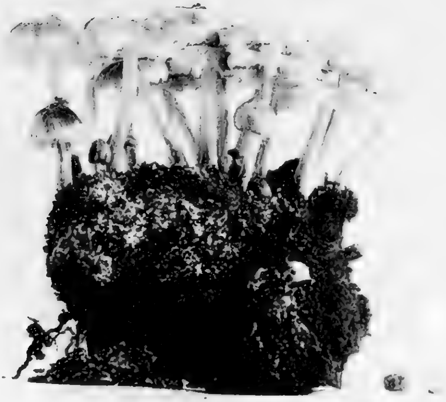
FUNGI OF TERMITE NESTS

FUNGI OF TERMITE NESTS



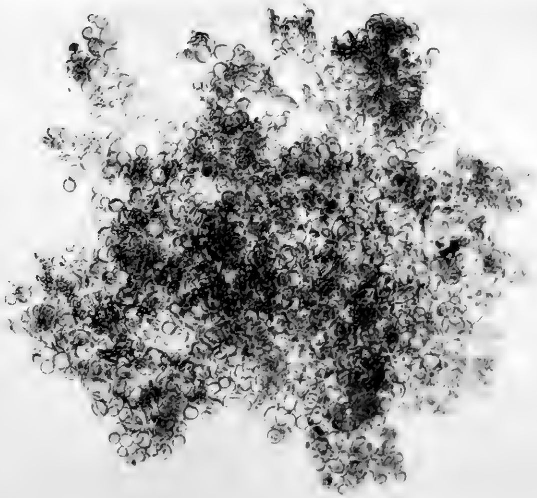
FUNGI OF TERMITE NESTS

A



ENTOLOMA MICROCARPUM B. & BR.

B

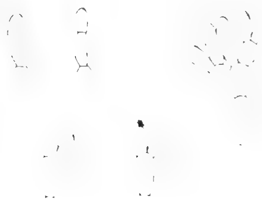


PART OF A TERMITE "SPHERE"

[illegible] [illegible]

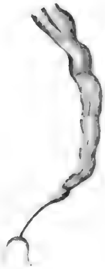
FUNGI OF TERMITE NESTS

9.



10.

14.



11.

12.

13.

16.

15.

17.

FUNGI OF TERMITE NESTS

18.

19.

22.

23.

21.

20.

24.

26.

25.

27.

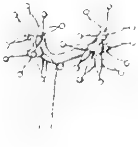
28.

29.

31.

32.

30.



FUNGI OF TERMITE NESTS

33.

34.

35.

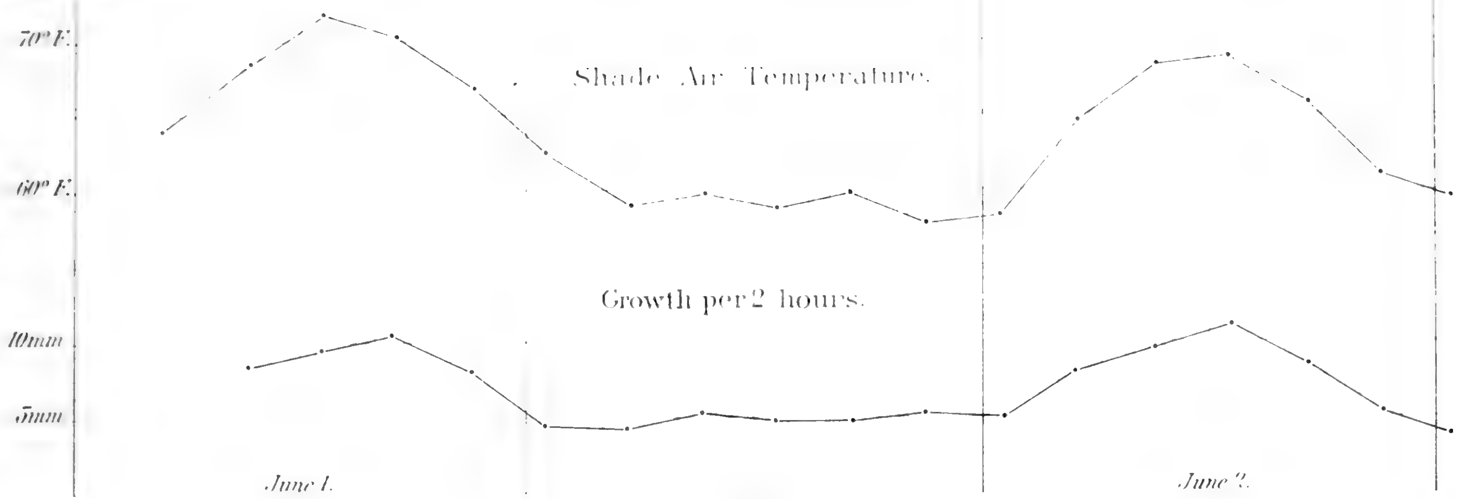
36.

37.

