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ANNALS OF BOTANY

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ASSISTED BY OTHER BOTANISTS

VOLUME XVI
With a Portrait, twenty-six Plates and thirty-one Figures in the Text

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ERRATA.

P. 383. The sentence beginning on line seven from bottom *should read:* 'Sometimes the protoxylem directly abuts upon the endodermis, but it may also be separated from it by a layer of parenchymatous (pericyclic) cells,' &c.

P. 391. The clause beginning on line six from bottom *should read:* 'nevertheless it may exhibit a variation which recalls that already described for the primary and first-formed lateral roots, namely, that the protoxylem of many or even all of the rays may abut immediately upon the endodermis (which is sharply marked from the first) whilst in others it is separated from it by one or more layers of pericyclic parenchyma.'

P. 549. Line 1. *For* 'mondesmic' *read* 'monodesmic.'

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THE extent of the valuable Memoir of Sir William Hooker with its comprehensive Appendices, has rendered it necessary to postpone the publication of other papers. The Editors have therefore decided to issue the first number of Vol. XVII in January instead of March, and to publish the succeeding numbers in the months of April, July, and October.

Walter L. Colls, Ph. Sc.

W. J. Hooker.

A SKETCH OF THE LIFE AND LABOURS

OF

SIR WILLIAM JACKSON HOOKER.

(*With Portrait*).

CHAPTER I.

NORWICH AND HALESWORTH, 1785–1820.

WILLIAM JACKSON HOOKER was born in St. Saviour's parish, Norwich, on July 6, 1785. He was the younger of two sons, the only children of Joseph and Lydia Hooker, of that city. His father was a native of Exeter, the home of many generations of the Devonshire Hookers[1], where he had been a confidential clerk in the house of Baring Brothers, wool-staplers, with whose family his was distantly connected. From Exeter he went to Norwich, and into business there, where he had a collection of 'Succulents,' the cultivation of which class of plants was a favourite pursuit of many of his fellow citizens[2]. He was mainly a self-educated man, and a fair German scholar. My father's mother was a daughter

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[1] Descendants of John Hooker, alias Vowell, First Chamberlain of Exeter and member for the city, editor of Holinshed's Chronicles, for which he wrote the history of the Irish Parliament and translated the Irish Histories of Giraldus Cambrensis, &c. He was uncle of Richard Hooker, whom he sent to college. My grandfather was seventh in descent from John, whose ancestors (fide Heralds' College) date back for six generations to a Seraph Voell, of Pembroke; but except John, Richard, and a John who was M.P. for Exeter, temp. Edward V, Richard III and Henry VII, not one of the long line, in so far as I know, emerged from obscurity.

[2] The best known of these collections was that of Thomas Hitchin, a dyer of Norwich, after whom Wallich named the noble Burmese plant *Hitchinia glauca*. In 1882 I could hear of but one collection remaining in the city, that of Dr. Masters, since dispersed, some of the contents coming to Kew.

of James Vincent, Esq., of Norwich, a worsted manufacturer, grandfather of George Vincent[1], one of the best of the Norwich School of artists, and whose works are now much sought for. Thus my father presumably derived his love of plants from his father's side, and his artistic powers from his mother's.

Of my father's early childhood I know no more than that he went to the Norwich Grammar School, under the then well-known pedagogue, Dr. Foster, but the records of that school having been destroyed it is impossible to say what progress he made there; at home he devoted himself to entomology, drawing, and reading books of travel and natural history. When only four years old he inherited the reversion to a fair competency in landed and personal property in Kent, through the death of his cousin and godfather, William Jackson, Esq.[2], of Canterbury, a young man of great promise. After leaving school he was sent to reside with a Mr. Paul, of Starston (a village on the borders of Suffolk), a gentleman farmer, who instructed sons of the landed gentry in the management of estates. Early in life he devoted himself to ornithology, visiting the Broads and sea-coast of Norfolk, which abounded in rare birds, shooting, stuffing, and drawing them, besides learning their habits and songs. Sixty years later he knew the birds in Kew Gardens by the eye and the ear, and in a manner which surprised me. Though a keen ornithologist and as keen an entomologist, he was almost morbidly averse from taking life; he never shot for sport or for the pot, and many years afterwards when instructing me in entomology he was ever urging me to kill with the least suffering, and never to take more specimens than were necessary. His was one of those temperaments that later in life

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[1] George Vincent was well educated and brought up, but lost himself. My father, his cousin, vainly endeavoured to trace his end in London.

[2] He was killed in 1789, being thrown from his horse at his father's door; see Hasted's Kent, iv. 427, and, for a long *éloge*, the Gentleman's Magazine, lxii (1790), 859. A sermon is to this day annually preached, in memory of him, in St. Mildred's Church, Canterbury, where is also his monument by the sculptor Bacon.

could not look on blood without a feeling of faintness, or on a wax model of the human face with equanimity.

That his entomological pursuits were, when still in his teens, appreciated by the veteran Kirby is evidenced by the latter having in 1805 dedicated to him and his brother a species of *Apion* with these words: 'I am indebted to an excellent naturalist, Mr. W. J. Hooker, of Norwich, who first discovered it, for this species. Many other nondescripts have been taken by him and his brother, Mr. J. Hooker, and I name this insect after them, as a memorial of my sense of their ability and exertions in the service of my favourite department of natural history[1].'

I do not know the age at which my father took up botany. The first evidence of his having done so is the fact, that he was the discoverer in Britain in 1805 of a very curious moss, *Buxbaumia aphylla*; but it may be inferred from this and from his correspondence with Mr. Turner (which I possess) that he had at the age of twenty-one thoroughly studied not only the flowering plants, but the mosses, Hepaticae, lichens[2], and fresh-water Algae of Norfolk. The *Buxbaumia* he took to his friend Dr. (afterwards Sir James) Smith[3], of Norwich, the possessor of the Linnean herbarium, who advised him to send specimens to Mr. Dawson Turner, F.R.S.[4], of Great

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[1] Transactions of the Linnean Society, vol. ix (1808), p. 70.

[2] In a letter dated March, 1806, he mentions having a cabinet made for his collection of lichens with twenty-eight or thirty drawers, each two inches deep with thirty-six partitions, in which to place cards with mounted specimens.

[3] In 1808 Sir James Smith dedicated a genus of mosses to him in the following words: 'I have great pleasure in dedicating this genus (*Hookeria*) to my young friend, William Jackson Hooker, F.L.S., a most assiduous and intelligent botanist, already well known by his interesting discovery of *Buxbaumia aphylla*, as well as by his scientific drawings of *Fuci* for Mr. Turner's work; and likely to be far more distinguished by his illustrations of the difficult genus *Jungermannia*, to which he has given particular attention' (Trans. Linn. Soc. ix. 1808, 275). The plate accompanying Sir James Smith's paper is of four species of the genus, signed 'W. J. Hook. delin^{t}.'

[4] Mr. Turner was a partner in Gurney's Bank, Great Yarmouth, of which his father was one of the founders. He was eminent as a scholar, botanist, antiquarian, and bibliophile. His collection of royal autographs and his illustrated copy of Blomfield's Norfolk are in the British Museum.

Yarmouth, author of 'Muscologiae Hibernicae Spicilegium,' and, with L. W. Dillwyn, F.L.S., of 'The Botanist's Guide through England and Wales.' This he did, and it was immediately followed by an invitation from Mr. Turner to visit him, which led to the colouring of his future life.

In 1806, when only four months over his majority, my father was elected a Fellow of the Linnean Society, probably the youngest individual so honoured. In the same year he visited London, and was introduced to Sir Joseph Banks, Konig, Brown, and other naturalists. The years 1806–9 were passed between Norwich, Yarmouth, and London, with intervals of travelling in Scotland and Iceland. In London he had rooms in Frith Street, Soho, to be near the British Museum, Linnean Society's rooms, his friends, R. Brown, Leach, Konig, Edward Foster, Macleay, and above all the Banksian library and collections, and Sir Joseph Banks himself, who treated him with great kindness, stimulating his zeal as a naturalist and his desire to travel. At Yarmouth, where he was a frequent guest for protracted periods, he devoted himself mainly to aiding Mr. Turner in his great work, the 'Historia Fucorum[1],' of which aid the latter makes frequent grateful mention in his correspondence with Mr. Borrer. During the same period he was occupied with preparing his 'British Jungermanniae' for publication[2], and in studying Buchanan-Hamilton's Nepal mosses in Sir James Smith's herbarium, upon some of which he wrote his first published paper. It is entitled 'Musci Nepalenses,' and was read before the Linnean Society in June, 1807 (Linn. Trans., ix. 1807, pp. 26-8, with three plates).

In 1807, when botanizing in the neighbourhood of Yarmouth, he was bitten by a viper. Fancying he had been pricked by a thorn he paid no heed to the pain till giddiness came on,

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[1] Of the 258 coloured plates of this work, 231 are inscribed 'W. J. H., Esq^{r}. delt.' in minute letters; 12 signed 'M. T.,' or 'D^{na} T.,' are by Mrs. Turner; 7 by Miss Hutchins, of Bantry; 2 by Professor Martens, of Bremen, and 1 by Sir Thomas Frankland.

[2] Writing to Mr. Turner in 1808 he mentions that Dr. Smith had lent him the whole Linnean collection of *Jungermanniae* for study, together with his own.

under which he succumbed. After lying for some time in a state of collapse[1] he was accidentally found by some friends, who carried him to Mr. Turner's, where violent fever supervened, followed by a tedious illness. On recovery he started with Mr. and Mrs. Turner on a botanical tour in Scotland. Their route was, first, Croft in Yorkshire, visiting the Rev. James Dalton, F.L.S., the discoverer of the *Scheuzeria* in England, after whom the moss *Daltonia* is named; then Carlisle, Branksome, Melrose, Edinburgh, the Falls of Clyde, Glasgow, Dumbarton, Luss, Ben Lomond—ascended in cloud and rain, guided by the Rev. Dr. Stuart, of Luss, an excellent botanist, a friend of Lightfoot, and the translator of the New Testament in Gaelic. Thence they proceeded to Inverary, Loch Awe, Oban, Mull, Ulva, Staffa, Fort William, ascending Ben Nevis in terrible weather, Fort Augustus, Elgin, visiting Mr. Brodie of Brodie, F.R.S., the discoverer of *Moneses* and other rare plants in Scotland. Thence to Loch Tay, ascending Ben Lawers twice, Killin, ascending Ben Cruachan, Craighalliach and Ben More, Stirling, Edinburgh, and Newcastle, visiting Mr. J. Winch, F.L.S., author of the 'Geographical Distribution of Northumbrian Plants,' and Mr. J. Thornhill, of Gateshead, a good local botanist; thence to Darlington on a visit to Mr. Backhouse, banker, who showed them *Cypripedium Calceolus*, and so back to Yarmouth.

In 1808 my father undertook a much longer journey in Scotland, accompanied by his friend Mr. Borrer[2]. On this occasion he reascended Ben Lawers, Ben Lomond, Ben Cruachan, and Ben Nevis, and for the first time Shichallion, Ben Hope, and Ben Loyal. After visiting Mr. Brodie of Brodie, they went to Caithness and the Orkneys, returning to Sutherland. In a letter to Mr. Turner he thus describes their reception in Sutherland: 'We did not leave North Sutherland with the good wishes of the inhabitants, at least

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[1] The symptoms, as described in a letter from Turner to Borrer, were dreadful giddiness, pain about the navel, shivering, drowsiness, vomiting, purging, and exhaustion.

[2] William Borrer, Esq., of Henfield, Sussex, F.R.S., F.L.S., died 1862, aged 81; the Nestor of British botanists.

the lower classes of them, most of whom took us for French spies, or, what is worse in their estimation, sheep-farmers. Daniel Forbes, who so often acted as our guide, was advised by some to conduct us by the worst way possible ; by others he was told that he might be better employed. Our lad heard some saying that we ought to be flogged and sent out of the country. They have not the least idea of persons travelling for mere curiosity, and could not be persuaded that we were not come to do them some ill.' Crossing Sutherland and Cromarty, they went by Moida and Lairg to Skye, where they found the *Eriocaulon*, and to the remarkable and little-visited cave of Slock Altramins. Recrossing the Sound to Glenelg, they proceeded to visit Sir George McKenzie at Coul, and Lord Seaforth at Brahan Castle, and again Mr. Brodie of Brodie, returning by Aviemore, Killiecrankie, and Edinburgh[1] to Norwich.

The journey through the North of Scotland was performed mainly on horses or ponies, and the difficulties met with were such as can now be experienced only in the out-of-the-way parts of the globe. My father made copious pencil sketches and kept a journal, which he was vainly urged by his friends to publish. I have no idea what became of it. The only recorded botanical result of the journey was the discovery of a new *Andreaea* (*A. nivalis*, Hook.) on the summit of Ben Nevis; which probably prompted the writing of his second published paper, 'Some Observations on the Genus *Andreaea*,' read before the Linnean Society in May, 1810 (Linn. Trans., x. 381, tab. xxxi).

In 1809 Sir Joseph Banks, hearing of an opportunity for a naturalist visiting Iceland, where he himself had been in 1772, suggested my father's taking advantage of it. This he did, and all the more eagerly from having as a boy read 'Van Troil's Letters on Iceland,' with a longing to visit the hot springs and volcanoes therein described. The opportunity was the dispatch of a vessel, the *Margaret and Anne*, with

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[1] It was probably on this occasion that my father became one of the founders of the Wernerian Society of Edinburgh, the memoirs of which, commenced in 1808, were concluded in 1832, in six volumes.

a letter of marque, chartered by a London firm, Messrs. Phelps & Co., for the purpose of obtaining a cargo of tallow. The venture was a risky one, for Denmark, to which country Iceland belonged, was at war with England, and the firm were enticed to undertake it by a Danish prisoner of war, Jorgen Jorgensen by name, who was now for the second time about to break his parole and accompany the ship in the interests of the firm. The *Margaret and Anne* sailed June 2, and on arriving June 21 at Reikevik Jorgensen, finding that commerce with England was prohibited, effected a revolution in the island, proclaimed its independence of the Danish crown and himself its 'Protector,' imprisoned the governor, Count Tramp, erected a fort armed with six guns, equipped troops, remodelled the laws, established representative government and trial by jury, reduced the taxes, and raised the salaries of the clergy; all without shedding a drop of blood, or an attempt at resistance on the part of the people[1]!

On his arrival at Reikevik my father received a hearty welcome from the Stiftsamptman (Icelandic governor of the island), to whom he had brought from Sir Joseph Banks a letter of introduction, together with a handsome present of books, engravings, &c. The delight of the old man on receiving these was affecting; he spoke of Sir Joseph with veneration, describing his philanthropic efforts to avert the

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[1] An account of the career of this extraordinary man is given in his Autobiography, published anonymously in Ross's Hobart Town Almanack for 1835; and is retold in a little work entitled 'The Convict King, being the Life and Adventures of Jorgen Jorgensen, Monarch of Iceland, Naval Captain, Revolutionist, British Diplomatic Agent, Author, Dramatist, Preacher, Political Prisoner, Gambler, Hospital Dispenser, Continental Traveller, Explorer, Editor, Expatriated Exile, and Colonial Constable, retold by James Francis Hogan': 12mo, London, Ward and Downey, 1891. What most concerns botany in Jorgensen's career are the facts that he served as a seaman under Capt. Flinders, R.N., in his voyage to Terra Australis (1802–5), with Robert Brown as botanist, and J. Franklin (afterwards Sir John, the Arctic traveller) as midshipman; and that it was through the exertions of Mrs. Fry, Sir Joseph Banks, and my father, that the sentence of death passed on Jorgensen in 1825 was commuted into penal servitude for life in Tasmania, where I saw him in 1840. He died there in that or the following year, his fellow-voyager, Sir John Franklin, being governor of the colony at the time! See 'Tour in Iceland,' by W. J. H., for details of Jorgensen's acts, &c.

famine that threatened the Icelanders at the beginning of the war, when the activity of our cruisers intercepted their supplies of food from Denmark and Norway [1], adding that Sir Joseph had obtained the release of Danish prisoners in England, and at his own expense furnished them with the means of living and returning to their homes.

As may be taken for granted, under such circumstances every facility was given to the visitor for travelling to the most interesting places in the island, Thingewalla, the Geysers, Skalholt, Reykholt, &c., and for making collections and observations on natural history.

On August 6, H.M.S. *Talbot* anchored in Reikevik harbour, when her commander, the Hon. Captain Jones, promptly deposing and making a prisoner of Jorgensen, replaced Count Tramp in the governorship.

On August 25, after bidding adieu to his kind friend the Stiftsamptman, who gave him a valuable collection of Icelandic books, my father embarked on his return voyage in the *Margaret and Anne*. On this occasion the vessel carried besides the passengers and crew some Danish prisoners of war, and she was ordered by Captain Jones to sail in company with the *Orion* [2], now a prize of the *Talbot*, carrying Mr. Jorgensen and another party of Danish prisoners. The two ships left in the afternoon, but the *Orion* becoming suddenly becalmed could not proceed till the following day. The *Margaret and Anne*, on the other hand, being favoured by the wind, pursued her voyage till the morning of the 27th, when being twenty leagues from the land, in a dead calm, she was discovered to be on fire. Being loaded with oil and tallow, the progress of the flames was rapid; smoke burst out at once from all the hatches, and to add to the horror of the situation, she did not

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[1] Sir Joseph Banks being himself a Privy Councillor obtained an Order in Council, dated Feb. 10, 1810, strictly forbidding acts of hostility against the poor and defenceless colonies of the Danish dominion, and permitting them to trade with the parent-country, unmolested by British cruisers.

[2] The *Orion* was a Danish ship of war, that had brought Count Tramp to Iceland a few weeks before the arrival of the *Margaret and Anne*, which, in virtue of her letter of marque, had, under Jorgensen's orders, seized her as a prize.

carry boats enough to hold the number of souls on board. All attempts to subdue the fire were vain, when providentially a rescuer appeared on the horizon. This was the *Orion* with the irrepressible Jorgensen[1] on board, who, to enable that vessel to rejoin her consort, had insisted on being allowed to run her through a dangerous passage between the reefs and the mainland of Reikevik harbour, and who by thus saving a day saved the lives of all hands on the burning ship, whom he carried back to Reikevik.

My father's description[2] of the progress of the conflagration, as seen from the *Orion*, is graphic—of the flames seizing the sails and rigging, of the falling of the masts, of the discharge of the guns, and of the reduction of a ship of 500 tons burthen, worth £25,000, to a hull with cataracts of blazing oil and tallow pouring over its sides.

Unfortunately the fire broke out in a part of the ship where his collections were stowed, and he lost everything but a few weeks of his journal, the clothes he stood in, and an Icelandic lady's wedding dress[3], which the ship's steward flung into the boat as she shoved off from the burning wreck.

The fire was proved to have been planned before leaving Reikevik by some of the Danish prisoners, two of whom had lit it in the previous night. A search in the bedding of the prisoners in the *Orion* resulted in finding combustible materials, no doubt secreted for the same object.

On her return to Reikevik Captain Jones offered my father a passage home on board the *Talbot*, which he gladly accepted. The voyage was a tempestuous one of sixteen days' duration, during which the *Talbot* lost her foremast. She arrived in Leith roads on September 20.

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[1] Jorgensen had proved himself to be a first-rate seaman, with all the qualities of a commander, when serving under Captain Flinders; and subsequently in 1807, as a captain in the Danish navy, when in a ship with eighty-three hands and twenty-eight guns, he engaged for three-quarters of an hour the British sloop *Sappho*, with 120 men. On this occasion he was taken prisoner and put on parole, which he twice broke as stated above, in making this and a former visit to Iceland in the interests of Messrs. Phelps & Co.

[2] See Tour in Iceland, vol. i, pp. 362–4.

[3] Now in the Victoria and Albert Museum, South Kensington.

Soon after his return, and yielding to the wishes of his friends, he commenced writing his 'Journal of a Tour in Iceland.' On hearing of this Sir Joseph Banks most liberally offered him the use of his own manuscript journal, and various other papers relating to the island, together with the magnificent drawings of the scenery, dresses of the inhabitants, &c., which were made by the artist who accompanied him in his voyage thither in 1772. With these materials, his own journal of four weeks out of the twelve which he passed in the island, and a retentive memory, refreshed by a reference to all available works and all documents relating to the revolution, he compiled and printed, for *private distribution only*, in 1811, an 8vo volume of upwards of 400 pages and four plates. Sir Joseph Banks was so pleased with it that he induced my father to reproduce it for publication. The second edition with additions, in two volumes, with two maps and four plates, dedicated to Sir Joseph, appeared in 1813, and is to this day a standard work. A *résumé* of its contents may be welcome to those interested in the author's career. Volume i contains the history and present condition of Iceland, its productions, institutions, commerce, &c., followed by his 'Recollections of Iceland' in journal form. Volume ii consists of six appendices: (1) details of the Icelandic Revolution, drawn up with singular impartiality; (2) proclamations relating to it; (3) Hecla and the volcanic mountains of Iceland; (4) Odes and Letters presented by the literati of Iceland to the Right Honourable Sir Joseph Banks and the Honourable Captain Jones; (5) a list of Icelandic plants; (6) Danish ordinances concerning the trade of Iceland.

Reverting to the destruction of his collections, my impression is that the loss to science of the cryptogamic plants was the most serious, for he was a keen student of mosses, Hepaticae, lichens, and both marine and fresh-water Algae[1], and had gained invaluable knowledge on them during his excursions

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[1] When only twenty-one years old he was in correspondence, on the subject of fresh-water Algae, with Mr. Dillwyn for whose British Confervae he made drawings of species discovered by himself in Norfolk.

in the east and north of England, and especially during his two extended Scottish tours. Of flowering plants he probably added but few to the list he gives of 359 species taken from Zoega's 'Flora Islandica,' published in 1772, with the addition of twenty-two from his own observations and Sir George McKenzie's collections. Babington, in his very valuable 'Review of the Flora of Iceland' (Journ. Linn. Soc., xi. 1870, 282), enumerates 433 Icelandic flowering plants, which is an increase of 96 species.

The years immediately following my father's return from Iceland (1809–12) were the most embarrassing of his life. His unquenchable longing to travel in the tropics was kept alive by Banks's earnest endeavours to find him a fitting opportunity. On the other hand his botanical friends were unanimous in urging him to remain at home, publish his Icelandic and Scottish journals, continue his aid to Mr. Turner on the 'Historia Fucorum,' and, above all, proceed with his 'British Jungermanniae,' his drawings and analyses of which were of unrivalled beauty, and his contemplated 'Muscologia Britannica.' Meanwhile Mr. Turner, with real desire to benefit his young friend, induced him in 1809 to join in partnership with himself and Mr. Paget of Yarmouth (father of the late Sir James Paget) in a brewery at Halesworth, reside there, and undertake the management of a business for which he had neither experience nor inclination. This did not check either his botanical ardour or his desire to visit the tropics. In 1810 he sold his landed property and determined to accept an invitation, which Sir Joseph had procured for him, of accompanying Sir Robert Brownrigg, G.C.B., the newly appointed Governor of Ceylon, to that island. To this end he appointed his father locum tenens at the brewery and proceeded to London, where amongst other preparations for the undertaking he made, at the Museum of the India House, reduced pen and ink sketches from upwards of 2,000 folio drawings of Indian plants[1], which had been executed by native

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[1] These drawings, now in the Herbarium of the Royal Gardens, Kew, are

artists in the Botanical Gardens of Calcutta under Dr. Roxburgh's directions.

To his bitter disappointment this opportunity had to be put aside, for disturbances followed by a rebellion had broken out in Ceylon that would have rendered travelling in the island impossible. One more chance presented itself in 1813. Through his intercourse with Dr. Horsfield [1], the Keeper of the India House Museum, his attention was turned to Java, where that officer had resided under Sir Stamford Raffles's rule, and had made magnificent collections. Sir Joseph Banks encouraged the idea of his going there, and prevailed on Lord Bathurst, the President of the Board of Trade, to remunerate him if he would send living plants to Kew, and procure information regarding the cultivation of spice-bearing trees in the Dutch East Indies. But disappointment still pursued him. The climate of Java was reported to be notoriously malarious, and Banks's own experience of it, as narrated in Cook's 'First Voyage [2],' was cited in evidence. For there, not only had Banks been extremely ill, but Dr. Solander had been at death's door; and Mr. Parkinson his artist, the two Otaheitans in his suite, Mr. Green the astronomer, Mr. Monkhouse the surgeon, and Mr. Spring had all died from the effect of the climate at or shortly after leaving Batavia. No wonder that the entreaties of his parents and friends prevailed, notwithstanding Banks's well-founded assurance that the climate of Java itself was as exceptionally good as that of Batavia was bad. My father was hence compelled to confine his wanderings to nearer home, adding gardening to his pursuits, and this with some success, for he was the first to flower *Cattleya labiata* in his little stove in 1818, and he also flowered *Musa coccinea* and other tropical plants.

duplicates (exact copies) of the originals in the Royal Botanic Gardens, Calcutta. The reductions by my father occupy ten duodecimo volumes, also in the Kew Library.

[1] Thomas Horsfield, M.D., F.R.S., F.L.S., Keeper of the India House Museum, 1820–59. For a sketch of his travels see Brown and Bennett, Plantae Javanicae Rariores, postscript, pp. i–xvi.

[2] The *Endeavour* lost, from malarial fever or its effects, seven persons in Batavia, and twenty-five after leaving that port.