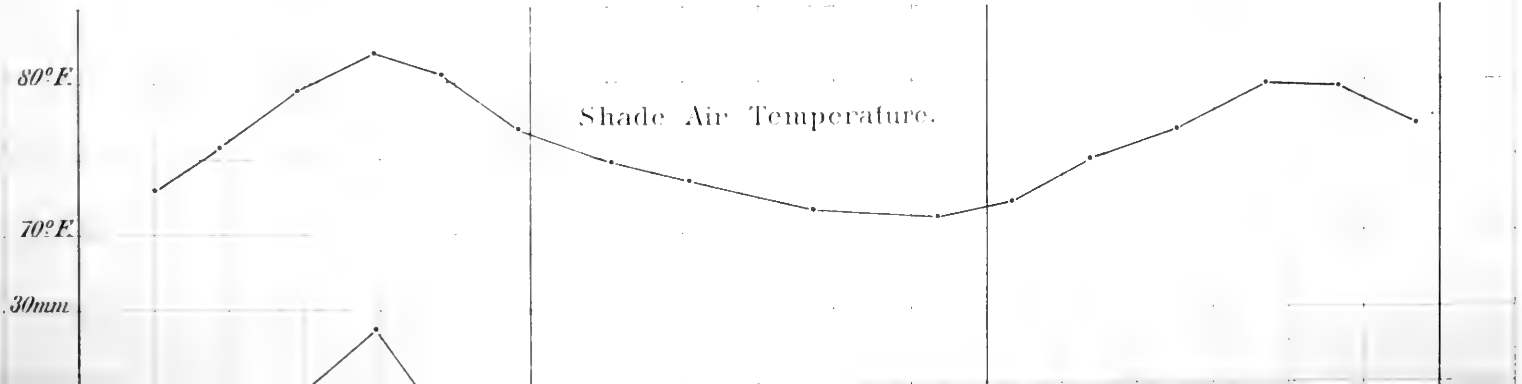
38.

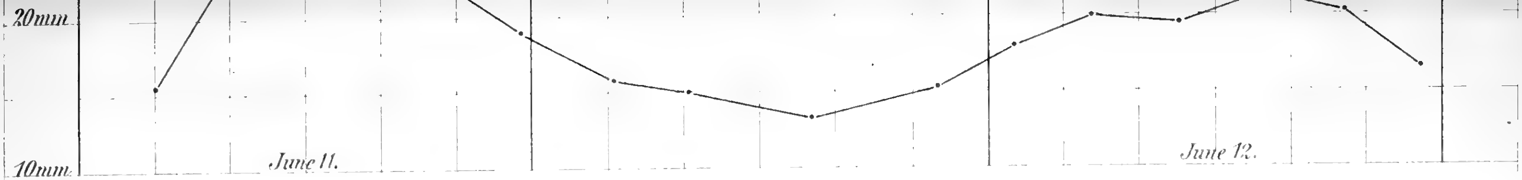
T. Petch and A. de Alwis del. [illegible]

ENTOLOMA MICROCARPUM ETC.

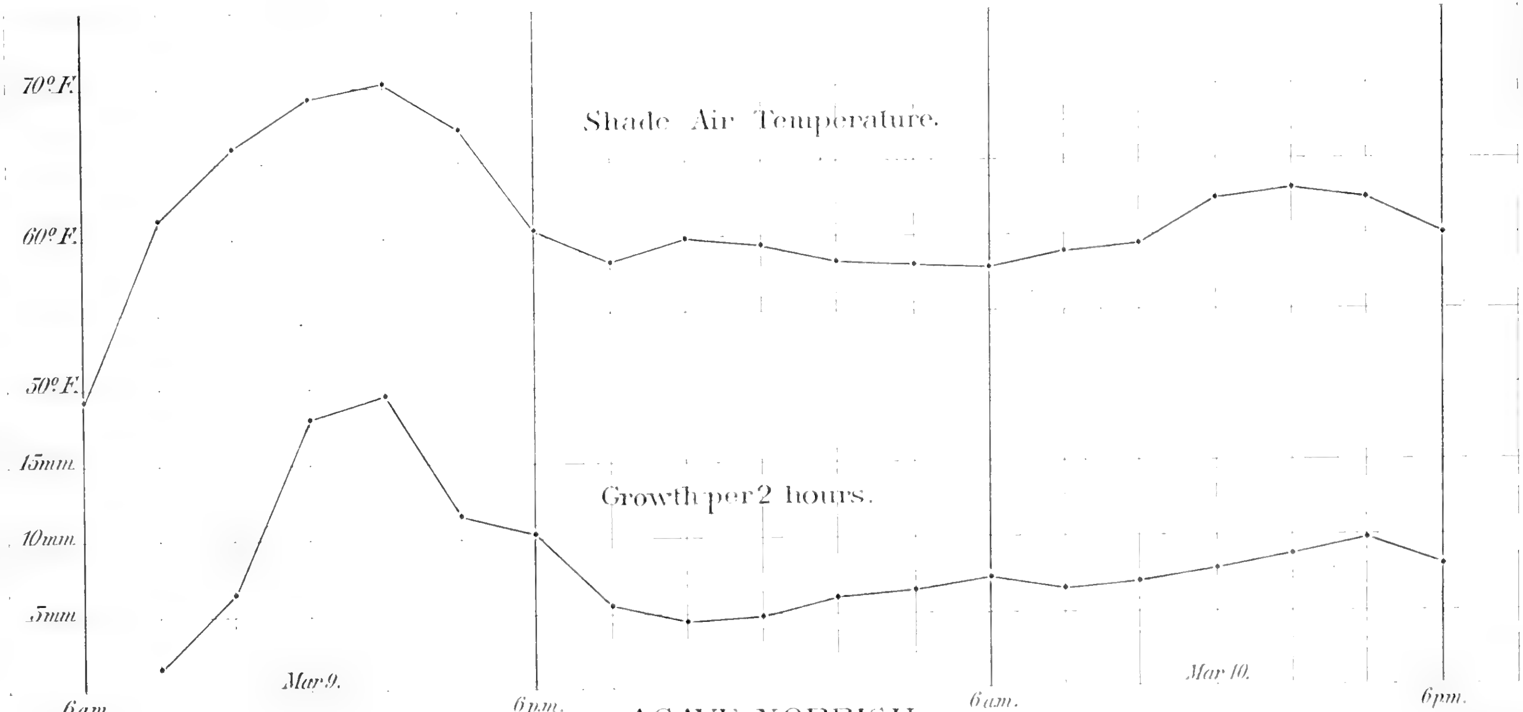


AGAVE AMERICANA.





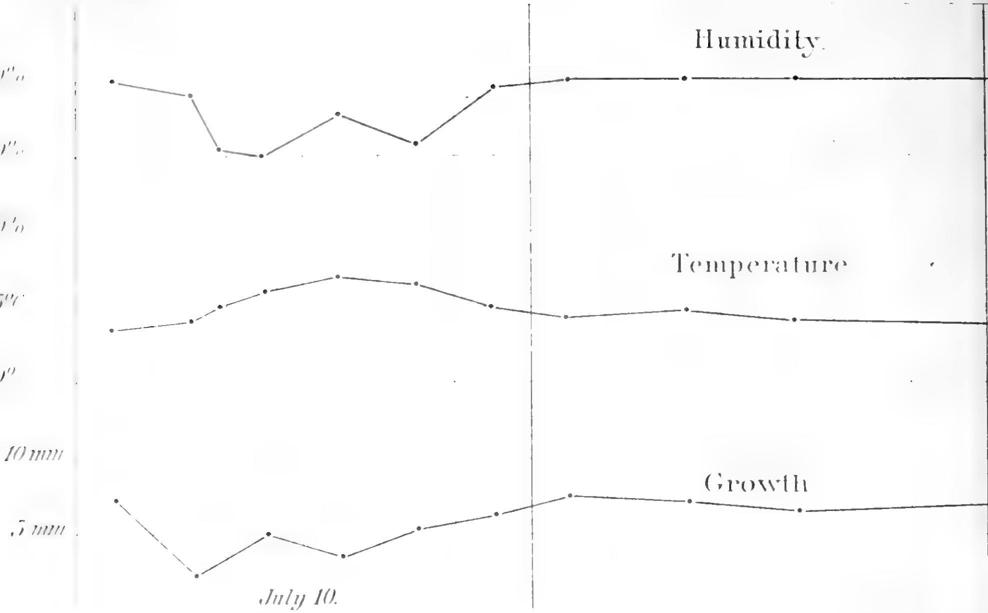
FURCRAEA GIGANTEA.



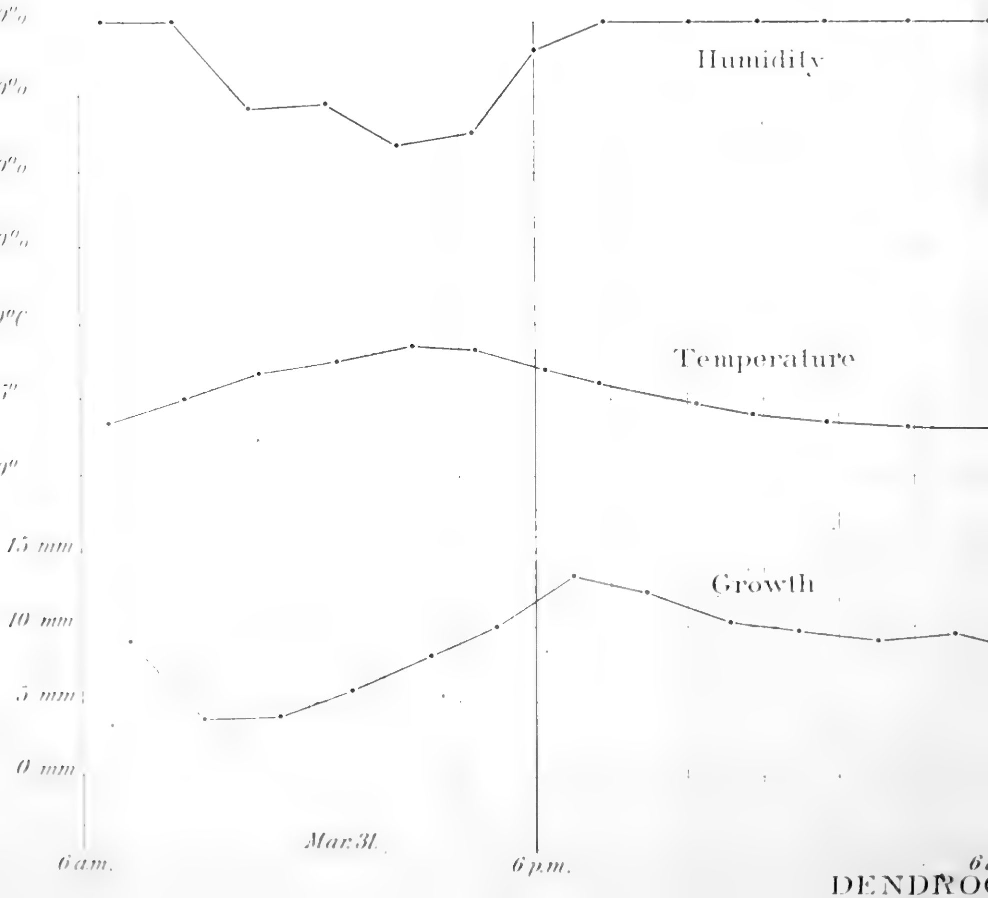
AGAVE NORRISII.

A.M.S. del.