In 1813, owing to the illness of his only brother[1], my father spent five months with him in Devonshire and Cornwall, which counties he diligently explored for Musci, Hepaticae, and lichens especially. The Trinity House yacht having been placed at his disposal, he visited the Scilly Islands, whence he writes to Mr. Turner: 'The first thing that caught my attention was the situation of the little town of St. Mary's, which so much resembled that of Reikevik that I could hardly help fancying for some time that I was in Iceland . . . nor is the surrounding country so much unlike as you would perhaps expect, for except where there are enclosures of stone the surface is equally barren.' He found mosses and lichens to be far from luxuriant in the islands, and at the time parched almost to a cinder, there having been no rain for many weeks.

In the same year he had two interesting visitors at Halesworth; one was his old friend Jorgen Jorgensen, who in a record of his life, printed in Tasmania[2], speaks of the hearty welcome he received, adding: 'Availing myself of the quiet retirement of this country residence I shut myself up and wrote an account of the Icelandic Revolution, in which I introduced various anecdotes of Scandinavian history. I presented it to Sir Joseph Banks.'

The other visitor was Dr. Thomas Taylor[3] of Dunkerron, Kerry, an excellent Irish muscologist, who spent three weeks with him over his own and Turner's herbarium. The latter was lent for the purpose, and was of especial interest as containing the types of the 'Muscologia Hibernica.' In a letter to Mr. Turner, Taylor is described as having been born in India, and up to his seventh year knowing no language but Hindustani; he was then shipped to Ireland in a vessel where

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[1] Joseph Hooker, junr., died in 1815 of consumption, for which the treatment in vogue then, and for many years afterwards, was 'powerful medicines and abstinence from nourishing food.' He was an excellent British entomologist. His collection of insects was purchased by the British Museum: my father's is now in the Norwich Museum.

[2] Ross's Hobart Town Almanack and Van Diemen's Land Annual for 1835, p. 138. The article is anonymous, entitled 'A Shred of Autobiography.'

[3] Died at Dunkerron, 1848. He was joint author of the Muscologia Britannica.

nothing but Portuguese was spoken, and on landing sent to a school at Cork where French alone was heard. It was thus comparatively late in life that he acquired English, and this with an Irish accent.

Early in 1814 my father accompanied Mr. and Mrs. Turner and family on a visit to Paris, then in the occupation of the Allies. There, at 'The Institute,' he made the acquaintance of the principal botanists resident in, or on visits to the city—Antoine Laurent de Jussieu, Desfontaines, Lamarck, Mirbel, Bory de St. Vincent[1], Thouin, and others. Leaving the party in Paris he spent the remainder of the year botanizing and seeing botanists, sketching and sight-seeing in the south of France, spending some days with de Candolle at Montpellier, and in Piedmont, Switzerland, and Lombardy. Returning to Paris early in 1815 he was introduced to Humboldt, who engaged him to publish a cryptogamic volume of his 'Plantae Equinoctiales.' This intention had to be abandoned owing to the publisher's refusal to continue that work. After much subsequent correspondence with Humboldt, that led to nothing, my father commenced the publication on his own account, and produced in 1816 the first part of a work entitled 'Plantae Cryptogamicae, quae in plaga orbis novi Aequinoctialis colligerunt Alex^{r}. von Humboldt et Aimat Bonpland.' It is a very thin quarto with four plates of species drawn by the author, and exquisitely etched by Edwards. The expense was great and the return nil; the work was therefore abandoned, and of the remaining Musci and Hepaticae many were included in the author's less expensive 'Musci Exotici.'

On June 12, 1815, my father married Maria Sarah, eldest daughter of Dawson Turner, and immediately started on a long wedding tour to the Lake District and to Ireland, which latter country the pair traversed in almost every direction, making sketches of scenery and ancient buildings; thence they went to Scotland on a visit to Mr. Lyell[2] at

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[1] Of the above, only two were alive to welcome me when I visited Paris in 1845; Mirbel died in 1854, Bory in 1846.

[2] Father of Sir Charles Lyell, translator of Dante. I have been unable to

Kinnordy in Forfarshire, with whom a close intimacy and correspondence on Hepaticae had long existed. Returning they passed through Manchester for the purpose of seeing Mr. Hobson[1], a packer in a warehouse, who with only the works of Withering, Hudson, and the 'Muscologia Hibernica' had acquired a critical knowledge of British mosses that surprised his visitor, who says of him: 'I never saw a man possessed of more enthusiasm than this poor fellow.'

Taking up his residence in Halesworth, my father was for the next four years seldom long without interesting and often distinguished botanical visitors. Early in 1816 he had staying with him, preparing to accompany Earl Amherst as medical attendant in his embassy to China, Dr. Clarke Abel[2], a young Norwich friend, whom he had recommended to Sir Joseph Banks for that appointment. Dr. Abel returned in 1817 and again stayed with my father at Halesworth, writing up his journal for publication and naming his plants.

In the same year M. de Candolle spent some days with him, of which the following account is given in the writer's own words[3]:—

'J'allai par les voitures publiques d'abord à Halesworth où demeurait M. Hooker. Il me reçut avec beaucoup d'amitié

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discover the beginning of my father's intimacy with Mr. Lyell. It commenced when the latter lived at Bartley Lodge, in the New Forest, which he diligently explored for Hepaticae. In the introduction to the British Jungermanniae Mr. Lyell is mentioned as having suggested alterations in the arrangement of the species adopted by Lamarck and de Candolle in the Flore Française. He was elected F.L.S. in 1813.

[1] Edward Hobson, who died in 1830, was the author of two volumes 8vo of Specimens of British Mosses.

[2] Clarke Abel, M.D., F.L.S., had practised for a short time as surgeon in Norwich, when his devotion to natural history led him to seek employment abroad. After returning from China he entered the service of the East India Company and went to Calcutta, where he won the regard of Dr. Roxburgh at the Botanical Gardens. He died at Cawnpore in 1826. His description of the tame orang-outang in the Asiatic Researches is classical, as are his works on the wild dog of the Himalaya and the crocodile of the Ganges. His Narrative of a Journey in the Interior of China (London, 1818) gives an account of the misfortunes of the embassy.

[3] Mémoires et Souvenirs d' Augustin-Pyramus de Candolle, écrits par lui-même et publiés par son fils, p. 272. Genève, 1862.

et je logais quelques jours avec lui. Sa femme, qui était aussi distinguée par la figure et par l'esprit, me reçut également d'une manière très amicale. Nous passions nos journées ensemble à causer, surtout de botanique, à voir son herbier et les plantes qu'il cultivait dans son petit jardin. J'y fis connaissance avec Lindley, alors jeune élève de Hooker, et qui depuis est l'un des premiers botanistes de l'Angleterre. Madame Hooker est fille de M. Dawson Turner, botaniste, connu par un bel ouvrage sur les *Fucus*. Elle m'engagea à aller à Yarmouth voir son père, et je fus, en effet, reçu avec la plus franche hospitalité. Madame Turner était une mère de famille très distinguée et elle dessinait assez bien et gravait à l'eau forte. Mon portrait a été gravé par elle.'

As alluded to by M. de Candolle, Lindley, then a youth of eighteen, was at the same time with himself a guest of my father. He was the son of a well-known nurseryman of Catton, near Norwich, and had shown such zeal and ability as a local botanist that with a view of encouraging him in its pursuit he was invited to Halesworth [1], and to occupy himself there with translating Richard's 'Analyse des Fruits.' This he did, introducing the author's latest corrections, and illustrating his translation with plates and original observations [2]. In the following year my father took Lindley to Sir Joseph Banks, who offered him temporary employment in his herbarium, and introduced him to Mr. Cattley, a wealthy merchant devoted to horticulture, who was desirous of having his rare plants handsomely illustrated [3]; and this again led eventually to the assistant secretaryship of the Horticultural Society of

[1] On this occasion Lindley was looking forward to employment as a botanical collector abroad, which led to an amusing incident. The housekeeper at Halesworth finding that his bed was never occupied, after a vain search for a reason, reported the fact. His distressed host had to ask for an explanation, which was simply that his guest was inuring himself to the hardships of a collector's calling by sleeping on hard boards! Dr. Lindley died in 1865, three months after my father.

[2] Published in London, under the title of Observations on the Structure of Fruits and Seeds, in 1819, pp. 100, and six plates; dedicated to W. J. Hooker.

[3] The result was the publication of the Collectanea Botanica, a folio with forty-one coloured plates. London, 1821.

London, which Lindley occupied till 1858. In the same year he was visited by Professor C. Martens of Bremen, an enthusiastic algologist, and father of Professor Martens who accompanied the Russian Captain Lutke on his voyage to Behring Sea, where he made valuable observations and collections of the wonderful Algae of that sea; and later received a second visit from Dr. Taylor, who was engaged with his host on the 'Muscologia Britannica,' published in 1818 with twenty-eight plates illustrating 269 species and three tables of genera with thirty-two species. This work had taken in all eight years of preparation, nearly every species having been collected by one or both authors. The number described is 269 as against 227 enumerated by de Candolle for France, including the Pyrenees and Alps. The number of synonyms is about 470. A second edition hereafter to be notified appeared in 1827.

The 'British Jungermanniae,' the most beautiful of all my father's works, in point of the drawing, analyses, and engraving of the plates, was concluded in 1816. It had occupied him for about ten years, and was the first work of any magnitude which he projected. It appeared in parts, in both a quarto and a folio form, with eighty-eight plates engraved by Edwards, illustrating 197 species.

In the same year he commenced working for the new edition, by G. Graves, of Curtis's 'Flora Londinensis,' a sumptuous work, the parts of which appeared at long intervals from 1819 to 1828. Its perplexing issue will be described later on.

1817 is one of the very few years of his life in which he published scarcely anything. The exception was an account of the very remarkable European moss named after his friend, *Tayloria splachnoides*, in 'Brand's Journal of Science and Art,' No. III, p. 144, and 'Musci Exotici,' tab. 173. Of a visit to London in August of this year, he writes: 'I met at Spring Grove (Sir Joseph Banks's) Abel, Brown, Leach, and a Mr. Manning of Diss, who passed many years among the Chinese endeavouring to get access into the interior, though he failed; though he tells me he saw much of Thibet.' Mr. Manning is, to this day, the only Englishman who ever entered the sacred city of Lhassa. What is more remarkable is, that his journal was lost to geographers till Sir Clements Markham happily found it in the possession of a cousin of his own in Norfolk. See 'Narratives of the Mission of G. Bogle to Thibet and of the Journey of T. Manning to Lhassa,' ed. 2, 1879, by Sir C. Markham, a book full of curious information.

In 1818 my father had the pleasure of receiving at Halesworth Robert Brown, Dr. Burchell [1], Mr. Lyell of Kinnordy, and Dr. Boott [2] of Boston, Mass. The first volume of the 'Musci Exotici' appeared in this year, the second in 1820, in both octavo and quarto forms. One of the objects of the work was to illustrate Humboldt's and Bonpland's discoveries, of which thirty-five are figured ; but the collections of Menzies during Captain Vancouver's voyage (1790-5), in New Zealand and North-West America especially, more than doubled that number. Other important contributions came from Burchell's Cape travels, Buchanan-Hamilton's Nepalese, and Brown's Australian. Altogether 176 species are figured, etched by Edwards, from coloured drawings by the author.

My father's Halesworth life was now drawing to a close: the brewery business, as might have been expected under the management of an enthusiastic naturalist and author, had proved unsatisfactory, and some of his investments were disappointing. Personally his ménage was entirely inexpensive

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[1] Dr. W. Burchell, D.C.L., F.L.S., was a great traveller. Embarking in 1804 on a voyage to the Cape for botanical purposes chiefly, he spent five years en route in St. Helena, then five in South Africa, penetrating into the Transvaal before the immigration of the Boers. He then went to Brazil and travelled for four years in the interior. On both journeys he made enormous collections of plants, estimated at 15,000 species, and many views of scenery, for he was a beautiful artist. But except two quarto volumes of travels in Africa and descriptions of three new African animals, he published nothing, and he shut himself up in his museum at Fulham, where I visited him about 1860. On his death in 1863 his herbarium was presented by his sister to the Royal Gardens, Kew.

[2] Dr. Boott, M.D., F.L.S., secretary and treasurer of the Linnean Society, resided in London and devoted his life to the illustration of the genus *Carex*, upon which he published four folio volumes with plates. He died in 1863. His collections and all the drawings he had made of the genus were presented to the Royal Gardens, Kew, by his widow.

and simple, and this was so throughout his life; but his lavish expenditure on his own unremunerative publications, and on the purchase and beautiful binding of expensive entomological, ornithological, and especially botanical and even archaeological and artistic works, had crippled his resources, and he had now a wife and family of four to provide for. Under these circumstances he wrote to his friend Sir Joseph Banks, requesting that he might be informed, should he hear of any opportunity of applying his botanical knowledge to the improvement of his income. Sir Joseph promptly answered, that the Professorship of Botany was vacant in the University of Glasgow, and that he was ready to use his influence to obtain it for him should he desire to become a candidate. My father answered favourably, and at once left for Spring Grove, where he was hospitably received by Sir Joseph[1], who told him that the emoluments of the Chair, though small, would certainly increase; that it was freed from all medical duties[2]; that a really noble botanical garden had been formed at Glasgow, to which the University had given £2,000 and the city £3,000, and towards the development of which he could assure him that Kew would place all its resources.

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[1] The securing this professorship for my father was probably the last of the good deeds of this truly noble soldier of science. He died in the following June (19), aged 77.

[2] The Chair had been held conjointly with that of medicine by Dr. R. Graham, who was now transferred to Edinburgh. The Edinburgh Chair, as was that of Glasgow, had been first offered to Robert Brown, who declined both, on the score of his obligations to the aged Sir Joseph Banks, whose librarian he was. Sir James Smith had been a candidate for the Edinburgh Chair.

CHAPTER II.

GLASGOW, 1820-1840.

EARLY in February, 1820, my father was appointed by the Crown to the Chair of Botany in Glasgow, and having dispatched his library, herbarium, and household effects to London, to be thence sent by smack to Leith, and on to Glasgow by canal, he severed his connexion with Halesworth and the brewery. In May he presented himself before the Senate of the University, who gave him a flattering reception, read his inaugural thesis[1] (the Latinity of which, thanks to his classical father-in-law, was highly praised), and was duly installed, with the welcome addition of having the honour of LL.D. conferred upon him.

Meanwhile the preparation for his course of botanical teaching, which commenced in May, had been for three months a grave anxiety. He had never taught, lectured, or even heard a course of lectures, and some important branches of the science he was called upon to profess were new to him. Such especially was the anatomy of plants, of which he writes: 'It is a subject to which I have never attended, and authors are so much at variance as to their opinions, and on facts too, that I really do not know whom to follow. Knight in every one of his papers contradicts what he himself asserted in former ones, and has got handsomely lashed for it in the second number of the 'British Review'; as has Sir James Smith, for adopting his theories and for

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[1] Of this thesis I find no copy amongst my father's papers; and in answer to a request that the records of the University might be searched for it, I am informed that it does not exist there. It was entitled De Laudibus Botanicis.

giving him the highest praise for his perspicuity. I have written for Kieser's work[1] on the subject, which Brown says is the best. Mirbel has seen what nobody else can; so nobody contradicts him, though many won't believe him.'

Before enlarging on my father's success as a lecturer, I may premise that the teaching of botany in the first quarter of the last century was very different from that which now prevails. It was regarded as ancillary to that of Materia Medica, and as a means of enabling the practitioner to recognize the plants used in medicine when there might be no druggist to appeal to. Furthermore, it was required by the principal examining bodies for medical degrees or licences, that the candidate should have attended a course of lectures delivered in a botanical garden registered for the purpose; and in these gardens the plants were invariably arranged according to the Linnean[2] system, which consequently had to be taught. The latter was, however, with the new Glasgow Professor a secondary consideration, his primary aim being to open the eyes and minds of his pupils to the principles upon which plants were classified, and their distribution and uses, which was as much, he thought, as could be comprehended in a course of sixty lectures by young men who did not even know the elements of biology, and had not been exercised in using their eyes, hands, and brain in unison in the examination of a plant or animal. The course was opened by a few introductory lectures on the history of botany and general character of plant life. As a rule the first half of each hour was occupied with lecturing on organography, morphology, and classification, and the second half with the analysis in the class-room of specimens supplied to the pupils, the most studious of whom took these home for further examination. An interesting event in these half-hours was the Professor frequently calling upon such students as volunteered for being examined, to demonstrate the structure of a plant or fruit placed in the

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[1] Grundzüge der Anatomie der Pflanzen. Jena, 1815.

[2] Some of the students of my father's first year's course remonstrated against his introducing the Natural System into his teaching.

hands of the whole class for this purpose. Throughout the course my father's artistic powers were exercised with chalk and the blackboard ; and he gradually accumulated a magnificent series of folio coloured drawings, especially of medicinal plants, which were suspended in the class-room as occasion required. I well remember the murmur, and even louder expression of applause with which he was greeted on taking the Chair, when the number or interest of these pictures was conspicuous. Before his second year's class had assembled he had published the 'Flora Scotica' for its use, and an oblong folio of lithographed illustrations of the organs of plants by his own pencil, with twenty-four plates and 327 figures, a copy of which was placed before every two students [1]. During the course three botanizing excursions were taken, two in the neighbourhood of Glasgow, and one towards the end of June, of five or six days' duration, to the Western Highlands, usually to the Breadalbane range. This latter was eagerly anticipated by a contingent of ten to thirty students, amongst whom were frequent accessions of botanists from Edinburgh and England. Further to stimulate their zeal, he habitually invited the more industrious students to breakfast with him after the class (which was from 8 to 9 a.m.), when he would show them books, and give them from his store of duplicates, specimens of rare British plants. To conclude this episode of his life, it must be recorded, that his success as a lecturer was phenomenal ; his tall figure, commanding presence, flexible features, good voice, eloquent delivery, and urbane manners are vouched for in every obituary notice of him. His lectures were often attended by gentlemen of the city, and even by officers from the barracks three miles distant. The students of his first year's course presented him with a handsome silver vasculum, chased with a design taken from the moss, *Hookeria lucens*, and those of the second year with a richly bound copy in ten volumes of Scott's Poetical Works.

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[1] A second series in quarto with twenty-six plates, comprising 395 illustrations, by Fitch, for class use, was published in 1837.

During the twenty years of my father's Glasgow residence his life was one of continuous but congenial labour. For the first fifteen years or so he gave only one course of lectures, from May 6 to the middle of July, in the Botanical Gardens; but towards the end of his professorship a winter course was given in the College buildings. These and the examinations in botany for degrees were his only professional duties; the rest of his time was devoted to his botanical studies, drawings, and publications, the increase and keep of his herbarium, and rapidly accumulating botanical correspondence. Except for short visits to London, Yarmouth, or the Highlands, botanizing with Greville or Arnott, and once to Paris, he rarely left home. He was at his desk with pen or pencil by 8 a.m., and never left it much before midnight. The late summer and autumn weeks were frequently passed with his family at watering-places on the Clyde, usually at Helensburgh, where he enjoyed the society of two neighbours of scientific tastes and culture, James Smith, Esq., F.R.S., of Jordan Hill[1], and Lord John Campbell, afterwards Duke of Argyll, father of the late Duke, who inherited his parent's scientific tastes. In 1837 he purchased a cottage with an acre of ground, 'Invereck[2],' near Kilmun, on the Holy Loch; a lovely spot where he could indulge his fondness for gardening. In the touring season he received many English and foreign friends, who took Glasgow on their route for the Highlands, both to visit him and to avail themselves of his experience of roads, conveyances, and accommodation.

My father's reputation as one of the foremost botanists in this country was confirmed by his success in the Glasgow Chair, and rapidly rose as his successive publications appeared. Very soon he had but one compeer in Great Britain, Dr. Lindley, for Robert Brown towered above both as 'Botanicorum facile princeps.' It was a happy augury for

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[1] Eminent as a geologist, and as author of The Voyage and Shipwreck of St. Paul.

[2] The site of the cottage is now occupied by a castellated mansion in the Scottish style of architecture.

the progress of the science which both worshipped with single-minded zeal, that Lindley and my father were regarded as meriting equal recognition as scientific botanists and indefatigable labourers throughout forty-five years of their active lives, and that they should have been fast friends till death, within three months of one another[1].

As his own reputation advanced so did that of his herbarium and library, which before he had been ten years in Glasgow were reckoned as amongst the richest private ones in Europe[2]. This was due to his active correspondence,

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[1] The following admirable summary of the life-works of my father and Lindley respectively, is extracted from the Proceedings of the American Academy of Arts and Sciences, May 29, 1866:—'The names of Hooker and Lindley, which stood side by side in our botanical section, are naturally associated as those of the two most eminent botanists in Great Britain—also by the parallel course, and near coincidence in the close of their lives. Born in the same neighbourhood, in youth receiving their education at the same school, and early drawn together by similar predilections, they both devoted themselves with singular energy and perseverance to their chosen pursuit; exerted for many years, although in somewhat different ways, a paramount influence upon the advancement of botanical science; and died near together in place and time—the elder at Kew, on August 13 last, at the age of eighty years; the younger at Turnham Green, on the first of the ensuing November, at the age of sixty-seven years. For a long time they were the two most distinguished teachers in Great Britain, one at a northern, the other at the metropolitan University. They severally conducted two of the principal serial works by which botany contributes to floriculture; and they developed into highest usefulness the two great establishments, the Royal Gardens at Kew, and the Horticultural Society of London. Both wrote and published largely—Hooker only upon descriptive botany, in which he greatly excelled, while Lindley traversed a wider field, and grappled with abstruser problems in every department of the science, always with confidence and facility, but not with unvarying success.'

[2] The following testimony to the value of the herbarium is an extract from an essay on European Herbaria by Asa Gray, written in 1841, and published in the American Journal of Science and Arts, xl. 1 (see also Scientific Papers of Asa Gray,' ii. 13): 'The herbarium of Sir William J. Hooker, at Glasgow, is not only the largest and most valuable collection in the world, in possession of a private individual, but it also comprises the richest collection of North American plants in Europe. Here we find nearly complete sets of plants collected in the Arctic voyages of discovery, the overland journeys of Franklin to the polar sea, the collections of Drummond and Douglas in the Rocky Mountains, Oregon, and California, as well as those of Professor Scouler, Mr. Tolmie, Dr. Gairdner, and numerous other officers of the Hudson's Bay Company, from almost every part of the vast territory embraced in their operations from one side of the continent to the other. By an active and prolonged correspondence with nearly all the botanists and lovers of plants in the United States and Canada, as well as by the collections

judicious purchases, the contributions of his former pupils, especially from abroad, to his methodical habits, and to the welcome he gave to all botanists who desired to consult his collections. For the operation of mounting specimens, &c., he employed aids, of whom I remember two; the first, in about 1827, I think, was a native of Dundee, a keen algologist, James Chalmers by name, who prepared fasciculi of named Algae, in quarto form[1], in the disposal of which my father aided him. The other was Dr. J. Klotzsch, who spent some years as curator of the herbarium. Klotzsch was an excellent fellow, a devoted mycologist, and whilst at Glasgow would study no other branch of botany than fungi. During the summer and autumn months he frequently rose at 4 a.m. and made a long excursion collecting in the environs of the city. On these occasions his appearance excited great curiosity; he was short and stout, wore a green doublet and German peaked cap, his long hair flowed over his shoulders, a huge tin vasculum was strapped to his back, he carried a stout staff with a pickaxe head, and his English was very German. Meeting the rough factory hands and miners on their way to work he was often hustled and even assailed, when he defended himself with this weapon, and, being quick of temper, on one occasion felled with it a too rash tormentor. Klotzsch was the founder of the mycologic portion of the herbarium. Returning to Berlin, he took up the study of flowering plants, acquired distinction as a botanist, and became eventually Keeper of the Royal Herbarium, Berlin. The only other aids my father had in Glasgow were my mother, as amanuensis, and myself; for having been attracted to

of travellers, this herbarium is rendered unusually rich in the botany of this country; while Drummond's Texan collections, and many contributions from Dr. Nuttall and others, very fully represent the flora of our southern and western confines. That these valuable materials have not been buried, or suffered to accumulate to no purpose or advantage to science, the pages of the Flora Boreali-Americana, the Botanical Magazine, the Botanical Miscellany, the Journal of Botany, the Icones Plantarum, and other works of this industrious botanist, abundantly testify; and no single herbarium will afford the student of North American botany such extensive aid as that of Sir William Hooker.'

[1] Algae Scoticae. See Hook. Journ. Bot., i. 158.

botany from my childhood, much of my spare school and college time was devoted to the Herbarium.

In 1820 there were few botanists in Scotland to welcome the newly-appointed Professor, and of these only two were known to him personally, his old friend Mr. Charles Lyell[1], of Kinnordy, in Forfarshire, who had, however, abandoned the study of *Hepaticae* for that of Dante; and the Rev. Dr. Stuart, of Luss, with whom he had botanized during two of his Highland tours (see p. xiii). Others were Dr. Robert Graham, his predecessor in the Glasgow Chair, then holding that of Edinburgh; with him there was maintained a close correspondence till his death in 1845, chiefly concerning plants flowering in the Edinburgh Botanical Garden, many of which were figured in the 'Botanical Magazine'; Dr. R. K. Greville, LL.D., of Edinburgh, with whom he had corresponded when in Suffolk on the structure of *Buxbaumia aphylla*, and with whom, as associate, he published the 'Icones Filicum' and many papers on mosses and ferns; he died the year after my father, in 1866; Dr. Hopkirk, LL.D., F.L.S., of Glasgow, author of the 'Flora Glottiana' and 'Flora Anomoia,' who had taken the leading part in the formation of the Glasgow Botanical Garden; Captain Dugald Carmichael, F.L.S., of Appin, Argyleshire, who had been a brother medical officer with Robert Brown in a fencible regiment stationed in Ireland; and Dr. F. Buchanan-Hamilton, F.R.S., F.L.S.[2], of the Indian Medical Service, who after a long and active career in India, including for a short period the superintendence of the Botanical Garden of Calcutta, had succeeded to an estate near Callender, where he died in 1829. These had all been correspondents except the now-forgotten

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[1] Mr. Lyell died in 1849; retaining to the last his interest in botany, corresponding with my father on his publications, and responding liberally to the calls for aid and counsel from struggling botanical workers, and their widows and families.

[2] Author of 'An Account of the Kingdom of Nepal,' of 'A Journey from Madras through Mysore, Canara, Malabar, &c.,' and 'A Commentary on Rheede's Hortus Malabaricus' (Trans. Linn. Soc., vols. xiii, xv, xvi). He was the earliest explorer of the Flora of Nepal, and, after Rheede (in 1670), of Malabar. His very large collections were distributed by Wallich.

soldier-botanist Carmichael, of whom he had heard when staying with Sir Joseph Banks in 1820 from R. Brown, as a man who had visited the all but unknown and inaccessible island of Tristan d'Acunha in the South Atlantic, and had left no branch of its natural history unexplored. Captain Carmichael, then retired, was living in seclusion in a farm of his own at Appin, in Argyleshire, devoting his whole energies to investigating the cryptogamic flora, especially the Algae and Fungi, of his vicinity. Ten years subsequently my father published in the 'Botanical Miscellany' (ii, pp. 1, 258; iii, p. 23) a very interesting memoir of Carmichael, written by his friend, the Rev. Colin Smith, of Inverary, giving a full account of his military services, first as a medical officer, and latterly as a lieutenant and captain in his regiment, which was actively employed under Sir David Baird at the taking of Cape Town. The memoir gives long extracts from his journals on the botany, zoology, and physical geography of the countries around Cape Town and Algoa Bay, and of the islands of Mauritius, Bourbon, and Tristan d'Acunha, in respect of which one cannot but admire his powers of observation, and wonder how under the obstacles and discouragements of a soldier's life in those days he obtained the thorough scientific knowledge he displays, of the botany especially, of the several countries he visited. Of these latter Tristan d'Acunha was virgin soil, and of its natural history little is as yet known beyond what he recorded. The occasion of his visiting it was, that being at the Cape when orders were sent to take possession of it (as an eye over our prisoner Napoleon in St. Helena[1]), he obtained leave to accompany the expedition. This enabled him to spend between six and seven months in the island, which he devoted to its exploration. The result is a paper entitled 'Some Account of the Island of Tristan d'Acunha, and its Natural Productions[2],' by Captain Dugald

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[1] The knowledge of geography possessed by the War Office of those days must have been rudimentary.

[2] Transactions of the Linnean Society of London, vol. xii, p. 483. This important paper is overlooked in the otherwise very full history of Tristan d'Acunha given in The Narrative of the Cruise of the *Challenger* (vol. i, p. 241).

Carmichael, which contains amongst other matters a complete account of its flowering plants and ferns.

Soon after his arrival at Glasgow my father had a visit from Captain Carmichael, bringing with him a collection of the mosses of Appin. Of him he writes[1]: 'It was impossible not to be struck with the varied knowledge he possessed, for though in botany he took the greatest delight, yet with almost every subject, and especially such as bore any relation to his extensive travels, his mind was richly stored. It was in examining these minute productions (Fungi and Algae) that he spent almost the whole of his life after his retirement from active service. And though his attention was wholly confined to the parish in which he lived, he was so eminently successful that among the Fungi alone he detected more species than had been before described as native of the whole of Scotland. My last interview with him was in the summer of 1826, when I invited him to join an excursion to the Western Islands with the students of my class. He met us in our vessel immediately opposite his residence, when we proceeded to Mull and Skye; thence returning through the Sound of Mull we visited Fort William, Ben Nevis, and the majestic scenery of Glencoe.' Captain Carmichael died in the following year. The results of his labour in Scotland appear in Part II of the 4th edition of 'The British Flora,' devoted to Algae and Fungi. Two manuscript volumes in 4to, 'Algae Appinenses' and 'Cryptogamiae Appinenses,' preserved in the Library at Kew, testify to his knowledge and skill as a botanist, microscopist, and artist.

Very soon after the settlement of the herbarium and library in Glasgow botanists from all parts of Europe flocked to it, amongst whom the following eight made the most frequent and longest sojourns, some of them becoming collaborators with the owner: R. K. Greville, G. Bentham, Sir J. Richardson, G. A. Walker-Arnott, W. Wilson, the Rev. M. J. Berkeley, H. C. Watson, and W. H. Harvey. Mr. Bentham's first visit was in 1823, from which occasion he dated his permanent

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[1] Botanical Miscellany, vol. ii, p. 4.

adhesion to botany as an occupation for life. The next (in 1823) was Dr. (afterwards Sir John) Richardson, R.N., the companion of Franklin in his Arctic expeditions, through whom my father was made known to the Lords of the Admiralty, the Directors of the Hudson's Bay Company, and the chiefs of the Colonial Office, thus becoming the recipient of many herbaria made by the officers of these departments, and the author of works published under their authority. It further led to his being asked to recommend young medical men fond of natural history, from amongst his pupils especially, to embark in their services abroad.

In 1825 he first met Mr. G. A. Walker-Arnott, of Arlary, a member of the Scottish Bar, then living in Edinburgh. I think I am correct in saying that their meeting took place in Paris, when my father being taken ill was kindly attended to by this fellow-countryman, a stranger to him, who was staying in the same hotel. Mr. Arnott must then have been on his way to join Mr. Bentham in his exploration of the botany of the Pyrenees [1]. He was a mathematician of considerable attainments [2], and had published an important paper on the 'Classification of Mosses [3].' With him as collaborator were published the 'Botany of Beechey's Voyage,' 'Contributions towards the Flora of South America and the Pacific Islands,' and the sixth and seventh editions of 'The British Flora.' As Dr. Arnott, LL.D., he succeeded Dr. Balfour in the botanical Chair of Glasgow, and died in 1868.

In 1827 my father's correspondence commenced with W. Wilson, of Warrington, who paid many visits, sedulously studying the mosses of the herbarium, and exploring the Highland mountains, sometimes joining in the botanical class excursions. Latterly he volunteered a revision of the whole collection of Musci in the herbarium, thereby adding very

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[1] This resulted in the publication by Mr. Bentham of his Catalogue des plantes indigènes des Pyrénées et du Bas Languedoc. Paris, 1826.

[2] Author of two papers, 'On the Solutions of Experimental Equations,' and 'A Comparison between the Chords of Arcs employed by Ptolemy, and those now in use' (Tilloch's Phil. Mag., 1817 and 1818).

[3] Mém. Soc. Hist. Nat. Paris, 1825.

largely to its value. He co-operated in the publication of many papers on exotic mosses in my father's 'Journals of Botany,' and edited a greatly enlarged edition of the 'Muscologia Britannica' under the title of 'Bryologia Britannica.'

In 1828 my father first became acquainted with the Rev. M. J. Berkeley, of Kings Cliffe, Northamptonshire, the mycologist, who was then, I believe, on his way to visit Captain Carmichael in Appin. This led to a very intimate friendship, and repeated visits to West Park and Kew. Mr. Berkeley took the same interest in the Fungi of the herbarium as Mr. Wilson did in the Musci, and but for him this order of plants would never have attained its present pre-eminence; for his zeal induced my father to urge his correspondents in all parts of the world to collect fungi; with what success is shown by the richness of his herbarium, and the numerous papers on exotic genera and species of the order published by Mr. Berkeley in the botanical Journals, in the 'Transactions of the Linnean Society,' and many other works. Mr. Berkeley also contributed the volume on fungi to the third edition of Hooker's 'British Flora' (vol. v, p. ii of Smith's 'English Flora'), and, dying in 1889, he bequeathed his herbarium to Kew, together with the choice of his botanical library.

In 1830 Mr. Hewett Cottrell Watson, the most accomplished of British botanists, then resident in Edinburgh, requested permission to accompany the students of the botanical course on an excursion to the Breadalbane Mountains, for the purpose of ascertaining the altitudes affected by their plants. Thus commenced a very active and interesting correspondence between my father and this acute botanist, which led to the publication of many papers in the Journals conducted by the former, to the botanical expedition of the latter to the Azores, and indirectly to his valuable account of the Flora of that interesting archipelago[1] in Godman's 'Natural History of the Azores' (London, 1870).

In 1831 Mr. W. H. Harvey, of Limerick (afterwards Pro-

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[1] London Journal of Botany, vols. ii, iii, and vi.

fessor of Botany in the Royal Dublin Society, and Keeper of the Herbarium, and eventually Professor of Botany in Trinity College, Dublin), introduced himself by letter with specimens from two new localities of a West Indian moss (*Hookeria laete-virens*) found nowhere in the eastern hemisphere but the south and west of Ireland. It was answered by an invitation to Glasgow, which resulted in an intimacy that amounted to his being regarded as a member of the family.

Mr. (afterwards Dr.) Harvey took the same interest in the Algae of the herbarium as Wilson did in the *Musci* and Berkeley in the Fungi, besides augmenting it largely by contributions from the splendid collections made during his voyages to North America, Ceylon, Australia, and the Pacific Ocean, for the sole purpose of investigating their marine Floras. Many illustrations of his classical works 'Nereis Boreali-Americana,' 'Nereis Australis,' 'Phycologia Britannica,' and 'Phycologia Australis,' were lithographed by himself under my father's roof at Glasgow, West Park, and Kew. He died the year after the latter[1], when staying with my mother at Torquay.

I must not close this brief notice of my father's activity in encouraging others without an allusion to the solicitude with which he fostered my own aspirations to become a traveller and a botanist; the interest he took in my ambitious projects; the energy with which he aided me in overcoming every obstacle thrown in my way, and prevailed on the higher powers to grant me facilities and the necessary funds; and, last but not least, the liberality with which he helped me whenever other resources were exhausted. In this connexion I refer especially to four crises in my scientific career:—my appointment to accompany Sir James Ross in the Antarctic Expedition in 1839 (for which he supplied all my scientific outfit); my (unsuccessful) candidature for the Professorship

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[1] No fewer than ten of my father's botanical friends died within three years of his own end, including seven who were amongst his most intimate associates: Borrer, 1862; Boott, 1863; Lindley and Richardson in the same year (1865); Greville and Harvey, 1866; Arnott, 1868. The others were Burchell, 1863; Woods, 1864; Daubeny, 1867.

of Botany in Edinburgh University in 1845; my mission to India in 1847; and my appointment as Assistant Director of Kew in 1855. Add to these benefits, the legacy of his herbarium and library, and the truth of the saying 'one soweth, another reapeth' forcibly applies.

The works published by my father when in Glasgow are very numerous. A complete list of them, with details regarding the more important, will be given at the end of this sketch. They may be grouped under four headings—British Botany, American Botany, Miscellaneous Works, and Serials.

In the British Botany there was the 'Flora Scotica,' the new edition of Curtis's 'Flora Londinensis,' four editions of the 'British Flora,' and many contributions to a knowledge of British plants in the volumes of his botanical Journals.

The more important works on American Botany were the 'Flora Boreali-Americana'; Botanical Appendices to the Narratives of Sir E. Parry's three last voyages to the Polar Seas. There were also, in his botanical Journals, descriptions of T. Drummond's and of Geyers' United States and Oregon plants, and articles on the botany of Peru and Chili; and, in conjunction with Arnott, the 'Flora of South America and the Pacific Islands.' Also many American plants are described in the 'Botany of Beechey's Voyage' by himself and Dr. Arnott, and in his 'Icones Plantarum.'

Under Miscellaneous Works may be classed as most important Greville's and Hooker's 'Icones Filicum,' and the commencement of an 'Enumeration of all known Filices and Lycopodiaceae' by the same authors in the 'Botanical Miscellany'; the 'Botany of Captain Beechey's Voyage to Behring's Sea, the Pacific Ocean, and China' by himself and Arnott; the third edition of Woodville's 'Medical Botany'; the botanical articles in Murray's 'Encyclopedia of Geography,' and the first three volumes of the 'Icones Plantarum,' or figures and descriptions of new or rare and otherwise interesting plants contained in his herbarium, with 300 plates by W. Fitch[1].

[1] Walter Fitch, F.L.S., who by his artistic talents contributed so largely to

Of the Serial Works the first was the 'Exotic Flora,' inspired by the interest he took in the Glasgow Botanical Gardens. It was commenced in 1823 and concluded in 1827, with 232 coloured plates, from drawings mostly executed by himself, of exotic cultivated plants. It was followed in 1827 by his undertaking the authorship of the 'Botanical Magazine.' Of this work thirteen volumes were issued from Glasgow, the drawings for the first ten of which (about 720) were by his own pencil.

In the same year (1827), finding that his extensive correspondence with botanists and travellers abroad provided him with information of great value that might otherwise never see the light, and that his herbarium was at the same time teeming with plants unknown to science, my father formed the plan of himself editing a periodical for the diffusion amongst botanists of the information obtained from these sources. As a model he took Konig and Sims's 'Annals of Botany,' of which two volumes only had been published (London, 1805–6). He never stopped or stooped to calculate the time, worry, and cost that this undertaking would entail upon him, which occupied him for the next thirty years of his life; for he had throughout no assistant editor, and was dependent solely on my mother, and at intervals on myself when at home, for aid in proof-reading, &c. The heavy correspondence it entailed was conducted by himself alone.

Including the continuation of the series issued from Kew, these periodicals embrace twenty-eight volumes with 548 plates, of which seven volumes with 247 plates, the greater number of them drawn by himself, were issued from Glasgow. These were the 'Botanical Miscellany,' three volumes with 152 plates (1830–3), the 'Journal of Botany,' two volumes with 44 plates (1834 and 1840), and the 'Companion to the Botanical Magazine,' two volumes with 51 plates (1835–6).

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the value of my father's works, was, when he entered the service of the latter (1834), a pattern-drawer in a calico-printing establishment in Glasgow, aged 18. His earliest work was for the Botanical Magazine and Icones Plantarum. He died at Kew, in 1892, in the receipt of a pension from the Crown (Civil List).

In the interval between the publication of the 'Companion to the Botanical Magazine' and the resumption of the 'Journal,' he undertook the editorship with Sir William Jardine and others of Taylor's 'Annals of Natural History,' which for three years (1837–40) was the recipient of much of his botanical matter; but the latter became too copious to be included in the numbers of the 'Annals,' and, the result proving otherwise embarrassing, that editorship was abandoned. After leaving Glasgow for Kew he resumed the 'Journal,' three volumes (1840–2) of which were followed by the 'London Journal of Botany,' seven volumes (1842–7), and that by the 'Journal of Botany and Kew Garden Miscellany,' nine volumes (1849–57).

Regarding the conduct of this series of journals under their different titles, it is impossible to overrate the value of the assistance and encouragement which he received throughout in contributions from fellow botanists at home and abroad; especially Arnott, Bentham, Berkeley, Harvey, W. Wilson, Hewett Watson, and Asa Gray: and this though, owing to the limited circulation of the volumes, the publishers (of whom there were consecutively seven) gave the contributors neither the work nor copies of their papers, except on payment. The editor contented himself with one copy, and gave his services, and in many cases the drawings on stone, gratuitously.

As a contribution to the history of botany during three decades of the nineteenth century these periodicals were unique; no period or subsequent decade of that century can show so rich a store of valuable botanical material. Amongst their most interesting contents are the letters from correspondents abroad—Jameson and Hall from Ecuador, Douglas from North-West America, T. Drummond from Canada and the United States, Spruce from the Amazon, Peru, and the Pyrenees, Purdie from Jamaica and New Grenada, Bromfield from the United States, Geyer from Oregon and the Rocky Mountains, Seemann from Panama and the North Pacific, Gardner from Brazil, Walker from Ceylon, Stocks from Sind and Beluchistan, A. Cunningham from New South Wales, Fraser from Queensland, J. Drummond from South-West Australia, von Mueller from Victoria and tropical Australia, and many others. The articles headed 'Botanical Information' and 'Notices of Books' are full of instructive information written for the most part by himself.

Towards the end of his Glasgow life my father resumed a systematic study of ferns, which he had begun with Greville soon after his arrival there, the first result of which was the commencement of an 'Enumeration of all known Ferns,' published in the 'Botanical Miscellany.' The issue in parts of Hooker and Bauer's 'Genera of Ferns' was begun in 1838; it originated in his having been shown the beautiful analyses of many genera of the order by the veteran botanical artist Francis Bauer[1], who offered the loan of these for publication to my father; not that the order had in the meantime been neglected by him, as is proved by the numerous genera and species described and figured in his journals, in the 'Icones Plantarum' and other works, and by his publication of J. Smith's 'Genera of Ferns[2].' As I propose to give in an appendix to this sketch of his life a complete account of my father's works, I shall not further dwell here on those devoted to ferns.

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[1] Francis Bauer, an Austrian by birth, came to England in 1788, and was through Sir Joseph Banks's influence attached to the Royal Gardens, Kew, with the title of Botanical Painter to the King. He resided in a cottage on Kew Green, where I visited him with my father in 1835, when he showed us the original daguerreotype plates of Niepce. He died at Kew in 1840, aged eighty-two, in the enjoyment of a pension left him by Banks. A handsome tablet in Kew Church records his career, and a fine oil painting of him hangs in the Kew Gardens Museum, No. 1. His published works are not numerous; the principal are, besides the Genera Filicum, Illustrations of Orchideous Plants, 20 plates, with a preface by Lindley; Strelitzia depicta, with 4 plates; and the plates (20) in Aiton's Delineations of Exotic Plants cultivated in the Royal Gardens of Kew, a huge folio (1796). His brother Ferdinand, equally celebrated as a botanical artist, accompanied Brown in that capacity on Flinders's survey of the coasts of Australia (1802–5).

[2] 'An Arrangement and Definition of the Genera of Ferns, with Observations on the Affinities of each Genus,' by J. Smith, Curator of the Royal Gardens, Kew (Journ. Bot., iv. 38–147; Kew Gard. Misc., i. 419, 659, ii. 378).

CHAPTER III.

WEST PARK AND KEW, 1841–1865.

DURING his occupation of the Professorship of Botany in Glasgow University my father, feeling keenly his severance from the scientific society of London, was always on the look-out for a congenial position there, even if of less emolument than that which he held. The Professorship of Botany in the newly created University College of London (then entitled London University) was pressed on him by Lord Brougham, but the possibility of an appointment to the Royal Botanic Gardens of Kew had for some years eclipsed all other prospects. Nor were his aspirations in this direction unreasonable, for over and above his botanical qualifications he had inherited a taste for cultivating plants, encouraged by ten years' experience in his own garden, greenhouse, and stove at Halesworth ; he had twenty years' of good work in and for the Royal Botanic Gardens of Glasgow, and had been for thirteen years author of the 'Botanical Magazine,' a serial devoted to the illustration and description of cultivated plants. Added to this was the fact that Mr. Aiton, who as 'Gardener to Her Majesty' had controlled the Gardens of Kew since 1793, was approaching the age for retirement. Meanwhile the Kew Botanic Gardens, which for upwards of half a century had ranked as the richest in the world, had since the deaths, almost contemporaneously, of King George III and Sir Joseph Banks, been officially cold-shouldered, and had retrograded scientifically. Their early history is summarized in the official 'Guide-book to the Royal Gardens,' and need not be repeated here. The following is a *résumé* of the circumstances that led to their transference from the private property of the Sovereign to the nation as a scientific establishment under my father, who came forward as a candidate for their control on the first hint of a change in their management being contemplated.

Soon after the accession of Her late Majesty a revision of the royal household became necessary, and the question of retaining the Botanic Gardens at Kew as a royal appanage having to be considered, a Commission was appointed by Parliament to report upon them. The Commission, the chairman of which was Dr. Lindley, reported favourably on the whole, and concluded with the recommendation that they should be retained and extended, in the following words:—'The importance of Botanic Gardens has for centuries been recognized by the governments of civilized states, and at this time there is no European nation without such an establishment except England. The wealthiest and most civilized country in Europe offers the only European example of the want of one of the first proofs of wealth and civilization. There are many gardens in the British colonies and dependencies, as Calcutta, Bombay, Saharunpore, the Mauritius, Sydney, and Trinidad, costing many thousands a year: their utility is much diminished by the want of some system under which they can all be regulated and controlled. There is no unity of purpose among them; their objects are unsettled, their powers wasted from not receiving a proper direction; they afford no aid to each other, and, it is to be feared, but little to the countries where they are established; and yet they are capable of conferring very important benefits on commerce, and of conducing essentially to colonial prosperity. . . . A National Botanic Garden would be the centre around which all these lesser establishments should be arranged; they should all be placed under the control of the chief of that garden, acting with him and through him with each other, recording constantly their proceedings, explaining their wants, receiving supplies, and aiding the mother country in everything useful in the vegetable kingdom; medicine, commerce, agriculture, horticulture, and many branches of manufacture would derive considerable advantage from the establishment of such a system. . . . From a garden of this kind Government could always obtain authentic and official information upon points connected with the establishment of new colonies: it would afford the plants required on these occasions, without its being necessary, as now, to apply to the officers of private establishments for advice and help. . . . Such a garden would be the great source of new and valuable plants to be introduced and dispersed through this country, and a powerful means of increasing the pleasures of those who already possess gardens; while, what is far more important, it would undoubtedly become an efficient instrument in refining the taste, increasing the knowledge, and augmenting the amount of rational pleasures of that important class of society, to provide for whose instruction is so great and wise an object of the present administration.'

Dr. Lindley's recommendations as embodied in the Report having become widely known, enthusiastic advocates of them soon made themselves heard, and a memorial urging their adoption, drawn up by the Linnean and Horticultural Societies and the University of London jointly, was addressed to the Government, and transmitted through the Treasury.

But to carry out such a scheme was not so simple a matter as at first sight appeared. There were many conflicting interests in high places to be consulted and conciliated during the three years' interval that elapsed between the sending of the Report to the Treasury and its presentation to Parliament. These were the Lord Steward (Earl of Surrey), under whose control the Royal Gardens were placed; the Commissioners of Woods and Forests, the Chancellor of the Exchequer, and Parliament itself. The initial difficulty arose from the position of the Botanic Gardens. These, though comparatively small, occupied a very important site in the royal demesne at Kew, by far the greater part of which latter, including a royal palace, were to be under any circumstances retained as such. It was not the Botanic Garden only that was wanted, but the attached Arboretum and space for indefinite extension, and hence inevitable interference with the amenities and privacy of the palace and its approaches. Even more formidable obstacles were the large expenditure which would have to be incurred on creating such an establishment as Dr. Lindley had outlined, and the best means of controlling it.

In the above-cited interval the fate of the Botanic Gardens was all but sealed, as the following extract taken from a little work, the author of which was a witness of the occurrence which he describes, proves:—'In the autumn of 1839 the Lord Steward, then Lord Surrey, who in virtue of his office had the whole management of the Royal Gardens, paid frequent visits to the Botanic Gardens, always accompanied by the superintendent of the kitchen garden, and carefully examined the greenhouses and pits; and it became known that it was his intention to convert them into vineries and pine stoves, and that the plants had been offered to the Horticultural Society for their garden at Chiswick, and also to the Royal Botanic Society for their garden at Regent's Park; but the offer was in both cases declined. The vinery scheme was, however, intended to be carried out, and on February 18, 1840, the kitchen gardener informed me that he had received instructions from Lord Surrey to take possession of the "Botany Bay House" and convert it as soon as possible into a vinery, and that the "Cape House" was to follow; and to enable him to do so he was to destroy the plants[1]. This becoming known to the public led to articles in the public journals condemning the scheme as being a disgrace to the nation. This had the desired effect, and Lord Surrey's scheme was abandoned[2].'

[1] The collections of Australian and S. African plants were unique. Some of the specimens were half a century old.

[2] Records of the Royal Botanic Gardens, Kew, by John Smith, ex-Curator. London, 1880. That the Royal Botanic Gardens maintained any position as a scientific establishment in the interval between the death of Sir Joseph Banks in 1820 and the appointment of the new Director in 1841, was wholly due to the unaided exertions of Mr. Smith, who, from being a foreman under Mr. Aiton, became Curator from 1841 till 1864 under my father. He kept up the correspondence with the colonial Gardens in the West Indies, S. Africa, and Australia, himself sowing the seeds and raising the plants that these contributed, and carefully recording their scientific names, habitats, and donors' names. For

Meanwhile unobtrusive but powerful influence was being exerted in favour of Dr. Lindley's recommendations by John, sixth Duke of Bedford, a nobleman distinguished for his devotion to botany, horticulture, and agriculture, who delighted in having the plants in his gardens at Woburn Abbey scientifically classified and named, as objects for his own gratification and study, and as materials for the production of botanical works of high scientific value, which he had printed and distributed at his own cost[1].

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a notice of his life and labours see vol. ii, p. 429 of these 'Annals,' where it is stated that the characters of twenty new genera of ferns published in Hooker and Bauer's Genera of Ferns, are by him. But except *Ochropteris*, only sub-genera or sections of genera of ferns are there referred to.