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

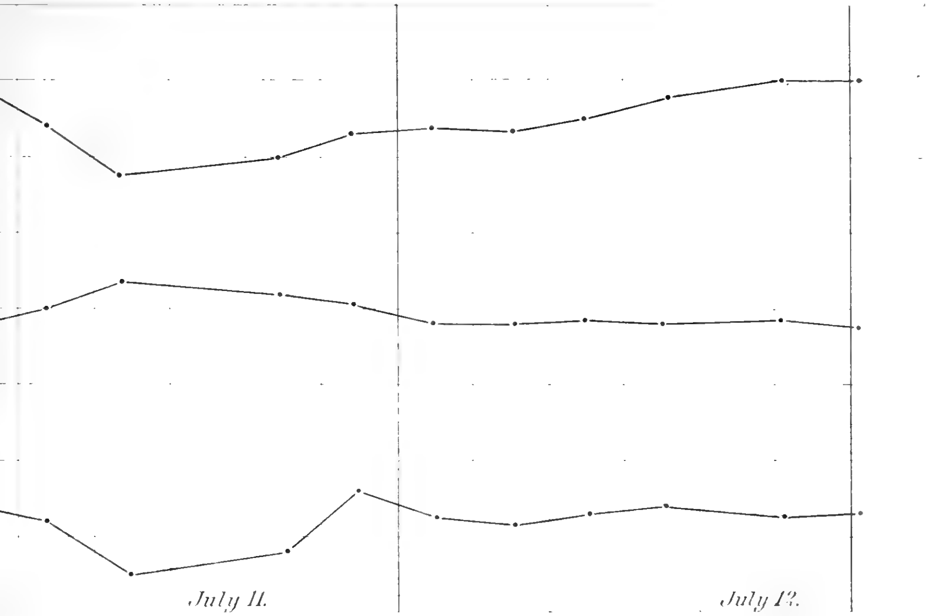


DENDROC

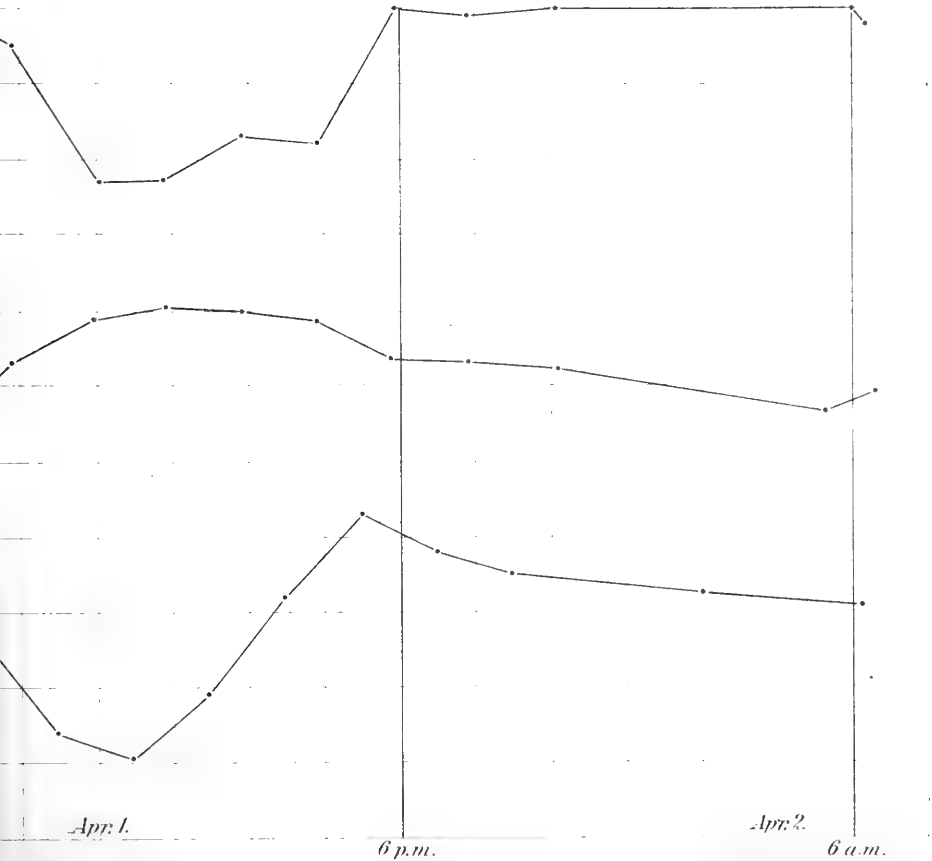


DENDROC

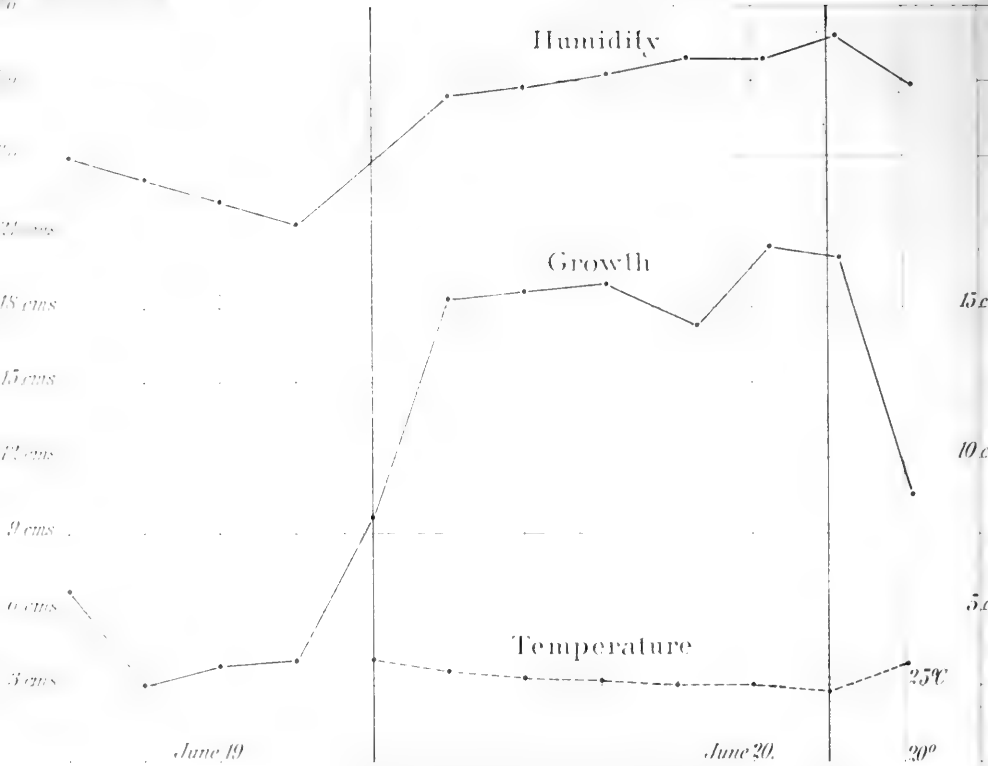
Pl. XXIII.



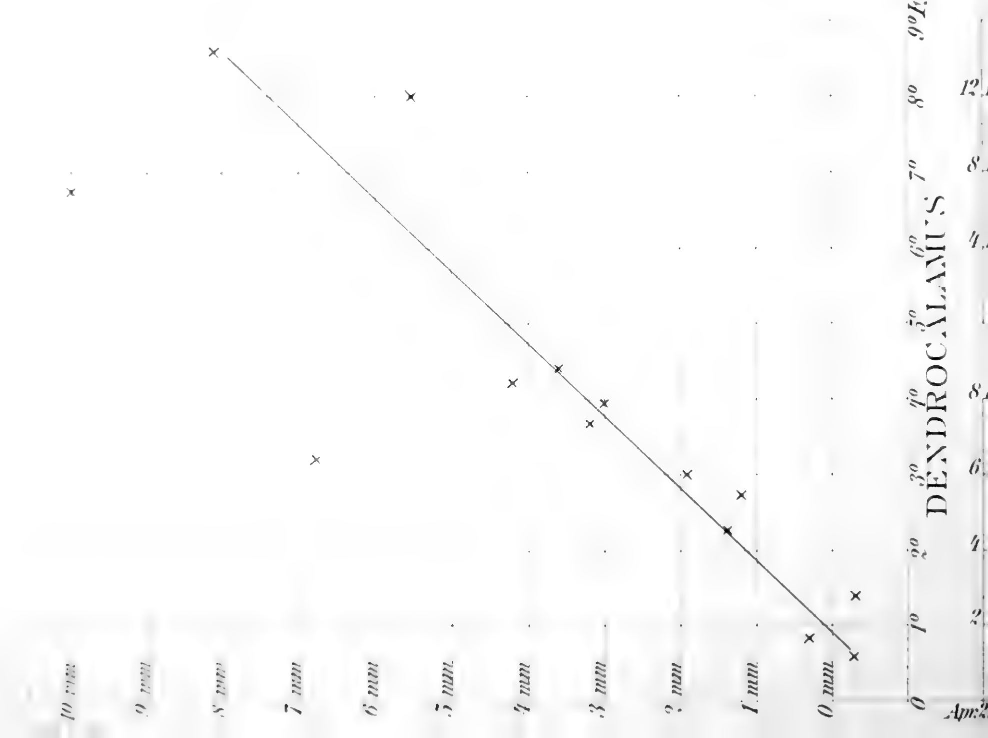
AMUS



LAMUS

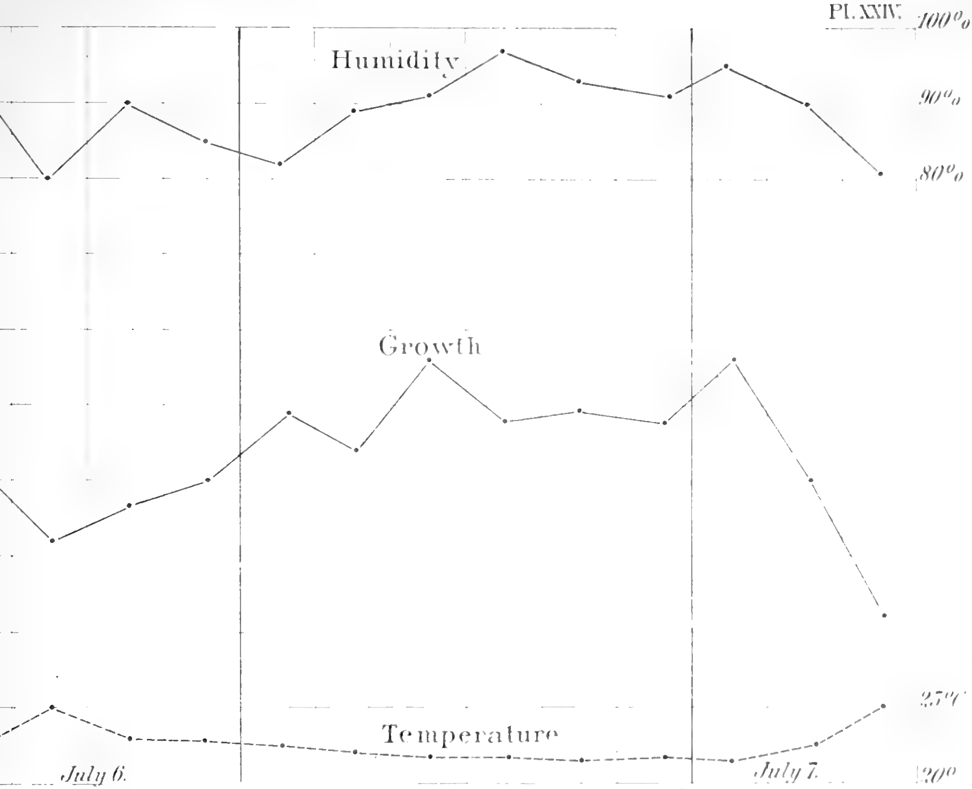


DENDROCALAMUS

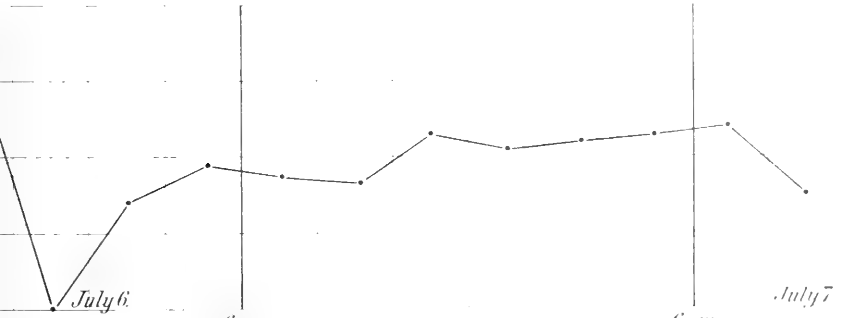


DENDROCALAMUS

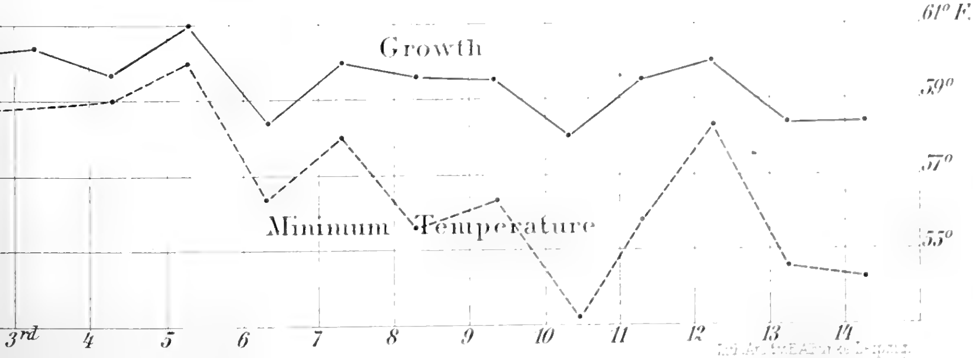
PL. XXIV.