[1] The services rendered to botany, horticulture, and agriculture by the sixth Duke of Bedford have been veiled through the suppression of his own personality in all he undertook for the encouragement of science and art. They were known well to few besides my father, whose botanical reputation the Duke recognized as early as 1817, and with whom he corresponded actively during his later years. Besides contributing liberally to the botanical missions of Schomburgk in Guiana, Purdie in New Grenada, Gardner in Brazil, Drummond in Florida and Texas, Tweedie in Argentina, Lippold in Madeira, and Cuming in Luzon, he established at Woburn a *Hortus gramineus*, an *Ericetum*, a *Salictum*, and a *Pinetum*, all on a scientific basis; and during his last illness he was forming a collection of Cacti, of which he had 450 species, and was contemplating an *Arboretum*. The following works were due to his munificence :—Hortus Gramineus Woburnianus, a folio volume of specimens, with an account of the results and experiments on the produce and nutritive qualities of different grasses and other plants used for the foods of the more valuable domestic animals; instituted by John Duke of Bedford, pointing out the kinds most profitable for permanent pasture, irrigated meadows, dry and upland pasture and alternate husbandry, with characters of the species and varieties, by G. Sinclair, gardener to his Grace.' Ed. i appeared in 1816; ii in 1825; iii in 1838.

Hortus Ericeus Woburnensis, a catalogue of 400 heaths, with four coloured plates, four of views, houses, and plans, and two of schemes of colour by Sir G. Hayter.

Salictum Woburnense, a catalogue of the willows in the Woburn collection, with coloured plates and descriptions by James Forbes, gardener to his Grace, roy. 8vo, 1829 (160 species and varieties are included).

Hortus Woburnensis, a descriptive catalogue of upwards of 6,000 plants cultivated at Woburn Abbey, with a view of the Abbey, twenty-six plates of plans of houses and beds, and brief descriptions of the species, by James Forbes, 1833.

Journal of a Horticultural Tour on the Continent, taken under orders of the Duke, in Hamburgh, Germany, Belgium, Bavaria, and France, by James Forbes, 8vo, 1837. It resulted in the acquisition of 600 new species to the Woburn garden.

Pinetum Woburnense, a catalogue of Coniferous plants in the Woburn collection, Long before the issue of Dr. Lindley's Report to the Treasury the Duke, who knew the Gardens well, had entertained the hope that they might one day become the nucleus of a botanical establishment worthy of the nation ; and in 1834, on an (unfounded) rumour of coming changes in their management being circulated, he warmly impressed upon his most influential friends my father's claims to be employed in them. When, therefore, in 1838, Dr. Lindley's Report came to his knowledge he wrote to my father expressing his satisfaction with it, entirely agreeing in its recommendations, and adding: 'though the outlay of restoring the Gardens to their original design and intention must of course be considerable, he should nevertheless think that no House of Commons would refuse a grant for an object so important in a national point of view.' In a letter dated Geneva, March 24, he writes: 'I look with hope and confident expectation to the prospect of seeing Kew Gardens and the whole of the surrounding demesne converted into a great national establishment, which may not only rival but be superior to the *Jardin des Plantes* at Paris. I have written to some influential friends to interest them in the subject.' And in another letter, alluding to his being solicited to patronize the establishment of a Garden in London, he says: 'I have uniformly refused, thinking that it would interfere with the more important plan of a great National Botanic Garden at Kew. I do not know if you are acquainted with the locale, but there is a large space behind the present Garden, now occupied as an unprofitable lawn and useless pasture, which is capable of being converted into a range of Gardens more useful as well as more ornamental than those of Paris.'

The Duke continued his efforts to induce the Government to give effect to the recommendations of the Report till within four days of his death[1]. This occurred on October 20, 1839,

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systematically arranged and described by James Forbes, with sixty-seven coloured plates, roy. 8vo, 1839. In my father's collected correspondence there are 200 letters from the Duke almost exclusively on botanical subjects.

[1] His last letter to my father, written on October 16, the day before he was

after earnestly commending the measure to the care of his two sons, the seventh Duke, Francis, and Lord John (afterwards Earl) Russell, who was then in the ministry; and faithfully the sons carried out their father's wishes.

On March 3, 1840, reports being still in circulation that the Government intended to abolish the Botanic Gardens, the Earl of Aberdeen in the Upper House rose to inquire if such was the case, adding that he considered that establishment to constitute a part of the state and dignity of the Crown, which ought by no means to be alienated from it. He was answered by Viscount Duncannon that there was not only not the least intention to break up those Gardens, but there never had been such intention. To this Lord Aberdeen rejoined that he could assure the noble Viscount that an offer of the plants had been made to the Horticultural Society of London, and that the Society refused the offer, thinking it would be injurious to the public interest that the establishment should be broken up. Viscount Duncannon replied that though the care of the Gardens was not in his department, he had the authority of the Lord Steward for stating that no intention of breaking them up now existed.

It cannot but have been a source of regret with the Duke of Bedford's family and friends that he should not have lived to greet this, the dawn of the realization of his long-cherished wishes and hopes, together with the announcement which soon followed, that Her Majesty had graciously relinquished the Botanic Gardens and Arboretum of Kew, with the view of their being available for the public good.

On March 31, 1840, the Gardens, Pleasure Grounds, and Deer Park of Kew were (with the exception of about 20 acres surrounding a Swiss cottage) transferred from the Lord Steward's department to the Commissioners of Woods and Forests, the chief of whom was Lord Duncannon, now virtually pledged, by his answer to Lord Aberdeen, to maintain the Botanic Gardens. But that nobleman being firmly opposed

stricken with paralysis, ends with 'I have written to-day to Lord John to urge him strongly not to relax his efforts in pursuit of this grand object.'

to any enlargement of them and to any further expenditure upon them, all hopes of their forming the nucleus of an establishment worthy of the nation appeared, for the time at any rate, to be frustrated. The view taken by the Government of the expenditure and the responsibilities to be incurred in establishing the Gardens on a national footing, may be learned from a Report addressed to the Treasury by the Commissioners of Woods and Forests, signed by Lord Duncannon and other members, dated April 24, 1839. It points out that Parliament must find, in addition to the present annual expenditure on the Botanic Gardens, £20,000 for new works; and goes on to say, that though the services of the Board are available for the execution of the new works and supervision of the annual expenditure, neither it nor its officers can efficiently assist in the scientific management of the establishment and its adaptation to useful purposes; adding that such management and control would be most properly invested in trustees to be named by Her Majesty and to consist of persons holding high office in the State, and others at the head of institutions in the metropolis for education and science, as suggested in the Report of the Committee[1].

It is difficult to see how £20,000 could be profitably expended on new works in so confined an area as the Botanic Gardens then occupied.

After the Bedford family, Lord Monteagle, when, as Mr. Spring Rice, he was Chancellor of the Exchequer, was the most powerful advocate for the retention of the Botanic Gardens and for my father's being placed at their head; but at that particular time the national finances were in a straitened condition, and he could not propose a vote in the House of Commons for a Kew subsidy; nor could he influence Lord Duncannon in favour of the Botanic Gardens. Writing from Glasgow to Mr. Turner in December, 1840, my father says: 'From Lord Monteagle, indeed, I hear that the obstacles to my having an appointment at Kew are insurmountable.

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[1] To which Report this refers does not appear. It is certainly not that of February, 1838, drawn up by Dr. Lindley, which contains no such recommendation.

My vexation, however, would have been greater than it is, had I not almost on the same day received a long and most kind letter from the Duke of Bedford, from which it does appear that I may now safely leave the matter in the hands of Lord John Russell; and I think I may infer from one or two parts of the Duke's letter, that however influential Lord Monteagle may have been when I first applied to him, when he was Chancellor of the Exchequer, he is now, being out of place, out of power. Lord Monteagle's letter was so decisive that I thought it right to thank him for all he had done in my behalf, and to close altogether the correspondence as bearing on Kew; and I have told the Duke that I should leave the matter in his brother's hands.'

The following letter from the Duke further explains the situation:—

'WOBURN, *December* 5, 1840.

. . . 'With respect to yourself and your own views and wishes, I do not like to be too sanguine or to hold out expectations that may not be realized, since we all know how much there is often between the cup and the lip, but I can give you some information which you will be pleased to hear. Lord Melbourne and my brother are here, and yesterday I had a full conversation with them and Lord Duncannon after breakfast on the subject in question. The result is that my brother, who is in truth your best friend, has desired Lord Duncannon to give him in writing a statement of the expenses that would be incurred to the public or to the Woods and Forests by your taking the place of Mr. Aiton at Kew. If that statement is satisfactory to him, which I have no doubt it will be, after what you stated to me in your letter of the first, he will himself prepare the matter to go to the House of Commons. I am sure from the decided manner in which he has taken it up that he will go through with it, if nothing unforeseen arises. In short, he will take it upon himself to make the proposition he is disposed to do in a way that justifies me in saying that he is your *best friend* in this matter; but I beg you to consider this as confidential.

'I have now got to the end of a long letter, written in great haste, but I trust I have answered all your points satisfactorily.

'Yours faithfully,
'BEDFORD.'

The continuation of the proceedings is best described in the following letter to Mr. Dawson Turner:—

'London, *January* 24, 1841.

'I had received two letters from the Duke of Bedford, telling me how actively his brother Lord John was engaged in my interest in respect of Kew; and together with the last of them, one from Lord John, or rather from his private secretary, Lord E. Howard, written on the fourteenth, sent to me in Scotland, requesting that I would see Lord John in Downing Street the middle of this last week. I therefore felt it my duty to start immediately (from Jersey), and there was fortunately a vessel about to sail on Friday morning about 8 o'clock in which I embarked. We did not reach Southampton till nearly two on Saturday morning (yesterday), and the earliest train I could take was eight, and then I was obliged to leave my luggage in the Custom House, which I am sorry to say has not yet followed me. All dirty as I was I called in Downing Street, and had soon after an interview with Lord John, who seemed pleased with the promptitude with which I had come, and said he thought it much better that we should talk than write on this subject of Kew. He then again asked my opinion of Lindley's estimate[1], and for how much less expense the Garden could be carried on. I told him, knowing that economy was a great point with Lord Duncannon, that if, as I understood, £3,700 a year was now expended upon the Gardens, irrespective of Aiton's salary, I should feel well satisfied to conduct them with that income, feeling that with zeal and energy a great deal might be done which money could not buy. He asked what accommodation I should require on account of my herbarium and library (which he seemed duly to appreciate), which with that and my small salary was all the additional expense to be incurred. If, then he said, the £3,700 a year now paid from the Civil List did include Aiton's salary, he should have no hesitation in asking the House of Commons for £1,000 a year to cover that, and upon that ground the difficulties he thought might be removed. He further told me that Lord Duncannon had a serious objection to any additional ground being taken from the adjoining parks.

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[1] This refers to a communication between Dr. Lindley and the Treasury on the subject of the cost of making Kew a botanical establishment worthy of the nation.

Then I said, "There are eighteen acres, let us see what can be done with them." "Now then," he added, "you had better see Lord Duncannon" (with whom, as with Lord Melbourne, he has had frequent communications). I told him I did not know him, and would be glad of a line from him. "Say I begged you might have an interview." I called, sent up my card with the above message, but the answer was, "His Lordship is very busy, and will be so busy on Monday and Tuesday that he cannot see you till Wednesday." This is always the kind of reception I have met with in attempting to see Lord Duncannon [1]. I am sure that with him, in reality the most influential man connected with Kew, there are obstacles that Lord Monteagle was justified in considering "insuperable." I believe more than ever that Lord Duncannon's great *desire* is to abolish the Gardens and save the expense to the Civil List. If he is determined on this I then think that Lord John will appeal to Parliament, for the Duke of Bedford was very explicit in assuring me that if his brother failed in one way he was prepared to try another.'

It was not till the following March that my father was officially informed that the Treasury had sanctioned his being appointed Director of the Botanic Gardens at Kew, with a salary of £300 and £200 allowance for the rent of a house. On the 26th of that month Mr. Aiton, under instructions from the Commissioners of Woods and Forests, transferred the Botanic Gardens and Arboretum to the new Director, reserving all printed books and drawings as being his private property, and all journals [2], accounts, correspondence,

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[1] More than a month elapsed before he could obtain an interview with Lord Duncannon, and then only through his having been introduced at a breakfast party to one of the Commissioners, Mr. Milne, who arranged the meeting for him. He found his lordship, he writes, very communicative; he told him of the difficulties and obstacles, but that they were not insurmountable, that he would with the greatest pleasure further all Lord John's views to the utmost of his power, and that all he wished was, that there should be no more ground taken into the Gardens, and that the Civil List should not be further burthened.

[2] The journals, &c., were for the most part, I believe, transferred to the Commissioners on the death of Mr. Aiton, who had retained his official residence, and they are now at Kew. The collection of drawings, made under Mr. Aiton's supervision, was subsequently presented to the Royal Gardens by Mr. Atwell Smith, a relative of Mr. Aiton. There had been in the office a considerable herbarium of garden plants and of others made by collectors sent from the

and other documents as not being the property of the Commissioners. On April 1, 1841, my father received his commission, the acceptance of which was regarded by his friends as a very insecure foundation on which to build the object of his ambition, a Botanic Garden worthy of the nation. But he was confident of the support of the scientific public in whatever he should undertake, and, I suspect, of that of more than one of the Commissioners of Woods and Forests.

The next step was to find a residence within a reasonable distance from the Gardens. There was none to be had within two-thirds of a mile, where, in the adjoining parish of Mortlake, there stood a commodious three-storied many-roomed building, of which he took a lease. It was pleasantly situated on 7½ acres of ground with some fine trees that stretched down to the Thames, had a walled garden, orchard, stables, and coach-house, and was in good repair. It bore the name of Brick-stables, for which its owner, the possessor of large property in the vicinage, substituted that of West Park[1].

The translation from Glasgow to West Park occupied my father for three months, during which he was heavily and painfully handicapped by the absence of my mother, who was nursing a dying daughter in Jersey, and the illness of his father, who was nearer ninety than eighty years of age, and had lived with him for ten years. His only surviving son was serving in the Antarctic Expedition under Captain (afterwards Admiral Sir James Clarke) Ross. There being no railroad available in those days, he hired a smack for the conveyance by sea of his furniture, household goods and gods, herbarium and library, from Glasgow to London, where they were put into lighters and landed on the banks of the Thames at West Park itself. Previous to this he had lightened his library by the sale of 1,000 volumes, chiefly of classics, Delphine, Aldine, and Elzevir editions, collected in the middle of the previous

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Gardens to Australia, the Cape, &c., but these had already been sent to the British Museum.

[1] West Park has disappeared. Its former site is occupied by the sewage works of Kew and Richmond.

century by his godfather, Mr. Jackson of Canterbury. The cost of the move was about £300, his first year's salary.

Early in July he was settled at West Park, where the drawing-room, ante-drawing-room, and study, were shelved from floor to ceiling and filled with books, and five rooms were occupied with the herbarium.

Nothing was allowed him for the conveyance and fittings necessary for these indispensable working materials[1], which he kept up mainly at his own cost, for the use of the establishment, for twenty-four years.

On entering upon his duties under the Commissioners of Woods and Forests the new Director was cordially welcomed, and to his surprise and gratification found that he had a free hand, and promise of favourable consideration in projecting improvements in the Botanic Gardens. His plan of operations is tersely and best given in his first Report presented to Parliament on the condition of the Gardens, which begins with, 'Having no instructions for my guidance I determined to follow the suggestions of Dr. Lindley's Report.' Meanwhile Lord Lincoln (afterwards fifth Duke of Newcastle) had succeeded Lord Duncannon, and in him, Mr. Milne, the Honourable C. Gore, and Mr. Philipps, secretary to the Board, he found gentlemen as interested as himself in the development of the establishment, who made frequent visits, going into every detail of garden works, and giving much of that 'efficient assistance in scientific management and adaptation to useful purpose' which their former Chief Commissioner had declared the Board to be incapable of affording.

To give a clear account of the additions made and improvements carried out in the establishment of Kew, it will be convenient to consider them as far as possible under the four heads of Botanic Gardens proper, Pleasure Ground or Arboretum, Museum, Herbarium and Library.

Botanic Gardens proper. The first recommendation of the new Director was that these should be open to visitors on

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[1] In Dr. Lindley's Report, the necessity of a herbarium and library for the performance of the Garden duties was indicated.

week-day afternoons throughout the year ; of which privilege upwards of 9,000 persons availed themselves during the remaining nine months of the year[1]. The next, in 1842, was that the permission of Her Majesty should be asked to add a few acres of the Pleasure Ground to the old Arboretum for the purpose of opening a new entrance[2] to the Gardens from Kew Green. This was graciously granted, as were the far larger areas from time to time asked for, of which the next (in 1843) was for forty-eight acres, to afford sites for a new Pinetum, and for the erection of a Palm House far exceeding in dimensions any previously constructed.

In 1846 the Royal Kitchen Gardens, which had remained under Mr. Aiton's management, were annexed to the Botanic Gardens. They occupied an area of about fifteen acres skirting the Richmond Road. A good-sized building used as a storehouse for fruit stood on this site, together with a large vinery and several forcing-houses, frames, melon and other pits. The vinery and some of the latter were in such disrepair as to be condemned, others were retained ; but a considerable area being provided with excellent garden soil was devoted to the formation of a new collection of hardy herbaceous plants arranged according to the Natural System. This, according to a printed catalogue drawn up by Mr. Niven, foreman of the department, in 1853, contained about 5,500 species, a number no doubt swollen by the admission of half-hardy plants, varieties, and synonyms. The first hardy herbaceous collection in the Royal Gardens was formed in 1760, near the Temple of the Sun. It was an acre in extent, contained 2,712 species, and was called the Physic Garden. According to the first edition of Aiton's *Hortus Kewensis* (1789), there were about 2,824 hardy herbaceous plants cultivated in the Royal Botanic Gardens, and in the second edition (1810–1813) 3,946 species.

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[1] In the last year of his Directorship (1865), Sundays having in the interim been included with the open days, 73,307 persons were admitted. In 1883 the numbers had risen to 1,240,489.

[2] The noble gates erected on this spot in 1845 are from designs by Decimus Burton, F.R.S.

Of the plant-houses existing in 1841 about ten were of considerable size, and of these two only, an Orangery and the architectural Conservatory near the entrance gates, are still (1902) standing. The Orangery was built by Sir W. Chambers in 1761 for wintering orange trees. It is the first plant-house of any importance erected in the grounds, and had been latterly used as a conservatory for the reception of such trees as had overgrown the height of the New Holland House. It was so occupied till the completion of the Temperate House in the Arboretum in 1863, when its contents were transferred to the latter, and replaced by Museum objects, as will be more fully described under Museums. It was almost the only remaining house heated by flues under the floor, the dry air from which was very unfavourable to the plants, as was the want of light.

The other permanent building was the architectural Conservatory near the entrance gates. It is one of a pair erected in 1836, the other is at Buckingham Palace. It was heated on Perkin's system of innumerable coils of pipes, the size of ordinary gas-pipes, charged with steam[1] from twelve furnaces in the vaults. It was used for the same purposes as was the Orangery, and its contents were similarly disposed of at the same time, when these were replaced by tropical plants, chiefly small palms, tree-ferns, and aroids, not a few of which are still flourishing. With regard to the other old houses, some were destroyed and better provided, others were improved and added to, and the majority had the old system of heating by hot air from flues passing under the floor replaced by that of hot-water pipes. In the case of six of these houses the flues from their furnaces were conducted into one shaft, thus contributing much to the cleanliness of their surroundings. Two span-roofed houses were doubled, one for tropical, especially economic plants, the other for Australian and New Zealand ones.

The building of the great Palm House was commenced in 1844 from the designs of Decimus Burton, F.R.S., and the

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[1] At a later period this system was replaced by one of hot-water pipes.

Director. It was completed in 1848, together with the campanile, which was intended to serve the purposes of a smoke-shaft and water-tower, and the ornamental terrace facing the water. The flues of six furnaces which heated the boiler of the hot-water apparatus were carried in a tunnel to the base of the campanile, where there was a furnace for the consumption of the smoke and for securing a powerful draught[1]. The tunnel also served for the conveyance of fuel from the coke yard by the Richmond Road to the furnaces, thus avoiding the necessity of carting over the lawns. The dimensions of this building are—length 362 feet, centre 262 feet by 100 wide, and 66½ feet in height; the wings are each 50 feet long and 30 feet in height. It is glazed with about 45,000 square feet of sheet glass. A gallery runs round the central portion at a height of 30 feet; there are 19,500 feet of hot-water pipes 4 inches in diameter. It is, except the Crystal Palace and subsequently erected Temperate House at Kew, I believe, the largest glass house in existence.

At this time the activity of the Commissioners of Woods and Forests was far-reaching, for it was in their contemplation to annex the Chelsea Botanic Gardens to Kew and to form a Medical Garden for the use of the colleges and schools of London. Referring to these schemes in letters to Mr. Dawson Turner, my father in 1843 writes in respect of the formation of a Medical Garden: 'It will be attended with many difficulties, but I shall encourage it, and have written a long memorial to the Board about it.' In 1845 he writes: 'I have to write to the "Woods" on an affair to be laid before the Queen respecting a Medical Garden adjoining the Botanical Garden.' And again in 1845: 'My Report on the Gardens is printed by the House of Commons, and my letter on the removing Chelsea Garden to Kew. Lord Lincoln thinks it will result

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[1] This arrangement proved unsatisfactory and had to be abandoned. The flues from the furnaces are now led to two shafts in the centre of the wings of the house, the projecting mouths of which are masked by octagon lanterns. This effected both a great saving of fuel and an increase of heat, but it was not till a double coil of pipes was led round the gallery in the central compartment that the house was heated sufficiently for its purpose.

in that Garden being removed here, or in Government forming here a Medical Garden on a national scale.' Both schemes were abandoned.

In 1846 a new Orchid House was built, and a wing 60 feet long was added to the New Holland House. The Orchid House was especially required for the accommodation, besides the Kew collection, of two others, one the Woburn Orchids, which had been presented by Duke Francis to Her Majesty with the view of their being transferred to Kew; the other that of the Rev. F. Clowes, of Broughton Hall, Manchester, a very large one, eminently rich in Andean species, generously presented by its owner.

In 1850 the Tropical Aquarium, or Water-lily House, was built, at a cost of about £2,000, chiefly for the cultivation of the *Victoria Regia.* It stands near to the north end of the Palm House, from one of the boilers underneath which it was heated[1].

In 1855 a Succulent House, 200 feet long by 30 feet wide, was erected and filled from end to end with Cactuses, Crassulaceae, Aloes, Agaves, S. African Mesembryanthemums, and allied plants of dry climates. This house became very popular, but it is difficult to say whether the visitors were more interested, or instructed, or puzzled, by the strange and novel forms it contained. One Cactus which lived for several years was the wonder of the Kew collections. It weighed one ton. It belonged to the genus *Echinocactus,* of which the species are more or less globular, and in this case was 9½ feet in girth. My father reported that he paid a bill of fifty guineas as the cost of its transport from the mountains to the coast of Mexico in a wagon drawn by six oxen. Owing to a bruise received in transit it very slowly rotted away.

Reverting to the greatly extended Botanic Gardens, now nearly 70 acres in extent, the laying out of the new ground,

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[1] This arrangement did not answer; the loss of heat in transmission was too great, and eventually the house had to be supplied with a separate boiler and furnace.

construction of main walks for the accommodation of large crowds of visitors, and of subsidiary ones leading to the various plant-houses, and the designing of extensive geometric flower-beds in character with the Palm House, the gates, and other great structures, demanded the genius of a professional landscape gardener, and Mr. Nesfield of Eton was selected for the purpose. The conditions to be met presented many difficulties, the views in all directions were dominated by conspicuous insurmountable objects, the imposing entrance gates, the Palace, the Orangery, the campanile, the Pagoda, the Temple of the Sun, a piece of water, and two large artificial mounds crowned with classical temples. The result has proved satisfactory, its main features called forth no adverse criticism, and remain to this day almost as they were planned upwards of half a century ago.

As these works were progressing, Her Majesty, accompanied by the Prince Consort, in 1843, paid her first visit to the Gardens. They were pleased to express their approval of all they saw, and were especially interested in a model of the Palm House, then about to be erected. They subsequently sent the Royal children on several occasions that my father might point out to them the more interesting plants in the houses. The Prince Consort paid several subsequent visits, and took a keen practical interest in all that was doing in the Pleasure Ground, which was separated from the Botanic Gardens by a light wire fence, and in the Deer Park beyond. He took the finer trees under his especial protection and forbad the cutting down of any without his sanction. The Deer Park he declared should never be built upon, and he approved of my father removing the wall that separated it from the Pleasure Grounds.

Now that I am in duty bound to introduce Royalty into a sketch of my father's life it would be disloyalty, as well as ingratitude, to pass over the life-long connexion of the late Duke of Cambridge and his family with Kew. The gardens of Cambridge Cottage abutted on the Royal Botanic Gardens, and for a great part of the year the family resided there, and daily walked in the grounds, or the Duchess drove in a light pony carriage, carefully keeping off the lawns and the edges of the walks. The Duke died before my father took up his residence at Kew itself, but the Duchess and the Princess Mary, afterwards the Duchess of Teck, constantly invited him to accompany them in their walks, and were not backward in giving him their opinion of his operations. The Princess would come and tap at his study window for him to come out and show her interesting plants in the houses and grounds, though he never (as has been reported in some biographies of Her Royal Highness) either taught her botany, or was ever asked to do so. Knowing as all do her charm of character, it is not surprising that my father, who was no courtier, greatly enjoyed such interviews with his Royal neighbours ; and he profited by them too, for he had the opportunity of meeting at Cambridge Cottage men of the highest distinction, and introducing them to the wonders of Kew.