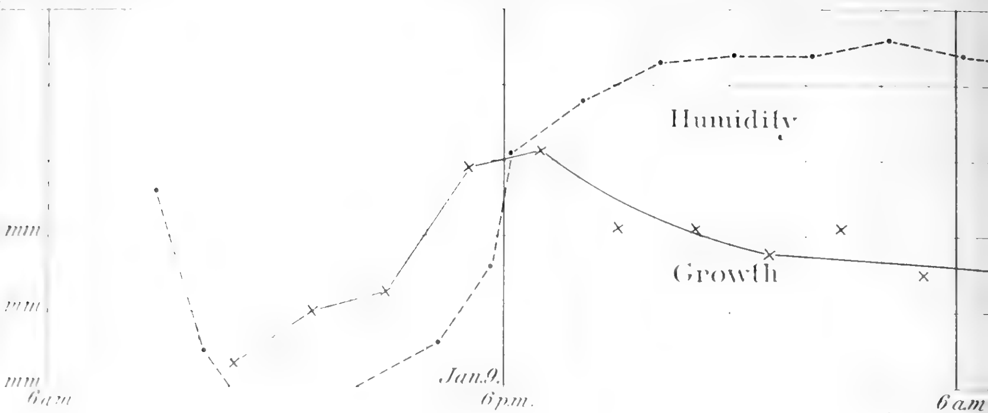
DENDROCALAMUS



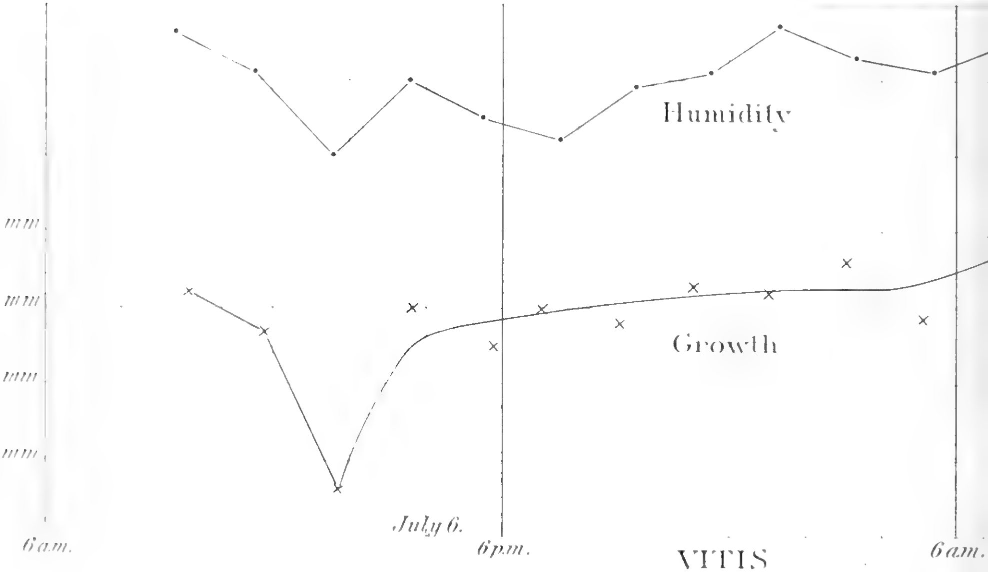
CAPPARIS



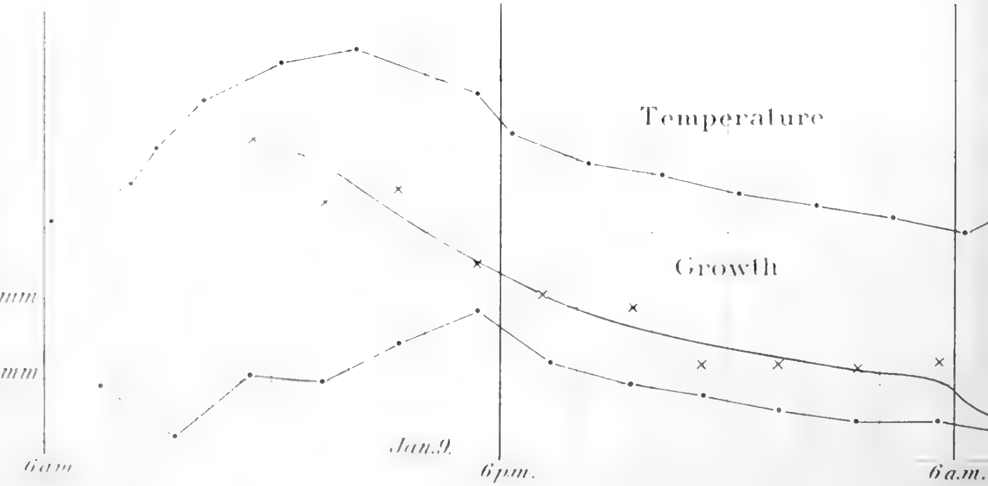
[illegible]



CAPPA

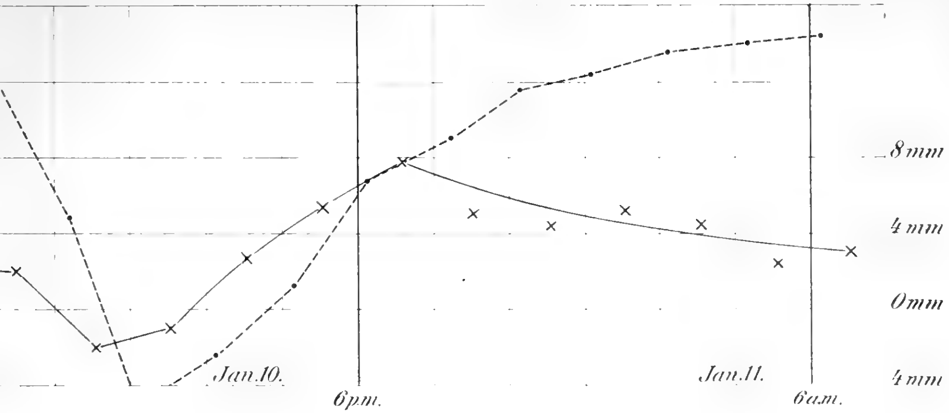


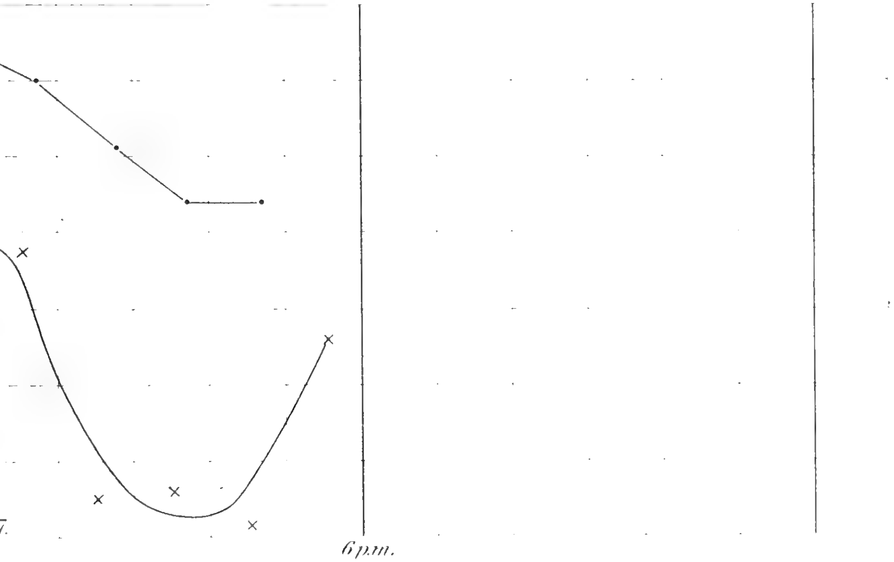
VITIS

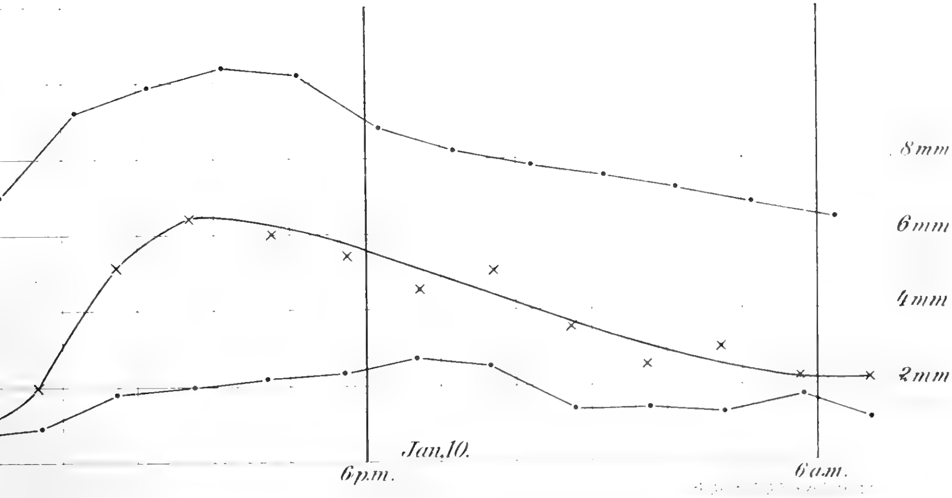


VITI

Pl. XXV.