The only other allusions to Royalty which I find in my father's correspondence are of a visit to Osborne by command of the Queen in 1850, and the following extract from a letter to Mr. Turner, dated August, 1854 : 'The Gardens are increasing amazingly in beauty, interest, and popularity. The Queen has been here three times in less than six weeks, and I was required by her to inquire if the Palace could not be put in repair for her and her children. The Duchess of Gloucester[1] commanded my attendance last week ; the Queen Dowager came on Friday with a very large suite, and remained three hours in the Gardens and Museum. The Palm House, now that it is filled, is the admiration of everybody, and the view of the palms from the gallery is most striking. The Queen was enchanted with it. But the Museum is, if possible, more attractive still, and is crowded daily.'

In 1843 my father reverted to the plan followed during the palmy days of Kew, when under the patronage of Sir

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[1] The Duchess of Gloucester and Princess Sophia were the last of the Royal family to reside at the Palace of Kew.

Joseph Banks, of sending collectors to distant countries for the purpose of transmitting plants and seeds to the Royal Gardens; and by way of lightening the demand on the Treasury he on several occasions, with the Commissioners' approval, invited the Duke of Northumberland and the Earl of Derby to contribute to such expeditions and share the produce. At the same time, through his influence at the Admiralty, he obtained the privilege of having all packages addressed to Kew coming by the Royal Mail West India steam packet sent freight free. By these means Mr. Purdie was sent to New Grenada, and Burke and Geyer to California and Oregon, with the most satisfactory results to all parties; and by similar arrangements with the Treasury, Foreign, Indian, and Colonial Offices there were subsequently sent Oldham and Wilfred to Japan, Formosa, and Corea, Mann to the Cameroons, Gaboon River, and Fernando Po, Baikie and Barter to the Niger, Kirk to the Zambesi with Livingstone, Meller to East Africa and Madagascar, myself to the Himalaya, Bourgeau to Canada, Lyall to British Columbia, Edmonstone, followed by Seemann, to Western and Arctic America in H.M.S. *Herald*, and the latter to the Fiji Islands with Col. Smythe's mission, Macgillivray to Torres Straits in H.M.S. *Rattlesnake*, Milne to the Pacific in H.M.S. *Herald*, Spruce to Ecuador for Cinchona seeds, and Hewett Watson to the Azores. The practice was definitely abandoned when the great nurserymen took it up, and liberally shared their proceeds with Kew in exchange for its Director's services in indicating countries worth exploring, giving the collectors letters of recommendation to his correspondents abroad, naming and publishing their novelties and rarities, &c.

In 1844 my father was instructed to prepare a Guide-book to the Gardens for sale at the entrance, and to make an annual Report on the progress and condition of the Gardens, to be laid before Parliament. The first edition of the Guide-book contains fifty-six pages and sixty-one woodcuts of objects exhibited. It was entitled 'Kew Gardens, or a Popular Guide to the Royal Botanic Gardens of Kew,' by Sir W. J. Hooker, Director. After bringing out twenty-one successive editions he transferred the duty to Prof. Oliver, the keeper of the Library and Herbarium, who in 1863 included the Arboretum in the Guide book.

In 1850 the Board of 'Woods and Forests' was divided into two, that of 'Works and Public Buildings,' of which latter the Chief Commissioner became a Minister of the Crown; and that of 'Woods, Forests, and Land Revenues,' which became practically a department of the Treasury. The Botanic Gardens and Pleasure Grounds were transferred to the first of these as revenue-expending establishments; the Deer Park to the second as revenue-yielding. The Palace and its domains, together with the Swiss Cottage in the Pleasure Ground and the ground around it, remained under the control of the Queen's Household[1].

On this fission of the office its chief, Lord Seymour (afterwards twelfth Duke of Somerset), became Chief Commissioner of Works and Public Buildings, of which Mr. Philipps retained the secretaryship. Mr. Milne, on the other hand, remained a Commissioner of Woods and Forests, &c., to my father's great regret, for this gentleman had from the first taken a special interest in the development of Kew Gardens, and had in many ways smoothed the Director's path. Happily in Lord Seymour and Mr. Philipps my father had excellent friends, and I have heard him say that Lord Seymour was on the whole, as a man of business and intelligence, the most efficient chief he had served under. I must add that as First Lord of the Admiralty the Duke continued to show his zeal for the establishment he had ruled over.

The following passages from my father's correspondence are interesting as referring to effects retained by Mr. Aiton (who died in 1849), on resigning the Directorship of Kew:—

'Kew, August 13, 1851. I have just received a catalogue of the *two* brothers Aiton's combined sale, which is to take

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[1] Her late Majesty latterly transferred these also to the Department of Works and Public Buildings, when they came under the control of the Director of Kew.

place to-day and three following days at Kensington, and I am happy to tell you that the botanical portion (600 volumes), herbarium, botanical drawings, &c., are excluded ; from which I can only infer that Lord Seymour has so far accepted my recommendation as either to have purchased them by private contract or to have arranged for their being kept back with a view to their being valued. Otherwise they were certainly to have been sold to-day, the books being all catalogued and numbered for the purpose by the auctioneer. It is odd that Lord Seymour should not have written further to me; but with best desire to do everything he can for the advantage of the Garden, he seems to feel that he is put into the office to keep a jealous watch over all the officers, and to take care there is no jobbing.'

'Sept. 2. In spite of Lord Seymour's refusing to purchase the books, &c., of the Aiton representatives, Mr. Atwell Smith has sent to me for the Garden Zoffany's very fine portrait of old William Aiton, and sundry MS. books which ought never to have been removed from the Garden. Lord Seymour little knows he has to thank me and the attentions I was able to pay to Mr. Atwell Smith by attending the two Aitons' funerals, &c., for these objects having come here at all. The picture is suspended in the Museum, and I am getting sixty of my large folio drawings (made for my Glasgow lectures) framed for the walls in the rooms now being added to the Museum.'

Referring to the above effects of the brothers Aiton, the books were sold, but the collection of drawings, which is of great value, was retained, and subsequently presented to Kew by Mr. Atwell Smith.

In 1853 a house in Kew, in possession of the Queen, having become vacant through the death of its tenant (Sir George Quentin, Riding-master to the family of George III), Her Majesty was pleased to place it at the disposal of the Commissioners of Works, to be in future the residence of the Director of the Botanic Gardens, in which it was situated. This was to my father a very great boon. He was in his sixty-ninth year, and burthened with the duty of creating a National Arboretum in the Pleasure Grounds, nearly two miles distant from West Park, and demanding unremitting scientific supervision. Nor must it be forgotten that his herbarium was outgrowing his accommodation for it, and that his expenses all along far exceeded his official salary[1]. The house was a good one, facing the Green, with its back in the Gardens, but it would not accommodate his library and herbarium, which, together with his study and artist's room, occupied thirteen apartments in West Park.

Fortunately a large house[2] closely adjacent to the Botanic Gardens, which had formerly been occupied by the King of Hanover, afforded abundant space for the herbarium and library, of which last he kept in his study such works as were in frequent use. A history of the Herbarium and Library at Kew during my father's lifetime will be found further on.

Returning to the operations in the Botanic Gardens, in about 1855 instructions were given to the Director (to his great discomfiture) to decorate the lawns and borders of the paths over a considerable area of the Botanic Gardens with 'carpet-beds' of flowers. These he regarded as out of place in a garden where objects of as great beauty, and far greater interest both popular and scientific, abounded. He further regretted the great expenditure on propagating-pits, frames, soil, and labour, on a show of but a few weeks' annual duration, whilst some scientific branches of the establishment

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[1] On taking up his residence at Kew he was allowed to retain with his salary (by this time £500) the allowance for rent (£200) which he had at West Park; in 1855, after several appeals for aid in conducting his enormously increased duties, I was appointed Assistant Director of the Royal Gardens, Kew.

[2] This house, with the grounds around it, had belonged to a Mr. Hunter, from whom it was purchased in 1818 by King George III, at the instigation of Sir Joseph Banks, to provide for a Herbarium and Library to be attached to the Royal Botanic Gardens. The only objective evidence of its original destination was that one of the rooms was shelved for books. In 1823 George IV sold the house and grounds to the nation: in 1830 William IV granted it to the Duchess of Cumberland for her life. On the accession of the Duke of Cumberland to the throne of Hanover, it became known as 'The King of Hanover's house.' It is now entitled 'The Herbarium of the Royal Gardens.'

were being starved, and a structure of the dimensions at least of the Palm House, to rescue the magnificent collection of colonial trees, &c., from destruction or deformity, was urgently needed. The object of the proposed decorations seemed to be to rival the London parks, where such an attraction was eminently suitable and admirably carried out. In the end he came to an arrangement with his chief (Sir Benjamin Hall, I think), that a sum of money should be added to the estimates and appropriated to this decorative work, and that he be supplied with a skilled foreman to carry it out. The system was continued for several years, and was thereafter gradually suppressed.

The years 1860 to 1862 were notable for the successful efforts in introducing the Peruvian barks into India and our tropical colonies. Mr. (now Sir Clements) Markham had induced the Indian Government to undertake this measure, which had been urged upon it by Sir Joseph Banks more than half a century before, and by various botanists since. Mr. Markham himself went to Peru, and brought to England living plants, which, after a short nursing at Kew, he took on to India and established in the Nilghiri Hills. Meanwhile my father, to whom the Indian Government applied for advice, not trusting wholly to the risky transport of living plants, urged that collectors should be sent to Ecuador and Bolivia for seeds of the different species, recommending at the same time the employment in Ecuador of Mr. R. Spruce, an able botanist and collector, who happened at the time to be in that country.

In the Report on the progress and condition of the Royal Gardens during the year 1861 it is stated that:—'The means adopted for introducing Cinchonas (trees yielding quinine) into the East Indies and our tropical colonies rank first in point of interest and importance of the works of the past year. In my Report for 1860 I mentioned the erection, at the desire of the Secretary of State for India in Council, of a forcing-house, especially for the cultivation of the Cinchonas, with the view of establishing plantations of them in

India. The operations of the several parties organized to proceed into the Andes and procure young plants and seeds have been described in detailed reports laid before the Secretary of State for India by Clements R. Markham, Esq. Upon the Royal Gardens devolved the duties of receiving and transmitting the seeds and plants to India, of raising a large crop of seedlings, of nursing the young stock, lest those sent on should perish or the seeds lose their vitality, and of recommending competent gardeners to take charge of the living plants from their native forests to the hill country of India, and to have the care of the new plantations there. Further, with the sanction of the Indian and Colonial Governments, it was arranged that our West Indian colonies and Ceylon should be supplied with a portion of the seeds.'

In the Report for 1862 the number of plants established in the Nilghiris is 117,706; in the Sikkim Himalaya 2,000[1], in Ceylon about 3,000. In the Report for 1863 the number of plants in the Nilghiris is stated to be 259,356, and in the Himalaya 8,000, where applications have been made to the superintendent of the plantation from private individuals for 1,500,000 plants; in Ceylon 22,050.

In 1864 and subsequently great efforts were made to introduce the Ipecacuanha plant into India from Brazil, but with little success. The plant was impatient of removal from its native forest and of transportation, and was further one of extraordinary slow growth. Such specimens as arrived in India in a living state made no progress, and the attempt had to be abandoned.

In 1861 a reading-room and some books and horticultural journals were provided for the gardeners, and Professor Oliver, keeper of the Library and Herbarium, volunteered a course of elementary lectures on botany. It was not till some ten

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[1] Manufactories of quinine have been established in the Sikkim Himalaya and the Nilghiri Hills. The most signal proof of the success of the experiment is, that a dose of five grains of quinine in a paper bearing a Government stamp may be bought at any post office in Bengal for half a farthing. This supply is from the Sikkim manufactory.

years had elapsed that a system of paid lectures was organized, which have proved a great boon and success.

In 1865, the last year of my father's life, he received from the Lords of the Admiralty the gratifying intelligence, that his long-sustained exertions in sending such plants to the sterile Island of Ascension as would most effectively and speedily clothe its naked soil, and thus conserve a water supply, had been crowned with success. It was in 1843, after the return of Sir James Ross's Antarctic Expedition, which had touched at the island on its homeward voyage, that the idea of planting that island extensively with such trees, herbs, and shrubs as were best suited to its soil and climate originated. Ascension being a naval station, the Admiralty favoured the idea, and Kew was applied to for aid in giving effect to it; which it did by sending out seeds and cases of living plants year after year, and a succession of young gardeners to plant and sow. According to Captain Barnard's Report to the Admiralty, 'the island in 1865 possessed thickets of upwards of forty kinds of trees, besides numerous shrubs and fruit trees, of which, however, only the Guava ripens. These afford timber for fencing cattle-yards.' In 1843 there was but one tree on the island and no shrubs, and there were not enough vegetables produced to supply the Commandant's table. The Report goes on to say: 'Through the spread of vegetation the water supply is excellent, and the garrison and the ships visiting the island are supplied with abundance of vegetables of various kinds.'

The *Arboretum*, formerly the *Royal Pleasure Grounds of Kew.* In 1845 Mr. Aiton[1] was relieved of the charge of that portion of the Pleasure Grounds (about 178 acres) then in occupation of the King of Hanover as a game preserve, which had not been as yet added to the Botanic Gardens, together with the Deer Park (350 acres), and my father was asked to

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[1] Mr. Aiton, on retiring with a pension of £1,000 per annum, had begged to be allowed to retain the Directorship of some portion of his realm, on the very natural plea that his services under the Royal Family might, if possible, be lifelong. He died in Kensington, October 9, 1849, in his eighty-fourth year.

include these in his Directorate. This he agreed to do, though no hint of an increase of salary accompanied the request, and though the duties involved were neither botanical nor horticultural, but rather agricultural. He had no doubt two good reasons for this compliance, one in having an eye to the remainder of the Pleasure Ground as the site for an Arboretum worthy of the nation; the other, that to have allowed these to be placed under any other authority might have led to complications.

Thus the Director's rule was extended in four years from a Botanic Garden of eighteen acres and a few hundred yards in length, to an area of nearly 650 acres, extending from Kew Green to the Thames at Richmond, two miles distant. Some idea may be formed of the labour which this acceptance of extra duty entailed from the following extract of a letter dated March, 1846, and addressed to Mr. Turner: he says, 'For myself the Gardens have never made such demands on my time as at the present season, when the most extensive operations are being carried on in the Pleasure Ground, as well as in the Botanic Gardens. In each place our usual complement of men is much more than doubled. In the former, owing to the severe illness of the foreman, I have to superintend everything, and there is literally not a man in whom I can put confidence about the place. I have lately detected very gross abuses, which there is every reason to believe have been practised for a long time under the régime of my predecessor.'

With regard to the Deer Park, often then called Richmond Old Park, except for planting some clumps of trees and shrubs, it suffered no change so long as my father had charge of it. It was let to a grazier and yielded large crops of hay. The Observatory[1], which stands towards the centre of it, was

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[1] The Observatory was erected in 1798 by George III for the purpose of observing the transit of Venus, and for the instruction of the younger members of the Royal family in astronomy. For many years it was devoted to scientific purposes, under the direction of accomplished astronomers; and served for regulating the clocks in the Horse Guards, St. James's Palace, and elsewhere in London. In 1840 its contents were dispersed, and the principal instruments sent to King's

then unoccupied, but shortly afterwards it was placed at the disposal of the Meteorological Committee of the Royal Society.

In the Pleasure Grounds the only improvement at first effected was the removal of a wall about three-quarters of a mile long which separated them from the Deer Park, and replacing it by a ha-ha, thus opening the latter to view, together with the distant views of Isleworth Church, Sion House, and the woods on the opposite side of the Thames.

Then followed the formation of avenues in the grounds, upon which point Mr. Nesfield was consulted, the construction of paths, and the establishment of a nursery for the purpose of rearing accessions to the Arboretum and projected Temperate House or Winter Garden, and of propagating duplicates for distribution and exchange.

In the formation of the Arboretum, which occupied about three years, some of the principal nurseries of the United Kingdom and the Continent were laid under contribution for specimens often of great market value, and it is impossible to exaggerate the liberal spirit with which the owners of these responded to my father's call. All seemed to recognize the national character of the work, and that, as a means of enabling them to verify scientifically the nomenclature of their stock in trade, its services would be invaluable. The two most conspicuous and beautiful features in the Arboretum formed at this time were the Rhododendron walk and the Azalea beds. The number of species and marked varieties in the Arboretum was 3,500, grouped under their natural orders and genera.

College, London. It is well that the Botanic Gardens did not share the same fate.

I may here remind my readers that Kew has claims for the worship of astronomers, as well as of botanists, for that in a house which stood opposite the Palace, and which was taken down in 1803, resided the celebrated astronomer Samuel Molyneux, F.R.S., secretary to George II when Prince of Wales. It was with a telescope constructed by Mr. Molyneux and placed on the lawn near his house, that Dr. Bradley made in 1725 the first observations that led to his two great discoveries of the aberration of light, and the nutation of the earth's axis. To perpetuate the memory of so important a station, His Majesty King William IV had a sundial with a suitable inscription placed on the spot where the telescope had stood. It is no doubt to the fact of His Majesty's having had the education of a naval officer that this rare tribute to a scientific man and his discoveries was due.

Another nursery was established in 1855 in the private grounds near the Palace, for the very different purpose of supplying the London and other parks, the property of the Crown, with trees and shrubs. Up to the year 1865 more than 25,000 trees and shrubs had been supplied from these two nurseries, many to Battersea, Hyde, Victoria, and Richmond Parks; others to plant open spaces in the private grounds of the Queen around the Swiss Cottage for the encouragement of wild birds, and to form a belt a quarter of a mile long by the banks of the Thames to screen the Arboretum from Brentford. Many wagon-loads were sent to Aldershot, Deptford, and other yards.

In 1857 a lake four and a half acres in area was formed in a marshy depression that had communicated with the Thames opposite Sion House, and which had been enlarged and deepened by the removal of many cart-loads of gravel for the formation of paths, and for the terrace on which to place the Temperate House. The lake was finished in 1861, its banks planted, and a communication with the Thames re-established by a tunnel and sluices. It has been enlarged considerably in later years.

By far the greatest undertaking carried out in the Arboretum was the construction of the main body and octagons of the Temperate House, or Winter Garden, as it was at first proposed to call it. From 1856 onwards my father had annually urged on the Government the necessity for such a building, and I cannot do better than reproduce the words of his Report for 1857, 'On the condition of the Royal Gardens,' as showing cause for its construction not being delayed :—'All the plant-houses are progressing favourably, with one exception, to which I have already alluded, as a source of deep concern. Unless we have, at once, a structure suited to the reception of our large trees and shrubs which will not bear frost, especially that once celebrated collection of pines, Araucarias, Proteas, &c., they will soon be past recovery. Already they have suffered extremely for want of space; many have perished, many are deformed and crippled, being shorn every now and then of their graceful and stately heads in order to bring them under the shelter of a dark roof, that of the "Orangery," only twenty-three feet high, or in a hovel of a building long ago condemned as discreditable to the Gardens. The crying need of a new Conservatory has long been admitted. One very old and decayed greenhouse, which had been tenanted by a portion of the very plants in question, was pulled down four years ago with the understanding that it should be replaced by a better building; and numerous desirable works have been postponed that the money destined for them might be applied to erecting a structure commensurate to our wants. I do not know that I can express my views on this subject in stronger words than I used last year, and which I beg to repeat. In my Report for 1856 I said that I must speak almost in the past tense of those superb Mexican, Australian, and Norfolk Island Araucarias, conifers, &c., which were once the pride of Kew Gardens, but that while some had suffered past recovery, others might still be restored by affording them needful space, light, and temperature. I added, as a further proof of the evident necessity of the house in question, that during the whole sixteen (now seventeen) years of my Directorship, not any addition had been made to the accommodation for these kinds of plants; it had indeed, as above shown, sustained a diminution. The Gardens cannot be deemed complete till the trees and shrubs of temperate climates are as well cared for as the tropical plants, for whose reception our noble Palm House was erected thirteen years ago. Then, and not till then, will the national establishment be perfect. A botanical garden is not valuable, as was once thought, for the number, mainly, of the species which it includes, but for their usefulness and beauty; they should be a *selection* rather than a *collection*. The Conservatory in question would certainly cost a large sum of money, but not *nearly* so much as did the Palm House, which involved several items not requisite in a structure for hardier trees and plants. The price of glass, too, has fallen materially since 1844.'

In 1859 the design for such a conservatory, by Mr. Decimus Burton and my father, was approved. It consisted of a central building 212 feet long by 137 feet broad and 60 feet high, with a gallery running round it at a height of 30 feet; two wings, each 112 feet 6 inches long by 62 feet 6 inches broad, and 37 feet 9 inches high; and two octagons interposed between the centre and the wings, each 50 feet broad and long by 25 feet high. In 1860 tenders were accepted for the construction of the centre and octagons only, and the work was at once proceeded with. In 1861 the octagons were completed and filled with plants in tubs and pots from the Orangery, the old Conservatory, and the architectural house near the gates, all in the Botanic Gardens; and in 1862 the centre was completed and its floor provided with beds, in which the larger specimens from the above-named houses were planted. Unfortunately no representations availed to induce the Government to complete the building by the erection of the wings, the unoccupied naked gravel platforms for which were an eyesore to the Director for the remaining few years of his life[1].

The history of one more conspicuous feature in the Arboretum remains to be told. I allude to the stately flagstaff of Douglas fir, or rightly speaking flagstaffs, for there were two of them, though for obvious reasons the acquirement and fate of the first were not officially made public. In March, 1859, the Director received a letter from Mr. Edward Stamp, a gentleman engaged in the timber trade of British Columbia, offering to present to the Gardens a flag-staff of the Douglas fir, over 100 feet in height and not exceeding sixteen inches in diameter at the base. The offer was accepted by the Commissioners, and an excellent site fixed for it, on a mound in the Arboretum, not far from the Richmond Road, where it would be visible from the latter as well as from a great extent of both the Botanic Garden and the Arboretum. The spar, fully rigged for erection, was dispatched to Kew from the London Docks, floating, towed by a tiny steamer, but was wrecked

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[1] They have since been erected.

en route, having been cut in two by another boat. Nothing daunted, Mr. Stamp had it back and the two pieces 'scarped,' thus reducing its length by a few feet. It was then again committed to the Thames, and safely landed on the river bank opposite Sion House, from whence it was transferred to the mound, in the top of which a suitable well had been sunk for the reception of the butt. The question of the proper person to entrust with the hoisting had been discussed with the Commissioners, when my father's suggestion of application being made to the Lords of the Admiralty for an experienced man from one of the ship-building yards was overruled in favour of the Clerk of the Works of the Office. The decision was unfortunate. The method adopted was to erect a derrick over the well, sling the spar, securely guyed, raise it horizontally to the required height, and then by depressing the end bring it to a vertical position and lower it. The occasion was a memorable one; a large party, including Royalty, was assembled to witness the operation, which resulted in a puff of wind striking the spar when in mid air, and bringing it and the derrick to the ground, where the spar lay broken into three pieces. I was present on the occasion and shared in full my father's vexation and bitter disappointment. The hardest task remained, the communicating the Commissioners' regret, together with his own, to the generous donor of the spar, who promptly answered with the offer of sending a longer one on his return to British Columbia! This he did, and in 1861 a spar about 250 years old, when felled 159 feet long, and 20 inches in diameter at the butt, rigged and ready for erection, was landed at the same spot as the former one had been. On this occasion the Director's suggestion was followed, the First Lord of the Admiralty (the Duke of Somerset, who as Lord Seymour had been first Commissioner of Works, &c.) was applied to, and a gang of riggers was supplied from Deptford Dockyard. These carried the spar to the mound, there laid it down with its butt in position in the base of the well (which was reached through a cleft in the mound), and then tilted it up to the perpendicular.

The show concluded by one of the riggers offering to stand on the truck of the spar for the gratification of H.R.H. the Duchess of Cambridge, who was present on the occasion, but who declined the offer. It should be recorded that all expenses attending the transport of both spars from their native forest to Kew, together with their dressing and rigging, were borne by Mr. Stamp, and that this second spar is believed to be the finest in Europe.

Museums. Referring to the storehouse for fruit in the old kitchen garden of Kew, alluded to at p. lvii as left standing in 1846 when that piece of ground was added to the Botanic Gardens, it appeared to my father that it might be converted into a Museum of Economic Products of the vegetable kingdom, raw and manufactured, and for the exhibition of large fruits and other objects of varied interests, nowhere displayed to view. Of such objects he had a large collection, formed chiefly for the use of his class in Glasgow, and others were scattered about the offices of the Gardens, some of them being the property of Mr. Smith, the Curator. Procuring a few trestles and planks, he formed of them a long table in the central room of the building, arranged all these articles on it, ticketed them, and invited the Commissioners to come and see them. This they did (I happened to be present on the occasion), and listened to his eloquent discourse upon them, during which he showed how such a collection of vegetable products might, besides interesting and instructing the public, prove of great service to the scientific botanist, the physician, the merchant, the manufacturer, the chemist and druggist, the dyer, and to artisans of every description. All these might find in such a collection the raw material (and to a certain extent the manufactured article) employed in their several professions, trades, or arts, correctly named, together with their native country and some account of their history.

The suggestion was adopted by the Commissioners, and, being approved by the Treasury, the room was fitted with glazed cases filled with objects and opened to the public in 1848, as the first Museum of Economic Botany ever formed.