8 mm
4 mm
0 mm
4 mm
Jan.10.
Jan.11.
6 p.m.
6 a.m.


6 p.m.


8 mm
6 mm
4 mm
2 mm
Jan.10.
6 p.m.
6 a.m.

NOTICE.

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

Willis : a Revision of the Podostemaceæ of India and Ceylon, 70 pages	Re. 1·50 or 2*s*. 0*d*.
Willis : Studies in the Morphology and Ecology of the Podostemaceæ of Ceylon and India, 200 pages with 33 plates	Rs. 7·50 or 10*s*. 0*d*.
Wright : The Genus Diospyros in Ceylon : its Morphology, Anatomy, and Taxonomy, 185 pages with 20 plates	Rs. 6 or 8*s*. 0*d*.
Lock : On the Growth of Giant Bamboos, with special reference to the relations between conditions of Moisture and the Rate of Growth, 56 pages with 3 plates ...	Re. 1·50 or 2*s*. 0*d*.

CEYLON PUBLICATIONS.

FOR SALE AT THE GOVERNMENT RECORD OFFICE, COLOMBO.

Oriental Literature.

	Rs.	c.
The Mahawansa :—		
Original Pali Text, Part I. ...	7	50
Do. Part II. ...	7	50
Sinhalese Translation, Part I. ...	5	0
Do. Part II. ...	5	0
Wijesinha's English Translation of Part II., with Turnour's Translation of Part I. ...	7	50
The Mahawansa Tika, with original Pali, bound in stiff covers	7	50
Do. do. unbound ...	6	50
Saddharmalankaraya (Sinhalese) ...	2	0
Extracts from the Pujawaliya (English) ...	1	0
Do. do. (Sinhalese) ...	0	75
Nitinighanduwa, English	1	0
Do. Sinhalese... ...	1	0
Moggallana Panchika Pradipa (Pali) ...	1	0
Abhidhanappadipika, a Dictionary of the Pali Language	3	0
The Tesawalamai	0	50
Lapidarium Zeylanicum	31	50
Dravidian Comparative Grammar ...	13	0
Glossary of Native Words occurring in Official Documents (third edition) ...	0	30
Catalogue of Pali, Sinhalese, and Sanskrit Manuscripts in Temple Libraries ...	0	50
Alwis's Descriptive Catalogue of Sanskrit, Pali, and Sinhalese Works ...	5	0
Mugdhabodha Wyakarana (Sanskrit) ...	5	0
Mukhamatta Dipani (Pali) ...	5	0
Kawsilumina (Sinhalese)	1	50
Pybus's Mission to Kandy	0	50
Papers on the Custom of Polyandry as practised in Ceylon	0	15
The Rajavaliya; or, a Historical Narrative of Sinhalese Kings (in English and in Sinhalese) ... ... each	0	75

Archæology.

	Rs.	c.
Dr. Müller's Report on Inscriptions of Ceylon :—		
Text	5	0
Plates	5	0
Architectural Remains of Anuradhapura (with plates), by J. G. Smither, F.R.I.B.A. :—		
In boards	40	0
In cloth	60	0
Return of Architectural and Archæological Remains and other Antiquities in Ceylon...	1	20
Reports on the Archæological Survey of Ceylon :—		
Kegalla District	6	0
Anuradhapura (I.)	0	50
Do. (II.)	1	0
Do. (III.)	1	65
Do. (IV.)	1	0
Do. (V.)	2	20
Do. (VI.)	2	0
Do. (VII.)	4	0

Natural History.

	Rs.	c.
Report on Brown Scale (or Bug) on Coffee...	1	0
The Green-Scale Bug in connection with the Cultivation of Coffee.—Observations by Mr. E. Ernest Green (illustrated) ...	1	0
The Flora of Ceylon, by Dr. Trimen :—		
Parts III., IV., and V. (with plates) each	20	0
Lepidoptera of Ceylon, in 13 Parts, with coloured plates ... each Part	14	50
The Kitul Palm and its Uses, by T. B. Pohath-Kehelpannala	0	15
Report on the Ceylon Pearl Fisheries ...	1	35

District Manuals.

	Rs.	c.
Mannar, by W. J. S. Boake	1	0
Uva, by H. White	2	50
Nuwara Eliya, by C. J. R. Le Mesurier ...	5	0
Vanni Districts, by J. P. Lewis ...	5	0
North-Central Province, by R. W. Ievers ...	2	50

	Rs.	c.
Ceylon Civil List	1	0
Ceylon Blue Book	10	0
Administration Reports (annual volumes)	10	0
Sessional Papers (annual volumes)	10	0

TO BE OBTAINED OF H. W. CAVE & Co., COLOMBO.

	Rs.	c.
The Ruined Cities of Ceylon. Demy 8vo. Illustrated with collotypes	9	0
Golden Tips: A description of Ceylon and its great Tea Industry. 214 illustrations from photographs by the Author. Demy 8vo. ...	10	0
Kandy and Peradeniya: an illustrated description, with 33 full-page photogravures. Demy 4to., Roxburgh binding ...	18	0
Nuwara Eliya and Adam's Peak: an illustrated description of the Highlands of Ceylon, with 34 full-page photogravures. Demy 4to., Roxburgh binding	18	0

PUBLISHED AT THE "CEYLON OBSERVER" OFFICE.

	Rs.	c.
Ceylon in 1903, by J. Ferguson (illustrated)	5	0
Hevea Brasiliensis, or Para Rubber, by H. Wright (illustrated) ...	5	0
Skeen's Guide to Colombo (with maps and illustrations) ...	1	50
Do. to Kandy (do.) ...	1	0
Burrows' Guide to Kandy and Nuwara Eliya	1	50
Do. to the Buried Cities	2	0

New York Botanical Garden Library
3 5185 00257 7953