The Museum was no sooner sanctioned than my father began to cater for objects wherewith to fill it, by application to merchants and manufacturers and by interesting his correspondents all over the world, many of whose replies were published in the 'Journals of Botany' which he conducted. His enthusiasm was catching. The Secretary of State for Foreign Affairs (Lord Aberdeen), on hearing of it, caused circulars to be sent to our Ministers and Consuls in foreign countries, desiring them to transmit specimens intended for Kew; the First Lord of the Admiralty (Lord Auckland) requested him to draw up instructions[1] for collecting for officers in their service, and the Minister of the Colonies displayed the same interest.

Consequently contributions poured in in embarrassing quantities, especially on the close of the Great Exhibition of 1851, when Messrs. Lawson and Co. of Edinburgh presented their magnificent exhibit of the agricultural products of Scotland. Increased accommodation was hence necessary and was found in two wings of the building, which had been used (one or both) as dwellings of gardeners; these provided four additional rooms and a staircase to a gallery which was constructed in the main room, and which was lighted from the roof. These completed the Museum building, which presented within 6,000 square feet of glazed wall-cases, and eight glazed table-cases, most of them with glazed drawers underneath. To add to the interest of the exhibits, framed coloured drawings of economic plants, palms, &c., lent by the Director, were hung to the gallery rails all round. A Guide to the Museum was drawn up by him in 1855, for sale at the Garden gates; it contained a plan of the interior, eighty pages of descriptive matter, twenty-six woodcuts, and notices of 560 of the objects most worthy of the visitor's inspection[2]. In 1857, when the

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[1] The Admiralty Manual of Scientific Enquiry was the result, the botanical part of which was supplied by W. J. Hooker, assisted by D. Hanbury, Esq.

[2] In 1857, on the opening of the second Museum, he published a second edition of the Guide-book, in which 612 of the most interesting objects were described. In 1861 Professor Oliver brought out a third edition with notices of 1,000 exhibits.

larger Museum now to be described was opened, this one was numbered II in the Guide-book. Before proceeding to describe the second and third Museums erected by my father, it is gratifying to relate that within six years of the first being opened eight others, professedly on the lines of that at Kew, were established; they were in Edinburgh, in the India House (London), in Guiana, Jamaica, Melbourne, Calcutta, Madras, and in the Jardin des Plantes, Paris.

In the summer of 1855 the Director was invited by the Imperial Commissioners of the French International Exhibition of that year to take part in its functions, which resulted in his obtaining almost the entire collection of vegetable products there brought together. In aid of this he procured a grant of £400 from the Treasury, which the President of the Board of Trade, unasked, supplemented with a like sum. Thus provided, and with the ready assistance of the officers of the Board of Trade, and of the Science and Art Department, and enriched by donations of many exhibitors, he secured and transmitted to Kew forty-eight large cases of museum articles. This accumulation, and the facts that the Museum of 1848 was already overcrowded, and that great stores of specimens were being huddled away in the temples and sheds of the Gardens, led to the erection of a second and much larger building. This, which is Museum No. I of the Guide-books, was sanctioned by Parliament in 1854, was completed, fitted with 13,000 square feet of glazed cases, filled, and opened to the public in 1857. It is that now standing opposite the Palm House with the piece of water intervening. The expedience of following a classification of the contents of both Museums according to the Natural System necessitated the breaking up of the contents of the first, in which were retained all products of the Monocotyledonous and Cryptogamic divisions of the vegetable kingdom; the Dicotyledonous being transferred to the new building. In this laborious task the Director had the gratuitous aid of the Rev. Professor Henslow of Cambridge (Rector of Hitcham in Suffolk), who to his knowledge of botany and vegetable products, added singular skill in preparing and mounting the latter for exhibition[1]. His bust in marble (the gift of his sister) and that of the Director (the gift of Henry Christy, Esq.), both by Woolner, stand in the entrance hall of the new building, where are also, hung on the walls and projecting ends of the cases, a collection of nearly one hundred framed portraits of botanists[2], then the property of the Director. The third Museum (No. III of Guide-book), opened in 1863, originated in the timely conversion to this purpose of the Orangery, the oldest building in the establishment, 145 feet long in the interior. Timely it was in two senses; for the Orangery had hitherto been the main receptacle for such trees of Australia and New Zealand as had outgrown the old New Holland House, and in this very year the Temperate House was ready for their reception; also in 1862 my father had, thanks to the Secretary of State for the Colonies, the Duke of Newcastle (his first chief when Lord Lincoln), and to the Governors of several of the colonies themselves, acquired for Kew almost the whole of the vegetable products exhibited in the International Exhibition of that year, the East Indies being the chief exception. The colonies were, West Africa, the Cape of Good Hope, Natal, Mauritius, St. Helena, West Australia, New South Wales, Victoria, Tasmania, Queensland, Canada, New Brunswick, Vancouver's Island, British Columbia, Ceylon, Trinidad, the Bahamas, Dominica; together with these were exhibits from the Ionian Islands, Austria, Russia, and miscellaneous articles from other countries. Conspicuous amongst these acquisitions was the collection of colonial timbers, many as slabs of large

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[1] Nor should the services on these occasions of the keeper for ten years of both Museums be forgotten—Mr. Alexander Smith (son of the Curator of the Botanical Gardens), who had acquired a remarkable knowledge of vegetable products. Owing to his health breaking down he was obliged to retire in 1858. He died at Kew in 1864. He was succeeded by Mr. John Jackson, who showed equal ability, and who in the course of his forty-two years of keepership became a leading authority on vegetable products. He retired on his well-earned pension in 1901.

[2] There are now (1902) about 190 portraits of botanists in this No. 1 Museum. There are also in the Herbarium 275 mounted in portfolios, and a few hanging on the walls, amongst which latter are excellent oil paintings of the late Mr. Bentham and of Professors Oliver and Baker.

size, selected from sound trees, partially polished and often of uncommon beauty. Almost all these timbers were named by men of scientific attainments and practical knowledge, and they were accompanied by reports containing a vast amount of serviceable information on their uses, qualities, &c.

Herbarium and Library. As stated at p. lvi, when the new Director of Kew took up his appointment, neither books nor a herbarium were provided for him; but he was well equipped with those of his own; nor was it till he was moved into a residence in the Royal Gardens, that he received any other substantial aid towards their upkeep and increase than house-rent, and latterly stationery and some cabinets. It is also told that the new residence not affording that accommodation for these which the Government had guaranteed, they were placed in a building adjacent to the Botanic Gardens. On this occasion it was arranged between the Commissioners and my father, that, on the condition of his herbarium and library being accessible to botanists [1], he should be provided with such a scientific herbarium curator as he had himself hitherto salaried [2].

Four years afterwards, the Royal Gardens came into possession, by gift, of the very extensive library and herbarium of G. Bentham, Esq., F.R.S., which was second to my father's alone in England in extent, methodical arrangement, and nomenclature, and which was placed in the same building. Its formation was begun in 1816, in France, where and in the Pyrenees Mr. Bentham collected diligently; but its great expansion by the inclusion of exotic plants dated from his introduction to my father in Glasgow in 1823, when the friendship between the two commenced which remained

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[1] From the date of his taking up the Glasgow Professorship, his herbarium and library had been open to botanists, as was its owner's hospitable table to visitors from a distance.

[2] One of his curators, Dr. J. E. Planchon, subsequently attained to great eminence as Professor of Botany in Montpellier, where he carried out his researches in the vine disease caused by the ravages of the *Phylloxera*, which has cost France so many millions. He was the discoverer of the only effectual check to the propagation of this pest, by grafting *Vitis vinifera* on stocks of American species, which he proved to be almost immune from the attacks of that insect.

undisturbed for forty-two years[1]. From that date the two botanists may be said to have hunted in couples for the aggrandizement of their libraries and collections, sharing their duplicates, Mr. Bentham giving my father the preference in all cases of purchase, &c. The one great difference between their aims was, that the former confined his herbarium to flowering plants, whilst my father's rapidly grew to be the richest in the world in both flowering and flowerless plants. The offer of this gift was prearranged with my father, who with his wonted disinterestedness put aside the obvious fact, that its acceptance would greatly diminish the value of his own herbarium and library, should the Government ever contemplate its purchase[2].

The principal additions to the Herbarium and Library made during the last ten years of the Director's life were:—

(1) The large collection made in North-West India, Kashmere, and Little Thibet by Dr. Thomson, and in the East Himalaya, the Khasia, Mount Silhet, and Chittagong by Dr. Thomson and myself.

(2) In 1858 seven wagon-loads of collections from the cellars of the India House in Leadenhall Street, where they had been accumulating for many years. They arrived at Kew in the chests in which they had been packed in India, many of them partly open and their contents destroyed by vermin and damp. Amongst the most valuable of these herbaria were those of Falconer in the North-West Himalaya (in the worst condition), of Griffith in Afghanistan, Assam, Bhotan, Burma, and the Malay Peninsula, and of Helfer in Tenasserim.

(3) In 1862 the herbarium of W. Borrer, F.R.S., long the Nestor of British botanists, and the life-long friend

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[1] See Annals of Botany, vol. xii, p. 7.

[2] My father's herbarium had been offered to Government on several occasions, for a sum far below its value. After his death, it was (in 1866) purchased, with all such books, about 1,000 volumes (some of great rarity), as were not in Bentham's gift, together with a unique collection of botanical drawings, maps, MSS., portraits of botanists, and letters from his botanical correspondents from 1806–65, which amount to about 27,000.

and correspondent of my father, was presented by his widow[1].

(4) The Australian herbaria of Allan Cunningham, formed during that traveller's exploration of the interior of New South Wales and Queensland, made by himself in 1836 and 1838, and that made by his brother Richard Cunningham in 1835. Presented by R. Heward, Esq., F.L.S., of Kensington, in 1863.

(5) Mrs. Griffith's collection of British Algae. Presented by the Baroness Burdett Coutts in 1864.

(6) The specimens and original folio drawings, published and unpublished, upwards of 1,300 in number, illustrative of Dr. Boott's great work on the genus Carex. Presented by his widow in 1864.

(7) Dr. Lindley's Orchid herbarium, containing types of his 'Genera and Species of Orchideous Plants,' of his 'Folia Orchidacea,' and other works. Purchased in 1865.

(8) The immense herbaria of the traveller and naturalist Dr. Burchell, F.L.S., made in St. Helena, 1805–10, in South Africa (from the Cape to the Transvaal in 1811–5), and in Brazil in 1825–9. Estimated to contain 15,000 species, accurately ticketed for habitats and dates. Presented by his sister in 1864.

Turning now to my father's concluding botanical labours, the last of his efforts, the results of which have been far-reaching, was to address in 1863 a powerful appeal to H.M. Secretary of State for the Colonies, the Duke of Newcastle, K.G., in favour of H.M. Government undertaking to assist in the preparation and publication of a series of Floras of our colonial and Indian possessions. At the same time, for the information of the Secretary of State, he, in conference with Mr. Bentham, drew up and submitted the following estimate of the scope and cost of such a series of Floras,

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[1] The Hookerian correspondence in the Herbarium at Kew contains 145 letters from Mr. Borrer, dated from 1823 only. I am indebted to Miss Borrer, of Brookhill, Cowfield, Horsham, for a series of 139 letters dating from 1803 to 1839, addressed by my grandfather, Mr. Dawson Turner, to her grandfather, in which there are frequent references to my father which have been of great service to me in compiling this sketch.

which is interesting as giving the views of the two best informed botanists in Europe as to the number of species of flowering plants and ferns natives of the several colonies, specimens of which were assumed to be available in herbaria for description at that time.

Estimated numbers of species to be described:—

Australian Colonies,	8,000	Hong Kong,	1,000
South Africa,	10,000	Mauritius & Seychelles,	1,000
British North America,	2,000	British Guiana,	2,000
West Indies,	2,000	Honduras,	1,500
New Zealand,	1,200	West Africa,	2,000
Ceylon,	3,000	British India,	12,000

Of these colonies the Flora of one only had, previous to the appeal to the Secretary of State, been completed on the plan proposed; that of Hong Kong, by Bentham in 1861. Three others were in progress, and have since been completed; the 'Flora of the British West Indies' by Grisebach, 1859–64; the 'Handbook of the Flora of New Zealand,' 1864–7, which includes all the known Cryptogams of the island up to date; and the 'Flora Australiensis' of Bentham, commenced in 1863 and concluded in seven volumes in 1878. One other Flora was in progress, and is not yet completed; the 'Flora Capensis' of Harvey and Sonder, of which three volumes were published between 1859 and 1865. All the above works were subsidized by the home or colonial Governments.

The number of volumes required was estimated to be forty-three; the author's remuneration to be £150 per volume, payable at date of publication. The price proposed was £1 per volume containing not fewer than 500 species. To insure the publisher against loss, 100 copies were to be taken by Government on the day of publication. The authors were to have no pecuniary interest in the sales of the volumes. The Floras were to be limited to flowering plants, ferns, and their allies, and to be written in English.

Of the botanical works published by my father during the twenty-four years of his Directorship of Kew, the more important were, the continuation of the 'Botanical Magazine,' volumes lxvii to xc, with 1,440 plates; the 'Icones Plantarum,' volumes iv to x, 700 plates; the 'Journal of Botany,' volumes iii and iv, with 28 plates; the 'London Journal of Botany,' 7 volumes, with 166 plates; the 'Journal of Botany and Kew Gardens Miscellany[1],' 9 volumes, with 109 plates. On ferns alone there were the 'Species Filicum,' 5 volumes, with 304 plates illustrative of 526 species; 'Filices Exoticae,' 100 plates; 'A Second Century of Ferns,' 100 plates[2]; the 'British Ferns and their Allies,' 66 plates; 'Garden Ferns,' 64 plates; and lastly, a commencement of a 'Synopsis Filicum.' To these must be added his Guide-books to the Royal Gardens and to their Museums, and his annual 'Reports,' to be laid before Parliament, on 'the progress and condition of the Royal Gardens.'

Altogether, inclusive of the 'Icones Filicum' (in association with Dr. Greville), my father published upwards of 1,200 plates of ferns, and descriptions of 2,500 species.

Alphonse de Candolle, in his warm tribute to my father's memory (Archives des Sciences de la Bibliothèque universelle de Genève, July, 1866), gives 4,094 as the number of plates of plants published by my father, exclusive of those in the 'Flora Londinensis' (about 220). This is far short of the total number, which I make to be nearer 8,000; of which about 1,800 were from drawings executed by himself. I need hardly add that but for the fidelity, artistic skill, and extraordinary rapidity of execution of Walter Fitch, who was my father's botanical limner for thirty years, this number could not have been approached.

With the commencement of a 'Synopsis Filicum,' which the completed 'Species Filicum' made a comparatively easy task, my father's labours terminated. His end was unex-

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[1] This work was brought to a conclusion in 1857 with an almost pathetic farewell to the botanical helpers in his series of Journals, and to his botanical friends.

[2] The first Century of Ferns consisted of a re-issue of the plates and descriptions of the tenth volume of the Icones Plantarum (which volume was confined to ferns), on a larger sized paper, and coloured.

pected. On the Monday forenoon he spent two hours with me in inspecting Battersea Park, then in formation; here he left me and walked part of the way back to Kew, meeting by appointment the Queen of the Sandwich Islands and the Rev. Mr. Berkeley, with both of whom he spent the whole afternoon in the Gardens. On Tuesday morning his servant came to tell me that his master could not swallow. I followed immediately, and found him perfectly well except for this paralysis of the muscles of deglutition. I at once sent to London for the best advice, but to no purpose. I saw him no more, for sleeping on the floor by his bedside that night, under an open window, I was suddenly prostrated with rheumatic fever. Meanwhile he gradually sank, suffering no pain nor feeling the want of nourishment; and died from exhaustion, Saturday, August 12, in his eighty-first year[1]. He was buried in the churchyard of St. Anne's, Kew. A handsome tablet in the church with a central medallion profile by Woolner, and spandrels with groups of ferns in the corners, all in Wedgwood ware, record the dates of his birth, death, &c., with the motto, 'Thou, Lord, hast made me glad through Thy works.'

In person Sir William was over six feet high, erect, slim, muscular[2]; forehead broad and high, but receding, hair nearly black, complexion sanguine, eyes brown, nose aquiline—had been broken in a school fight; his mobile face, and especially mouth, was the despair of artists. Many chalk portraits of him were taken for friends by Sir Daniel Macnee[3], of which

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[1] I have given these details because some of the published statements regarding the cause of his decease are erroneous.

[2] He was a vigorous pedestrian, covering 60 miles a day with ease. When taking the week's end rest at Helensburgh, during his summer course of lectures, he habitually on Sunday walked to Glasgow, 22 miles, to be in time for his 8 o'clock Monday morning class.

[3] Macnee was a youth of fourteen living in Glasgow when my father, who was one of his earliest patrons, went there. He made for the latter chalk portraits of Arnott, Bentham, Allan and Richard Cunningham, Douglas, T. Drummond, Greville, A. Gray, Harvey, Richardson, Torrey, Wallich, and Wight; all now hanging in the Museum of the Royal Gardens. Sir D. Macnee rose to be President of the Royal Scottish Academy of Arts in 1876. He died in 1882.

the best known to me is that which prefaces this article. Other portraits of him are two life-size in oil by Thomas Phillips, R.A., one in my possession, and the other in that of Sir Leonard Lyell, Bart., of Kinnordy; the half-length in oil by Gambardella, in the Linnean Society's meeting room; a small engraving in the series of portraits of members of the Athenæum Club[1]; one by Maguire in the Ipswich series of portraits of scientific men; and an etching in profile by Mrs. Dawson Turner, from a profile by Cotman, unpublished, but widely distributed. There is also the bust in marble by Woolner in the Kew Museum, an excellent likeness.

His general health was excellent, but he suffered from deafness, and sometimes serious trouble in one ear, brought on by an attack of scarlet fever in Glasgow, when also his throat was severely cauterized, an operation which left that organ very susceptible to cold. His habits were of the simplest; he was at work by eight a.m., and again till near midnight. Under medical advice he dined for the last twenty years in the middle of the day, and took a light supper at seven or eight. Afternoon teas were unknown in those days. It rarely happened that the midday dinner was not also the lunch of some expected or unexpected guest or guests. His absence from London society, and especially from meetings of the Royal, Linnean, and Antiquarian Societies, of all which he had been a member for fifty years, was greatly regretted. But these were held at night, at a distance of seven miles from his dwelling-house, and for the ten years of his West Park life an omnibus that passed quite half a mile off was the only public conveyance from Kew to the metropolis.

He was a Fellow of the Royal, Linnean, Antiquarian, and Royal Geographical Societies, LL.D. of Glasgow, D.C.L. of Oxford, a Correspondent of the Academy of Sciences of France, Companion of the Legion of Honour, and member of almost every Academy in Europe and America which cultivated the Natural Sciences. In 1836 he received the honour of knighthood from His Majesty William IV,

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[1] Of which I find no copy in the Club.

together with the insignia of the Order of the Guelphs of Hanover, then an appanage of the British Crown.

In evidence of the estimation in which my father was held by his botanical contemporaries, I think I cannot better conclude this sketch of his life and labours than by giving the following extracts from the obituaries of him drawn up by the two most eminent then living botanists, one in America, the other in Europe. Of these, Prof. Asa Gray thus writes in the 'American Journal of Arts and Sciences,' 2nd Series, xli. 1 (1866):—'Our survey of what Sir William Hooker did for science would be incomplete indeed if it were confined to his published works—numerous and important as they are—and the wise and efficient administration through which, in a space of twenty-four years, a Queen's flower and kitchen garden and pleasure grounds have been transformed into an imperial botanical establishment of unrivalled interest and value. Account should be taken of the spirit in which he worked, of the researches and explorations he promoted, of the aid and encouragement he extended to his fellow labourers, especially to young and rising botanists, and of the means and appliances he gathered for their use no less than for his own.

'The single-mindedness with which he gave himself to his scientific work, and the conscientiousness with which he lived for science while he lived by it, were above all praise. Eminently fitted to shine in society, remarkably good-looking, and of the most pleasing address, frank, cordial, and withal of a very genial disposition, he never dissipated his time and energies in the round of fashionable life, but ever avoided the social prominence and worldly distinctions which some sedulously seek. So that, however it may or ought to be regarded in a country where Court honours and Government rewards have a fictitious importance, we count it a high compliment to his sense and modesty that no such distinctions were ever conferred upon him in recognition of all that he accomplished at Kew.

'Nor was there in him, while standing in a position like that occupied by Banks and Smith in his early days, the least manifestation of a tendency to overshadow the science with his own importance, or of indifference to its general advancement. Far from monopolizing even the choicest botanical materials which large expenditure of time and toil brought into his hands, he delighted in setting other botanists to work on whatever portion they wished to elaborate; not only imparting freely, even to young and untried men of promise, the multitude of specimens he could distribute, and giving to all comers full access to his whole herbarium, but sending portions of it to distant investigators, so long as this could be done without too great detriment or inconvenience. He not only watched for opportunities for attaching botanists to Government expeditions and voyages, and secured the publication of their results, but also largely assisted many private collectors, whose fullest sets are among the treasures of far the richest herbarium ever accumulated in one man's lifetime, if not the amplest anywhere in existence.'

From Prof. Alphonse de Candolle's long *éloge* (La vie et les écrits de Sir W. Hooker), published in the 'Archives des Sciences de la Bibliothèque universelle de Genève,' January, 1866, I have taken the following passages:—

'Et ici je me plais à répéter ce que beaucoup d'autres ont dit ou écrit. Hooker n'était pas de ces hommes qu'on oublie quand on les a vus une fois ou deux. Ses manières étaient aisées, affables, sa complaisance était réelle, son hospitalité charmante. La grâce de Lady Hooker y ajoutait beaucoup, j'en conviens, de sorte qu'il restait de la plus courte visite une impression durable. Sir William m'a toujours paru un type de vrai *gentleman* anglais. Il en avait les bonnes qualités et il en acceptait les charges. Poli envers tout le monde, libéral, oubliant ses intérêts au profit de la science, répondant à toutes les lettres et à toutes les demandes, il avait obtenu dans l'opinion publique une position exceptionnelle. Il était le protecteur des jeunes botanistes et des nombreux amateurs d'histoire naturelle qui partaient pour les colonies. S'il fallait créer un établissement public, donner des subventions, les ministres le consultaient. Sous ce rapport son influence directe ou indirecte s'est fait sentir dans le monde entier. Si l'on publie actuellement des Flores de presque toutes les colonies anglaises, on le doit principalement à ses conseils.

'Maintenant, dans quelle classe devons-nous ranger Sir William Hooker? Évidemment dans celle des botanistes actifs.

'Je pose la plume. Je parcours les rayons de ma bibliothèque, uniquement composée de livres de botanique et assez considérable, je consulte l'ouvrage précieux du *Thesaurus literaturae botanicae* de Pritzel, et je m'adresse la question suivante: en laissant de côté les compilateurs, quels sont les botanistes qui ont le plus écrit? La diversité des formats, la multiplicité des éditions, le mélange dans quelques ouvrages de morceaux de plusieurs auteurs, enfin la dispersion dans les journaux empêchent de répondre à cette question avec toute la précision désirable. Il me semble cependant que Linné, Augustin-Pyramus de Candolle et Sir William Hooker sont les trois botanistes qui ont été le plus laborieux.

'Peu de botanistes ayant eu à nommer des espèces de tous les pays, surtout des espèces de jardins, ont fait aussi rarement que lui des erreurs. Il avait eu soin de s'entourer de riches herbiers et d'une grande bibliothèque; il avait bonne mémoire; son coup d'œil était rapide. Grâce à tout cela ses descriptions marchaient vite et bien. On est rarement appelé à transporter d'un genre dans un autre les espèces qu'il a classées. Celles qu'il dit être nouvelles, le sont véritablement, à de rares exceptions près, et c'est un degré d'exactitude assez difficile à atteindre en ce qui concerne les plantes cultivées, et dans un ouvrage paraissant à jour fixe, comme le *Botanical Magazine.*

'Je me suis permis de caractériser nettement le botaniste en ce qui concerne ses travaux. Mais il y a, ne l'oublions pas, à côté des ouvrages de Hooker, l'action généreuse, incessante et éclairée qu'il a su exercer autour de lui et à distance. Il a inspiré le goût de la botanique à une foule de personnes, en particulier à son fils. Il a organisé l'établissement scientifique et horticole de Kew, un de ceux où l'on travaille le plus et où les botanistes de tous les pays trouvent le plus de ressources. En arrangeant et en démontrant les belles collections de ce jardin, il a rendu la science populaire. Grâce à ses antécédents et à l'agrément de ses manières, il a obtenu beaucoup en faveur soit de la botanique soit de l'horticulture. Ses recommandations étaient puissantes, même en Australie, dans l'Inde ou en Amérique, de telle sorte que bien des voyages, bien des découvertes et beaucoup de publications importantes sur la flore de pays lointains se rattachent déjà ou se rattacheront à lui, au moins par leur origine.'

J. D. HOOKER.

Nov. 1902.

APPENDIX A.

CATALOGUE, CHRONOLOGICALLY ARRANGED, OF SIR WILLIAM JACKSON HOOKER'S WORKS, WITH NOTES AND OBSERVATIONS.

1806–19. Assisting Mr. Turner in making Drawings and Analyses for his 'Fuci, sive plantarum Fucorum generi a botanicis adscriptarum icones, descriptiones et historia.' Four vols., 4to, with 258 coloured plates, of which 231 are signed W. J. H., Esq., delt.

1808. Musci Nepalenses, Trans. Linn. Soc. ix, 275, twelve species with three plates.

1810. On the Genus Andreaea, Trans. Linn. Soc. x, 381, with four species and one plate.

1811. Journal of a Tour in Iceland in the Summer of 1809, by William Jackson Hooker, Member of the Wernerian Society of Edinburgh. Four vols., 8vo, pp. 400, with four plates. Printed for private distribution.

1813. Ditto. Second Edition with additions, two vols., 8vo, with two maps and four plates. Dedicated to Sir Joseph Banks, Bart.

1816. British Jungermanniae, being a History and Descriptions, with coloured figures of each species of the genus, and microscopical analyses of the parts. 4to (a few copies also in folio), 197 species with 88 coloured plates. Dedicated to Dawson Turner, Esq., F.R.S., F.L.S.

1816. Plantae Cryptogamicae, quas in plaga orbis novi aequinoctialis collegerunt Alexander de Humboldt, et Aimat. Bonpland, adjectis tabulis species quasdam novas minusve cognitas exhibentibus; necnon Alexandri de Humboldt notationibus quibusdam Plantarum geographiam spectantibus. 4to, pp. 14, eight species, four coloured plates. (A fragment, never continued.) London, Paris, and Vienna.

1817. On Tayloria, a new Moss allied to the genus Splachnum. Brand's Journal of Science and Art, 1816, No. 3, p. 144, with one plate.

1817–28. Curtis's Flora Londinensis, new edition, by George Graves. This sumptuous but impracticable work in five vols. folio will be described under date of 1828.

1818–20. Musci Exotici, containing figures and descriptions of new or little known Foreign Mosses and other Cryptogamic subjects. 2 vols. 8vo, and a few copies 4to. 176 plates, coloured. Dedicated to James Brodie, Esq., of Brodie House, N.B.

1818. Muscologia Britannica, containing the Mosses of Great Britain and Ireland, systematically arranged and described, with plates illustrative of the characters of the Genera and Species, by W. J. Hooker and Thomas Taylor, M.D., &c. One vol. 8vo, with thirty-one coloured plates, by W. J. H. The plates also published separately in 4to form, coloured in a very superior manner, by George Graves. Species described, 269. Dedicated to Rev. James Dalton, M.A.

1819. Observations on the germination of Mosses, in a letter to William Jackson Hooker, Esq., F.L.S. By Mr. James Drummond, A.L.S. Trans. Linn. Soc. xiii, 24. The authorship of this article is erroneously attributed to W. J. H. in the Royal Society's Catalogue of Scientific Papers.

1821. Flora Scotica. Two parts, 8vo. Part I. Flowering Plants only, arranged according to the Linnean System. Part II. Including also the Cryptogamic Orders, &c., all arranged according to the Natural System. Of the second part the author says it may be considered as a joint work of himself and his friend Mr. Lindley; and the great assistance of his friend R. K. Greville, Esq., in respect of the minuter Fungi is acknowledged. Dedicated to the Chancellor of Glasgow University, James, Duke of Montrose. It gives an idea of the number of recorded Scottish plants in the first quarter of the nineteenth century, to find from this work, Acotyledons, 902, Monocotyledons, 159, Dicotyledons, 723; total, 1784.

1822. Botanical Illustrations for use in the Classroom. An oblong folio of twenty-four lithographed plates, with 327 figures of the organs of plants, &c., executed by the author.

1823–7. The Exotic Flora, containing figures and descriptions of new rare or otherwise interesting Exotic Plants, especially such as are deserving of being cultivated in our gardens, in three vols. 8vo, with 232 coloured plates chiefly by the author (which also appeared in 4to form). The work appeared in a serial. Dedicated to Charles Lyell, Esq., F.L.S., of Kinnordy. The subjects were supplied chiefly by the Botanical Gardens of Glasgow, Edinburgh, and Liverpool. Though financially a failure, the work benefited largely the above gardens, by attracting the attention especially of West Indian merchants, who directed their foreign agents and correspondents to collect and transmit living plants to them. One notable figure in the work is that of *Cattleya labiata*, Lindl., a plant which has, under its own and innumerable other varietal and hybrid names, received more horticultural awards than any other Orchid. It flowered for the first time in a stove in Mr. Hooker's garden in Halesworth in 1818, the plant having been sent him from Brazil by its discoverer, W. Swainson, Esq. This was six years before Lindley (in 1824) published the genus in the 'Collectanea Botanica,' p. 33.

1824–5. Hooker and Greville in Brewster's 'Edinburgh Journal of Science[1].' Four papers on ten genera of Mosses.

On *Orthotrichum* (including *Schlotheimia*, *Macromitrium*, and *Ulota*), *Glyphomitrium*, and *Zygodon*, vol. i, p. 110.

On *Tortula*, vol. i, p. 287.

On *Hookeria*, vol. ii, p. 221.

On *Calymperes* and *Syrrhopodon*, vol. iii, p. 218.

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[1] In this journal, vol. i, p. 173, the following announcement appeared:—'We may here mention, that Dr. Hooker, Professor of Botany in the University of Glasgow, is at this time engaged in preparing an Universal Flora in the English language, in which he will follow entirely the arrangements, and in many instances the generic and specific characters, which have been adopted by De Candolle in his Prodromus. Every new species to which Dr. Hooker can obtain access will besides be added, and the work will be accompanied by plates, drawn by himself, illustrative of the Natural Orders. The first part will appear at the commencement of the ensuing year.' My father did contemplate such a work, but I am very sure that he never put pen or pencil to paper in prosecution of it.

1825. Description of two West African plants in Gray and Douchard's 'Travels in West Africa.' Four species, with four plates.

—— **On the Botany of America.** Brewster's Edinburgh Journal of Science, vol. ii, p. 108.

—— **Catalogue of Plants contained in the Royal Botanic Gardens of Glasgow,** 8vo. About 7,000 species.

—— **Plants collected by Capt. (afterwards Sir Edward) Sabine, R.A.,** during the voyage in 1823 of H.M.S. *Griper* to Greenland, Melville Island, Spitzbergen, and the North Cape. Trans. Linn. Soc. xiv, 360. Ninety species, with one plate 4to.

—— **Appendix to Capt. (afterwards Sir Edward) Parry's 'Second Voyage in search of a North-West Passage,'** 4to. 173 species from the Polar Islands, with two plates 4to.

1826. Appendix to Capt. (afterwards Sir Edward) Parry's 'Third Voyage in search of a North-West Pasaage,' 4to. Eighty-four species from the American Polar Islands, 4to.

1827. The Botanical Magazine. The transition from the authorship of the 'Exotic Flora' to that of Curtis's 'Botanical Magazine' was direct. The latter publication, which had since its first appearance in 1787 been the leading illustrated botanical serial in Europe, with a sale of 3,200 copies in its early years, was in 1826 at a low ebb scientifically and financially, and was threatened with extinction. It had in England alone no fewer than ten illustrated competitors of various merit. At this critical period of its history my father was offered the editorship[1], and being assured of a supply of materials from the Gardens of Kew, Edinburgh, Liverpool, Glasgow, and some private collections, he accepted the offer, discontinued the 'Exotic Flora,' and threw all his energies into this new venture. For the first ten years he was for the most part his own artist, during which time he had

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[1] From 1827 till 1845 the title-page of the successive volumes proclaimed the work as 'conducted by Samuel Curtis, the descriptions by W. J. Hooker.' The fact was that the latter provided not only the plates, but the subjects for them, and was responsible for their execution and colouring. He was wholly author and editor of the work; of which the 'conductor' was the publisher and proprietor, nothing more.

succeeded in training a lad of remarkable promise as a botanical artist. This was the late Walter Fitch, F.L.S.[1], who executed about sixteen hundred plates for the 'Botanical Magazine' alone. Great improvements in the work were introduced by the new Editor, such as giving for the first time analyses of the plants, and by figuring species of economic interest, from specimens grown in England, or from drawings sent by foreign correspondents. At this time too the cultivation of Orchids was becoming a passion, and for twelve succeeding years Curtis's Magazine rivalled Edward's 'Botanical Register' (conducted latterly by Dr. Lindley) as an organ for depicting and describing them. In 1847 the Register came to an end deservedly regretted by all botanists and horticulturalists, and the Magazine soon after had outlived all its ten competitors of 1827. Another novelty introduced into it was the dedication of the successive annual volumes to individuals who had conspicuously advanced the study of botany or horticulture, and especially such as had contributed materials for the work. For the first person thus to be immortalized, the Editor had the satisfaction of selecting his early friend, Robert Barclay, Esq., of Bury Hill, one of the founders alike of the Magazine and of the great brewery. In the end my father produced thirty-eight volumes of the Magazine, with about 2,860 plates and descriptions.

In 1833, on the completion of the first series of the Magazine (vols. i–liii), the proprietor, S. Curtis, commenced the publication of a new edition, with amended characters of the species, the whole arranged according to the Natural Orders by W. J. Hooker; to which is added 'the most approved method of culture,' by S. Curtis. The work did not advance beyond the first volume, with 119 plates. In the Preface the proprietor announces that it was designed to 'afford an unprecedented opportunity for illustrating the Natural Orders of plants, by exhibiting nearly 2,800 figures, arranged according to that method.' An inspection of this fragment of the intended work shows that its discontinuance is regrettable.

The succeeding proprietor, Mr. Lovel Reeve, commenced in 1846 the issue of a work with the title 'A Century of Orchidaceous

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[1] See footnote to p. xl.

Plants, selected from the 'Botanical Magazine,' systematically arranged, accompanied with an introduction on the culture and general management of Orchidaceous plants, and with copious remarks on the treatment of each species,' by John Charles Lyons. Only one volume of this work appeared.

It may interest both the botanist and horticulturalist of the twentieth century to know the names of the individuals living in the first half of the nineteenth who were selected for the dedication of volumes of the Magazine. They were:

Vol. 54 (1827), Robert Barclay, Esq., of Bury Hill.
55 (1828), W. T. Aiton, Esq., Director of the Royal Gardens, Kew.
56 (1829), Joseph Sabine, Esq., F.R.S., L.S., &c., Secretary of the Horticultural Society.
57 (1830), Charles Telfair, Esq., of the Mauritius.
58 (1831), His Grace John, Duke of Bedford.
59 (1832), The Right Honourable Lord Viscount Milton.
60 (1833), The Right Honourable Countess of Dalhousie.
61 (1834), His Grace William, Duke of Devonshire, K.G.
62 (1835), L. F. H. von Ludwig, Ph.D., Cape of Good Hope.
63 (1836), D. Fischer, Counsellor of State, Director of the Imperial Botanic Garden of St. Petersburg.
64 (1837), James Bateman, Esq., of Knypersley Hall, Cheshire.
65 (1839[1]), The Honourable and Rev. William Herbert, of Spofforth.
66 (1840), James Parkinson, Esq., F.R.S. and L.S., H.B.M. Consul, Mexico.
67 (1841), Mrs. Wray, of Oakfield, Cheltenham.
68 (1842), Mrs. Lawrence, of Ealing Park, Middlesex.
69 (1843), Mrs. Sherbourne, of Hurst House, Prescot, Lancashire.
70 (1844), His Highness Prince de Salm Dyck, of Dyck.
71 (1845), The Right Honourable the Earl of Lincoln, Chief Commissioner of H. M. Woods and Forests, &c.

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[1] The apparent omission of 1838 is due to the dating the volume succeeding the sixty-fourth from the termination instead of the commencement of the year.

72 (1846), The Rev. J. Clowes, late of Broughton Hall, Manchester.

73 (1847), Capt. Sir Everard Home, Bart., R.N.

74 (1848), The Right Honourable the Earl of Carlisle, Chief Commissioner of H. M. Woods and Forests, &c.

75 (1849), Sir Lawrence Peel, Chief Justice of the Supreme Court of Calcutta.

76 (1850), Dr. John Torrey, of New York, Author of 'Flora of North America,' &c.

77 (1851), Dr. Asa Gray, Professor of Botany, University of Cambridge, Massachusetts.

78 (1852), N. B. Ward, Esq., F.R.S., F.L.S., Inventor of closely glazed cases.

79 (1853), His Excellency Sir Henry Barkly, K.C.B., &c., late Governor of British Guiana.

80 (1854), The Rev. M. J. Berkeley, M.A., F.R.S., Rector of Kings Cliffe, Northamptonshire.

81 (1855), Dr. Thomas Thomson, M.D., F.R.S., Superintendent of the Honourable East India Company's Botanic Garden, Calcutta.

82 (1856), Lady Dorothy Nevill, of Dangstein, Hants.

83 (1857), J. S. Mackay, Esq., LL.D., Author of 'Flora Hibernica.'

84 (1858), The Countess Doneraile, of Doneraile, Ireland.

85 (1859), Decimus Burton, Esq., F.R.S., Architect of the gates and Palm House of Kew.

86 (1860), G. H. K. Thwaites, Esq., F.L.S., Superintendent of the Royal Botanic Garden, Paradenia, Ceylon.

87 (1861), Dr. Ferd. Mueller, Ph. and M.D., F.R.S., Government Botanist, Victoria, Australia.

88 (1862), Thomas Bell, Esq., V.P.R.S., late President of the Linnean Society, London.

89 (1863), Dr. Robert Wight, M.D., Illustrator of Indian Botany.

90 (1864), Dr. Frederick Welwitsch, M.D., A.L.S., Traveller and Botanist. Explorer of tropical Western Africa.

1827. Additional testimony respecting the Sea Serpent of the American Seas. Edinb. Journn. Nat. Sc. vi (1827), p. 126. Consists of two evidently veracious accounts submitted to my father at second hand, of what the spectators believed to be sea-serpents, but which, as it appears to me, may have been shoals of porpoises.

—— **Muscologia Britannica,** second edition. Corrected and enlarged, with thirty-six plates and 378 species, including the Hepaticae which were not included in the first edition.

1828. Appendix to Parry's 'Fourth Voyage, An Attempt to reach the North Pole,' 4to; the species enumerated are eighty-eight from Spitzbergen, and forty-four from Hammerfest.

—— **Curtis's Flora Londinensis,** new edition[1], by Thomas Graves, F.L.S., in five vols. folio, with 666 plates, coloured, was in this year brought to an abrupt conclusion. This magnificent work taxed my father's time and artistic skill for ten years. Owing to incredible mismanagement on the part of the Editor, it never took the position in botanical literature which the excellence of the descriptions and beauty of the plates merited. The main cause of this was that (as in the case of the first edition), the plates not being numbered or referred to in the letter-press, which itself was not paged, citation was impossible. Furthermore, the title of the second edition is a misnomer; that of the first was 'Flora Londinensis, or Plates and Descriptions of such Plants as grow wild in the Environs of London'; that of the second is 'Flora Londinensis, containing a History of the Plants indigenous to Great Britain.' Neither edition has either Preface or Introduction, and the plates of the first bear no artist's signatures; they are no doubt by William Curtis himself, whose name on the title-page of the work is a guarantee for their truth and beauty. The accompanying descriptions are meagre. In the new edition the plates of vols. i–iii (443) are reprints from the coppers used in the first, and are of plants found in the environs of London; those of vols. iv and v are of plants very few indeed of which are indigenous anywhere near London. Of these,

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[1] The first edition was in two small folio volumes, with 434 coloured plates, published 1777–1787.

vol. iv (1821) contains 151 plates with rarely either an artist's or engraver's signature; most, if not all, of them are from drawings by my father. Vol. v (1828) contains seventy-two plates; all (except five of the Algae and Fungi signed R. K. Greville) were, I believe, by my father, and, like those of vol. iv, are recognizable as such by the drawings and analyses, and in the case of vol. v by many of them bearing the name of the well-known Glasgow engraver Swan, who engraved also for the 'Botanical Magazine' and for other of my father's publications. The descriptions throughout the five volumes were, except those of the plates signed R. K. Greville, I believe all written, enlarged, or rewritten by my father; but his name appears nowhere except on the title-pages of vols. iv and v, on which are inserted the words 'the Botanical descriptions arranged and corrected by W. J. Hooker,' words which apply to the preceding four volumes, as may be seen from a comparison of the two editions. Another anomaly in vols. iv and v is, that in their Indices but not on their title-pages they are entitled 'New Series.' To conclude, this rare and beautiful work was produced at great cost under financial embarrassment of the Editor (Mr. Graves), and its end is probably unique in the history of botanical works,—Chancery! under which I may add that the real author could hardly have been a beneficiary.

1828–31. Icones Filicum. Figures and Descriptions of Ferns, principally of such as have been altogether unnoticed by botanists, or as have not yet been correctly figured, by R. K. Greville and W. J. Hooker. Two vols. folio, with 240 coloured plates, all by R. K. G. The descriptions all by W. J. H. Dedicated to Dr. Wallich, Superintendent of the Honourable East India Company's Botanical Garden, Calcutta. The authors announce in the Preface that they contemplate a work to be called 'Filices Asiaticae,' of the size and plan of Wallich's 'Plantae Asiaticae Rariores,' which was never proceeded with.

1829–40. Flora Boreali Americana, two vols. 4to, with 138 uncoloured plates, 126 from drawings by the author. The work is founded chiefly on the collections made by Richardson and Drummond during Franklin's first Expedition to the Polar seas, by David Douglas and Mr. Tolmie in North-West America, and by Mr. Goldie in Canada. Including the Ferns and their allies the number of species described is 2,500. The only aid received was from Dr. Boott, who worked up the Carices (158 species).

1830. **The British Flora,** comprising the Phaenogamous or Flowering Plants and the Ferns, by Sir W. Jackson Hooker, LL.D., &c., 8vo. In the first edition of this work the Linnean system was adopted, followed by an Appendix on the Natural Orders. About 1,570 species are included. The second edition was published in 1831; the third in 1833, in two parts: Part I. Flowering Plants and Ferns, with four plates, containing analyses of eighty-two species; Part II. Cryptogamic Plants, also formed vol. v of Sir James Smith's 'English Flora.' This part did not accompany any future edition of the 'British Flora.' It appeared in two volumes, one, in 1833, comprising the Mosses, Characeae, Hepaticae, and Lichenes, by the author, and the Algae by Greville and Harvey; the other, in 1838, on the Fungi, is by the Rev. M. J. Berkeley. The fourth edition appeared in 1838; the succeeding four were issued from Kew. The fifth, in 1842, is the first in which the arrangement is throughout by Natural Orders. The sixth, in 1850, and succeeding, are by W. J. H. and G. A. Walker-Arnott, with twelve plates, containing the analyses of 118 species. The seventh appeared in 1855; the eighth and last in 1860; it contains about 1,636 species, or about sixty-six more than did the first edition published twenty-five years earlier.

1830. **An Encyclopaedia of Geography, by Hugh Murray,** assisted by the following gentlemen in their respective departments of Science:—William Wallace, Robert Jameson, W. J. Hooker, William Swainson. This is a ponderous 8vo volume of 800 pages, with eighty-two maps and upwards of 1,000 miniature woodcuts. My father contributed about 180 slight articles on the botany of thirty-seven countries or groups of countries, with about 220 woodcuts of plants by Fitch. In 1835 H. C. Watson contributed a paper to the 'Companion to the Botanical Magazine,' vol. i, p. 228, entitled 'Botany of Great Britain,' pointing out omissions and errors. A second edition appeared in 1840, 'thoroughly revised and brought down to the present time,' in which, however, the omissions and errors indicated by Watson in the first edition are not corrected. My impression is that the work was stereotyped, and the second edition is only a reissue of the first.

1830–41. The Botany of Capt. Beechey's Voyage in H.M.S. 'Blossom' to Behring's Sea, the Pacific Ocean, and China, by W. J. Hooker and G. A. Walker-Arnott. One vol. 4to, with ninety-nine uncoloured plates, mostly from drawings made by W. J. H. This work, which embraces nearly 2,700 species, is notable for the diversity of the Floras included. Its title conveys a very inadequate idea of its contents, for it includes not only the plants collected by the officers of the *Blossom*, Messrs. Lay and Collie, but the far larger collections made in British Columbia, Oregon, and California by Douglas, in British Columbia by Tolmie, in Mexico and Guatemala by Dr. Sinclair, and also in China by the Rev. G. H. Vachell and Charles Millett, Esq.

The approximate number of species brought together from the individual countries visited is as follows:—

Behring's Sea and Kotzebue's Sound (Arctic), 230; Kamchatka, 115.
Oregon and British Columbia, 500; California, 212.
Mexico, 275; Supplement, 162.
Chili, 300.
Society Islands, 194; Sandwich Islands, 240; Loochoo and Benin Islands, 261.
China, 335.

1830–3. The Botanical Miscellany, containing figures and descriptions of such plants as recommend themselves by their novelty, rarity, or history, or by the uses to which they are applied in the arts, medicine, and in domestic economy, together with occasional botanical notices and other information. Three vols. imp. 8vo, with 152 plates (112, and forty suppl.), some coloured, by the author and others. Dedicated to the Court of Directors of the Honourable East India Company.

Vol. 1 (1830), with seventy-five plates. Articles by the Editor[1]:—
On *Spiridens Reinwardtii*, Nees, p. 1, t. i.
Bryum Gilliesii, Hk., p. 3, t. ii.

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[1] In this and the other volumes of the Botanical Journals edited by my father, various unsigned articles attributed to him may have been supplied wholly or in part by botanical friends.

On *Astelia alpina*, Br., p. 5, t. iii.
Mutisia, 6 sp., pp. 7–12, t. iv–ix.
Jungermannia serrulata, Hk., β., p. 13, t. viii.
Usnea fasciata, Torr., and *sphacelata*, Br., p. 14, t. xi, xii.
Sticta macrophylla, Fée, and *Humboldtii*, Hk., pp. 17, 18, t. xiii, xiv.
Adenocaulon bicolor, Hk., p. 19, t. xv.
Swietenia Mahogani, Jacq., p. 21, t. xvi, xvii.
Scouleria aquatica, Hk., p. 33, t. xviii.
Bryum Menziesii, Hk., and *giganteum*, Hk., pp. 36, 37, t. xix, xx.
Dicranum phascoides, Hk., p. 39, t. xxi.
Riccia natans, L., p. 41, t. xxii.
Parnassia fimbriata, Kön., p. 43, t. xxiii.
Menyanthes Crista-galli, Menz., p. 45, t. xxiv.
Vohiria aphylla, Hk., and *tenella*, Guild., pp. 46, 47, t. xxv.
Monoclea crispata, Hk., p. 117, t. xxvii.
Sinapis frutescens, Ait., p. 119, t. xxviii.
Weissia verticillata, Hk., p. 121, t. xxix.
Guildingia psidioides, Hk., p. 122, t. xxx.
Phascum tetragonum, Hk., p. 124, t. xxxi.
Draba alyssoides, Hk., p. 126, t. xxxii.
Parmelia enteromorpha, Ach., p. 127, t. xxxiii.
Poinciana Gilliesii, Hk., p. 129, t. xxxiv.
Neckera Douglasii, Hk., p. 131, t. xxxv.
Grimmia crispata, Hk., p. 133, t. xxxvi.
Atropa rhomboidea, Hk., p. 135, t. xxxvii.
Brachymenium pulchrum, Hk., p. 136, t. xxxviii.
Colliguaja, Mol., 4 sp., p. 138, t. xxxix, xl.
Gymnostomum Wilsoni, Hk., p. 143, t. xli.
Colletia, Comm., *Discaria*, Hk., *Retanilla*, Brongn., *Trevoa*, Miers, pp. 150, 158, t. xliii–xlv.
Verbena and allied genera, p. 159, t. xlvi–xlix.
Macraea, Lindl., 4 sp., p. 176, t. l.
Castanospermum australe, Cunn. and Fras., p. 241, t. li, lii.
Gyrostemon attenuatum, Cunn., p. 243, t. liii.
Oxleya Xanthoxylon, Cunn., p. 246, t. liv.
Habenaria cordata, Br., p. 270, t. lv.
Castela Nicholsoni, Hk., p. 271, t. lvi.

Plates of t. lvii–lx of plants described by Jack in his 'Malayan Miscellanies,' p. 276, &c.

On *Byttneria heterophylla*, Hk., p. 291, t. lx.

Umbelliferae of South America, p. 323, t. lxiii–lxvi, lxvii, bis.

Macropodium nivale, Br., and *laciniatum*, Hk., p. 339, t. lxvii, lxviii.

Cardamine angulata, Hk., p. 343, t. lxix.

Lewisia rediviva, Pursh., p. 344, t. lxx.

Jaborosa caulescens, Gill. and Hook., p. 347, t. lxxi.

Hexaptera, 3 sp., p. 349, t. lxxii, lxxiv.

Gymnostomum amblyophyllum, Hk., p. 352, t. lxxv.

Vol. 2 (1831), with twenty plates, and suppl. Plates I–XIX. Articles by the Editor:—

On Burchell's 'Travels in Brazil,' p. 128.

Holboellia ornithocephala, Wall., p. 144, t. lxxvi.

Robert Barclay, memoir of, p. 122.

Spathicarpa hastifolia, Hk., p. 146, t. lxxvii.

Jungermannia Berteroana, Hk., p. 145, t. lxxviii.

Cyclomycas fusca, Kunze, p. 150, t. lxxix.

Gongora macrantha, Hk., p. 151, t. lxxx.

Telfairia pedata, Hk., p. 154, t. lxxxi, lxxxii.

Thelephora badia, Kl., and *Kunzei*, Kl., p. 162, t. lxxxiv, lxxxv.

Simblum periphragmoides, Kl., p. 164, t. lxxxvi.

Myonima multiflora, D.C., p. 165, t. lxxxvii.

Noronhia emarginata, p. 167, t. lxxxviii.

Chili plants of Mr. Cruckshanks, p. 205, t. lxxxix–xcv.

Greville and Hooker, *Enumeratio Filicum*, p. 360.

Vol. 3 (1832), with seventeen plates, and suppl. Plates XXI–XLI (Plate XX absent in all copies, and no reference to it in the text). Articles by the Editor:—

Greville and Hooker, *Enumeratio Filicum*, p. 104.

Greville and Hooker, on *Sarothria*, Linn., p. 232, t. cvii.

On *Cardamine rhomboidea*, D.C., and *rotundifolia*, Mich., p. 237, t. cviii, cix.

Greville and Hooker, *Polypodium melanopus*, Grev. and Hk., and *Gymnogramma* (Sphalm. *Cryptogramma*) *retrofracta*, Grev. and Hk., p. 384, t. cxi, cxii.

Hooker and Arnott, Contributions to the Flora of South America and the Pacific, pp. 129, 216, 302, t. xcvi–cvi; Journ. Bot. i, p. 276, t. cxxxvii; ii, pp. 19, 310; Comp. Bot. Mag. i, p. 29.

1832. The **Enumeratio Filicum**, by Greville and Hooker, recorded above under vols. i and iii of the 'Botanical Miscellany,' is not a mere enumeration, for it gives synonymy, citation of all authorities, habitats, and descriptions of new and imperfectly known species. Only thirteen genera are thus treated; they are referable to *Lycopodineae*, *Ophioglosseae*, *Marattiaceae*, and *Osmundaceae*, beyond which the work was not continued. The number enumerated under each is, *Psilotum*, 2 sp.; *Tmesipteris*, 1; *Lycopodium* (including *Selaginella*), 196; *Ophioglossum*, 17; *Botryopteris*, 1; *Helminthostachys*, 1; *Botrychium*, 13; *Marattia*, 10; *Angiopteris*, 1; *Danaea*, 5; *Kaulfussia*, 1; *Osmunda*, 12; *Todea*, 3. Some idea may be gained of the great changes in the history of Ferns that have supervened during the half-century or more that has passed since the publication of the 'Enumeratio,' by a reference to the condition of some of the above genera in the most recent works which include them:—*Lycopodium*, now generically separated from *Selaginella*, consists of ninety-four species, a singularly close approximation to the number (93) given by Greville and Hooker for this section of the genus. On the other hand, of *Selaginella* (sect. *Stachygynandrum* in the Enum.), of which only 104 species were known in 1832, there are 333 described in Baker's 'Handbook of Ferns and their Allies' (1887). Of *Ophioglossum*, the species are reduced from 27 to 10; of *Botrychium*, from 13 to 6; of *Marattia*, from 10 to 7; and of *Osmunda*, from 12 to 6. On the contrary, the species of *Danaea* have risen from 5 to 11, and of *Todea*, from 3 to 4.

1831–42. Supplement to the 'English Botany' of the late Sir James E. Smith and Mr. Sowerby, by Sir W. J. Hooker and other eminent botanists. Three vols., 8vo, with coloured plates.

Vol. 1 (1831), thirty-three plates and descriptions by Sir W. J. Hooker.

Vol. 2 (1834), seventeen plates and descriptions by Sir W. J Hooker.

Vol. 3 (1843), no plates.

1832. **William Woodville, 'Medical Botany,'** containing systematic and general descriptions with plates of all the medicinal plants comprehended in the catalogue of the Materia Medica, as published by the Royal College of Physicians of London and Edinburgh. Third edition, in which thirty-nine new plants have been introduced. The botanical descriptions arranged and corrected by W. J. Hooker. Five vols., 4to, 313 coloured plates. The first edition of this work was published in 1790–93, in three volumes, with 304 plates, from which time, till the appearance of Bentley and Trimen's 'Medicinal Plants' (1875–80), Woodville's 'Medical Botany' had been the standard work illustrating the plants of the British Pharmacopoeia.

1833. **An Introduction to the Study of Botany, by Sir J. E. Smith, M.D., F.R.S.** Seventh edition, corrected, in which the object of 'The Grammar of Botany,' by Sir J. E. Smith, is combined with that of the 'Introduction,' by W. J. Hooker. One vol., 8vo, with fourteen plates.

1834. **The Journal of Botany,** being a second series of the 'Botanical Miscellany.' Vol. 1 (1834), 8vo, with twenty-eight plates (CXIII–CXL), some coloured. The articles by the Editor are:—

New or rare *Orchideae*, p. 44, t. cxv–cxviii; p. 272, t. cxxxiv–cxxxvi.

Notice concerning T. Drummond's collections in south and west parts of the United States, pp. 50, 183. Comp. Bot. Mag. i, pp. 21, 39, 95, 170; ii, p. 60.

Greville and Hooker, Two *Gymnogrammae* from Peru, p. 61, t. cxix, cxx.

Arnott and Hooker, Mosses in the Dillenian Herbarium, p. 88.

Death of Mr. Telfair, p. 149, in note.

Botanical information, p. 157.

Contributions to a Flora of South America and the Pacific: see Bot. Misc. vol. iii.

Contributions to a Flora of Van Diemen's Land, p. 241, t. cxxxiii. Comp. Bot. Mag. i, p. 272.

Unio Itineraria, account of, p. 323.

Poeppig's 'Travels in South America,' p. 380.

1835. **Companion to the Botanical Magazine,** being a Journal containing such interesting botanical information as does not come within the prescribed limits of the Magazine; with occasional figures, by W. J. Hooker, LL.D., &c., in two vols., with thirty-two plates, royal 8vo.

Vol. 1 (1835), with nineteen plates. Articles by the Editor:—

Botanical information regarding collectors, travellers, and authors in North and South America, p. 14.

Notes concerning Drummond's collections. See under Journ. Bot. vol. 1.

Contributions towards a Flora of South America and the Pacific Islands. See under Journ. Bot. vol. 1.

Botanical information, pp. 14–20, 82–6, 119–21, 157–60, 186–95, 225–6, 282–8, 304–8.

Memoir and Works of William Jack, p. 121.

On Hewett Watson's 'Geography of British Plants and New Botanist's Guide,' p. 195.

Contributions towards a Flora of Van Diemen's Land. See under Journ. Bot. vol. 1.

On Webb and Berthelot's 'Natural History of Canary Islands,' pp. 283, 332.

On Belanger's 'Oriental Travels,' p. 285.

Vol. 2 (1836), with thirty-two plates, and portraits of David Douglas, Richard Cunningham, and John Fraser. Articles by the Editor:—

Botanical information, pp. 3–12, 72–9, 184–92, 222, 246–9, 338–52, 378–81.

On *Erythroxylon Coca*, Lam., p. 25, t. xxi.

Hooker and Arnott, Contributions to Flora of South America and Pacific, pp. 41, 250.

On T. Drummond's collections, p. 60.

Memoir of the life of David Douglas, p. 79.

On *Wardia hygrometrica*, Harv. and Hook., p. 183, t. xxv.

Biographical sketch of Richard Cunningham, p. 210.

Biographical sketch of John Fraser, p. 340.

1835. Appendix to Nightingale's 'Oceanic Sketches.' A list of twenty-nine species of Ferns, without habitats (one new?).

1836. Compendium of the English Flora of Sir James E. Smith. Second edition, with additions and corrections by W. J. Hooker, LL.D., &c., 12mo.

1836. Appendix to Captain (afterwards Sir George) Back's 'Arctic American Land Expedition': plants collected by Richard King, 136 species.

1837. Botanical Illustrations for Use in the Classroom. A thin 4to, with twenty-six plates, comprising 395 illustrations by W. Fitch. This replaced the oblong folio of 1822.

1837–65. Icones Plantarum, being figures with brief characters and remarks of new and rare plants selected from the Author's Herbarium. The first of ten vols., 8vo, with 1,000 plates by W. Fitch (of which 300 were issued from Glasgow). Dedicated to G. Bentham, Esq.

It may be recorded here that since Sir William's decease the title of the work has been modified by the substitution of 'Kew Herbarium' for 'Author's Herbarium,' and nine volumes have appeared under my editorship (1867–89), followed by five under that of Professor Oliver (1891–5); all the succeeding ones have been issued under that of Sir W. Thiselton-Dyer (1896–1902). The last part, vol. xxviii, Part II (1902), ends with Plate 2750, and Part III is in preparation. It remains to record that the drawings on stone of Plates 1001 to 1500 were delivered gratuitously to the publisher by Mr. Bentham, who supplied also most of the descriptions; and that since that gentleman's decease the expense of drawing the plates on stone has been defrayed from the proceeds of his bequest to the Kew Herbarium of a sum of money to be employed on such a work. Plates 1011 to 1200 were executed by W. Fitch; 1201 to 1353 by Miss A. M. Cockerill, and all subsequent by Miss Matilda Smith.

1838–40. Taylor's Annals of Natural History, or Magazine of Zoology, Botany, and Geology, with twenty-two botanical plates, conducted by Sir W. Jardine, Sir W. J. Hooker, and others. Vols. 1, 2, 3, 8vo. Articles by the Editor:—

Vol. 1. On the medical properties of *Lycopodium catharticum*, Hook., p. 428.

On *Erythraea diffusa*, Woods, p. 437.

Vol. 2. On two new Orchideous plants of Guiana, p. 329, t. xv.

On a state of *Viola lactea*, p. 383.

Vol. 3. On two South African genera of *Passifloreae*, p. 420, t. ix, x.

1838–40. Genera Filicum, or Illustrations of Ferns and other allied genera, from the original coloured drawings of Francis Bauer [1], Esq., Botanic Painter to His Majesty, with additions and descriptive letter-press, by Sir W. J. Hooker, K.H., &c., royal 8vo, with 126 coloured plates illustrating 135 genera, by W. Fitch. Dedicated to his Grace John, Duke of Bedford. This work, which is unique in point of artistic representation of Fern analyses, appeared in parts. It is really as regards the plates more the work of Fitch than of Bauer, and it is to be regretted that the artist's initials do not appear on these. Bauer's original drawings for the work are preserved in the British Museum, accompanied with the following note by Mr. Carruthers, F.R.S., written when that gentleman was Keeper of the Botanical Department:—'The original drawing of Tab. XXIV is wanting. The drawings for Tab. XLI–XLIX and LII–CXX were made by Mr. Fitch, who lithographed [2] the whole work.' Mr. Edmund Baker, Assistant in the Department, who gave me the above information, has kindly supplied me with a list of Bauer's drawings, with the dates of their execution (1833–6), and the sources of the specimens figured, of which twelve are from the Royal Gardens, Kew, and one, *Asplenium Ruta-mararia*, from Kew Churchyard (where it does not now exist); the remainder are presumably from herbarium specimens. Of Fitch's original drawings I have found no trace; they were no doubt made from analyses prepared by my father. Of the whole 135 genera depicted, I think that seventy-eight are by Fitch; and one of the most interesting features of the work is the marvellous power this artist exhibited in adopting so successfully Bauer's style [3] and treatment of his subjects (widely different from his own), that it is impossible to distinguish his work from that of his predecessor.

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[1] For a notice of Bauer's career, see p. xliii.

[2] A few of the plates were zincographed, but by far the greater number were printed from the stone by Messrs. Allan and Ferguson of Glasgow.

[3] To truthful delineation and colouring, perspective of every organ of a plant, and power of seizing its salient characters of habit, &c., Fitch added a marvellous rapidity in execution. In all these qualities but the last, both Francis and Ferdinand Bauer were his equals, and they added microscopic labour over the minutest details of colour, surface, and vestiture, thus reproducing not merely the likeness but almost the specimen itself, at the expense of as many days as it took Fitch hours to depict it.

1840. Copy of a Letter addressed by Sir W. J. H. to Dawson Turner, Esq., F.R.S. and L.S., on the occasion of the death of the late Duke of Bedford, particularly in reference to the services rendered by his Grace to Botany and Horticulture (printed only for private distribution). A thin 4to, with a coloured plate of *Bedfordia salicina.* Extracts from this letter relating to the Royal Gardens, Kew, will be found at p. xlix.

1840–4. The Journal of Botany, continued from vol. 1 (1834).

Vol. 2 (1840), with sixteen plates, including portraits of Olof Swartz and Dr. Robert Wight. Articles by the Editor:—

Botanical information, pp. 29–38, 103–27, 157–90, 194–210, 343–74, 432, 438.

Beeches of the Southern Hemisphere, p. 147, t. vi–viii.

Memoir of the life of Olof Swartz, with extracts from his letters, p. 382.

Vol. 3 (1841), with eighteen plates, including portrait of A. L. de Jussieu. Articles by the Editor:—

Botanical information, pp. 16–9, 134–47, 202–7, 280–307, 348–74, 441–2.

Hooker and Arnott, Contributions to the Flora of South America and the Pacific, pp. 19, 310. See Bot. Misc. vol. iii; Comp. Bot. Mag. i, 29.

On *Fissidens hyalinus,* Wils. and Hk., p. 89, t. ii.

On Torrey and Gray's 'Flora of North America,' p. 292.

Graham, John, of Bombay, Obituary notice of, p. 300.

Notes on the Banyan-tree, p. 351.

Vol. 4 (1842), with ten plates, including portraits of Allan Cunningham and L. C. Richard. Articles by the Editor:—

Botanical information, pp. 72–86, 198–229 (death of A. P. de Candolle).

On *Laurus australis,* A. Cunn. (*L. Bowiei,* Hk.), pp. 418 and 436, and erratum at end of Index.

1842. Notes on the Botany of the Antarctic Voyage of Captain J. C. Ross, R.N., by W. J. H., in Journ. R. Geograph. Soc. xii, 265. See also Lond. Journ. Bot. ii, 247, t. ix, x.

1842–8. The London Journal of Botany, containing figures and descriptions of such plants as recommend themselves by their novelty, rarity, history, or uses; together with botanical notices and occasional portraits and memoirs of eminent botanists (by W. J. H.). Seven vols., 8vo, with 166 uncoloured plates.

Vol. 1 (1842), with twenty-three plates. Articles by the Editor:—

Some accounts of the Paraguay Tea, p. 30, t. i–iii.

Botanical information, pp. 42–50, 86–106, 203–17, 258–63, 295–312, 392–418, 605–56.

On *Trichomanes Vittaria*, D.C., p. 137, t. v.

Cenomyce retipora, Ach., p. 292, t. x.

A new species of *Meniscium*, p. 294, t. xi.

Two species of *Chrysosplenium*, p. 457, t. xvi, xvii.

A new species of *Thuja* and *Podocarpus Totara*, Don., p. 570, t. xviii, xix.

Three species of *Podocarpus*, p. 656, t. xxi–xxiii.

Vol. 2 (1843), with twenty-four plates. Articles by the Editor:—

On *Juniperus bermudiana*, Linn., and *Dacrydium elatum*, Wall., p. 141, t. i, ii.

Botanical information, pp. 145–84.

On *Thuja chilensis*, Hk., p. 199, t. iv.

The Botany of H.M. Discovery Ships *Erebus* and *Terror* in the Antarctic Voyage, with account of the Tussac Grass, p. 247, t. ix, x. See also under 1842.

Two species of *Panax* from New Zealand, p. 421, t. xi, xii.

Baxteria, Br., p. 492, t. xiii–xv.

Castanea chrysophylla, Dougl., p. 495, t. xvi.

A new species of *Drapetes* from New Zealand, p. 497, t. xvii.

A new species of *Senebiera* from Patagonia, p. 506, t. xx.

Vol. 3 (1844), with twenty-four plates. Articles by the Editor:—

Botanical information, pp. 113–41, 263–314, 418–28, 481–533.

On *Oxalis lindseaefolia*, Hk., p. 141, t. i, ii.

The *Alerse* of Chili, p. 144, t. iv.

Mosses and Hepaticae of Brazil, by W. J. H. and W. Wilson, p. 149.

On *Exothea oblongifolia*, Macfad., p. 226, t. vii.

Notylia multiflora, Hk., p. 315, t. x.

Lunania, Hk., p. 316, t. xi, xii.

Vol. 4 (1845), with twenty-four plates. Articles by the Editor:—

Botanical information, pp. 14–42, 157–66, 197–249, 385–409, 479–97, 551–77, 643–62.

Vol. 5 (1846), with twenty-four plates. Articles by the Editor:—

Botanical information, pp. 7–41, 109–42, 19 -208, 242–50, 285–350, 417–43, 491–548, 656–62, 227.

On *Gymnopteris Vespertilio*, Hk., p. 193, t. vii, viii.

Vol. 6 (1847), with twenty-four plates. Articles by the Editor:—

Botanical information, pp. 31–79, t. v, vi; 206, 257–64, 465–60 bis, 604–8.

Geyer's 'Plants of Upper Missouri and Oregon,' pp. 65, 206. See Kew Gard. Misc. iii, 287; v, 257; vii, 371; viii, 16.

Botany of the Niger Expedition, by W. J. H. and J. D. H., p. 125.

On *Lisianthus splendens*, Hk., p. 264, t. viii.
Cardamine picta, Hk., p. 292, t. xii.
Isonandra Gutta, Hk., p. 463, t. xvii.

Vol. 7 (1848), with twenty-three plates. Articles by the Editor:—

Botanical information, pp. 28–56, 97–107, 161–4, 200–20, 237–71, 297–321, 370–94, 501–6, 537–62, 657–71.

On *Anemia Seemanni*, Hk., p. 564, t. xvi.
Ranunculus javanicus, Bl., p. 565, t. xvii.
Pentagonia pinnatifida, Seem., p. 566, t. xviii.
Sonerila scapigera, Hk., p. 672, t. xxiii.

1844. Kew Gardens, or a Popular Guide to the Royal Botanic Gardens of Kew, by W. J. H. 12mo, with pp. 60, and sixty-one woodcuts of exhibits by W. Fitch. This was the first of twenty-one editions brought out by W. J. H., the last in 1863.

1845–8. Companion to the Botanical Magazine, New Series[1], 8vo. Consists of articles bound up at the end of vols. lxxi–lxxiv of that Magazine, and should be cited as Bot. Mag. lxxi, Comp., with page.

Vol. 71 (1845). Articles by the Editor:—

Notice respecting the Botanical Gardens of Kew, p. 1.
On making Chinese paper, p. 42.
The Ivory Palm, *Phytelephas macrocarpa*, p. 44.

Vol. 72 (1846). Article by the Editor:—

Additions to the 'Hortus Kewensis,' p. 1.

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[1] These four appendices to the Botanical Magazine are not indexed. They have been overlooked in the Catalogue of Scientific Papers published by the Royal Society of London.

Vol. 73 (1847). Article by the Editor:—

Addition to the 'Hortus Kewensis,' pp. 1, 33.

Vol. 74 (1848). Article by the Editor:—

On the rediscovery of *Nelumbium jamaicense*, D.C., in Jamaica, p. 3.

1846–64. Species Filicum, being descriptions of the known Ferns, particularly of such as exist in the Author's Herbarium, or are with sufficient accuracy described in works to which he has had access, accompanied with numerous figures, by W. J. H. This, which will probably prove to be the most enduring monument to my father's labour as a systematist and descriptive pteridologist, is comprised in five 8vo volumes, embracing nearly 2,500 species, with 304 plates by Fitch, illustrating 520 of these. It occupied much of the latter eighteen years of his life, the last part appearing in 1864. The first volume is dedicated to Robert Brown.

1847. A Description of Victoria Regia, or the great Water Lily of South America, with four coloured plates by Walter Fitch. Small folio.

1849. The Admiralty Manual of Scientific Enquiry, prepared for the Use of H.M. Navy, and adapted for Travellers in general. Edited by Sir W. Herschel, Bt., published by authority of the Lords of the Admiralty. Botany by Sir W. J. Hooker. 8vo. Several editions of this work followed.

1849–57. Hooker's Journal of Botany and Kew Garden Miscellany[1]. Nine vols., 8vo, with 109 plates.

Vol. 1 (1849), with thirteen plates. Articles by the Editor:—

Botanical information and Notices of Books, pp. 20–32, 57–64, 90–6, 121–8, 144–60, 176–92, 213–24, 247–56, 282–8, 320, 336–61, 370–84.

Attalea funifera, Mart., p. 121, t. iv.

The Vegetable Ivory Palm, p. 204, t. vi, vii.

On *Pogostemon Patchouli*, Pell., p. 328, t. xi.

Vol. 2 (1850), with twelve plates. Articles by the Editor:—

Botanical information, pp. 23–32, 60–4, 92–6, 118–28, 151–60, 179–92, 218–24, 249–56, 285–8, 320, 248–352, 382–4.

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[1] To avoid confusion, this series of the Journals should be cited as 'Kew Garden Miscellany.'

Toddymen and Implements, p. 23, t. i, ii.

Lagetta lintearia, Lam., Lace-bark of Jamaica, t. iv, no description.

Rice-paper plant, pp. 27, 250, t. viii, ix.

Corchorus capsularis, Linn., p. 91, t. iii.

African Oak (*Oldfieldia africana*, Benth. and Hk.), p. 183, t. vi.

Eboe Nut (*Dipteryx oleifera*, Benth.), p. 249, t. vii.

On the Kooso (*Brayera anthelmintica*), p. 349, t. x.

On the Cedron (*Simaba Cedron*, Pl.), p. 377, t. xi. See also i, p. 204, and iii, p. 59.

Vol. 3 (1851), with twelve plates. Articles by the Editor:—

Botanical information and Notices of Books, pp. 21–32, 52–64, 91–6, 125–8, 154–60, 181–90, 217–22, 250–4, 283–6, 317–8, 346–50, 373–82.

Cedron (*Simaba Cedron*, Pl.), p. 59. See also ii, p. 377.

Ranunculus digitatus, Hk., p. 124, t. iv.

Arnebia fimbriopetala, Stocks' MSS., p. 180, t. vi.

Geyer's 'Plants of Upper Missouri and Oregon,' p. 287. See Lond. Journ. Bot. vi, 256.

Boehmeria nivea, Gaud., and *B. Puja*, Herb. Ham., p. 312, t. vii, viii.

Vol. 4 (1852), with twelve plates. Articles by the Editor: —

Botanical information and Notices of Books, pp. 26–32, 56–64, 93–6, 124–8, 155–61, 188–92, 217–24, 252–6, 278–88, 312–20, 347–52.

Rice-paper plant (*Aralia? papyrifera*, Hk.), pp. 50, 347, t. i, ii.

Dammara macrophylla, Lindl., p. 115, t. iv.

Tallow-tree and Insect Wax of China, p. 150.

Camphor-tree of Borneo (*Dryobalanops Camphora*, Coleb.), pp. 200, 285, t. vii, viii. See also vol. v, p. 220.

Vol. 5 (1853), with twelve plates. Articles by the Editor:—

Botanical information and Notices of Books, pp. 25–32, 59–64, 86–96, 122–8, 152–60, 187–99, 216–24, 247–56, 279–88, 312–20, 342–52, 396–416.

Rice-paper plant, p. 79. See also vii, p. 280.

The Camphor-tree of Borneo, p. 220.

New Fern from China, p. 236, t. i, ii.

Geyer's 'Plants of Upper Missouri and Oregon,' p. 257; vii, p.

371; viii, p. 16. See also iii, p. 287, and Lond. Journ. Bot. vi, pp. 65, 206.

Polypodium Lobbianum, Hk., p. 309, t. xi.

Kew Gardens Museum, pp. 239, 381. See also vi, p. 10; vii, p. 97.

Horkelia Gordoni, Hk., p. 341, t. xii.

Filices of Hong Kong, forty-one species, p. 353.

Eriogonum pyrolaefolium, Hk., p. 395, t. x (*staticifolium*).

Vol. 6 (1854), with twelve plates. Articles by the Editor:—

Kew Gardens Museums, p. 10. See also vii, p. 97, &c.

Botanical information, pp. 30–2, 54–64, 90–6, 123–8, 151–60, 185–92, 220–4, 247–56, 279–88, 315–20, 345–52.

Argania Sideroxylon, R. and S., p. 97, t. iii, iv.

Jumping Seeds, p. 304.

Obituary notice of J. E. Winterbottom, pp. 307, 345.

Obituary notice of J. E. Stocks, p. 308.

On *Cyperus polystachyus,* Rottb., in Ischia, p. 349.

On *Grevillea Gillivrayi,* Hk., and *Stenocarpus Milnei,* Hk., p. 358.

Vol. 7 (1855), with twelve plates. Articles by the Editor:—

Botanical information, pp. 23–32, 59–64, 87–96, 127–8, 151–60, 181–92, 213–24, 255–6, 280–8, 314–20, 343–52, 380–4.

Mora-tree (*Mora excelsa,* Bth.), p. 87.

Kew Gardens Museum, pp. 97, 129, 209, 245.

Asplenium fontanum, Br., in Britain, p. 340, viii. 25.

Vol. 8 (1856), with twelve plates. Articles by the Editor:—

Scirpus lacustris, L., in South America, p. 20.

Botanical information, pp. 22–32, 54–64, 81–96, 106–28, 150–60, 177–92, 210–24, 243–56, 281–8, 312–20, 347–52, 377–84.

Balsam-bog (*Bolax glebaria,* Comm.), p. 74.

Soap Plant of California (*Chlorogalum pomeridianum,* Kth.), p. 317.

Cuba Bast (*Paritium elatum,* Rich.), p. 347.

Polypodium anomalum, Hk., p. 360, t. xi.

Vol. 9 (1857), with twelve plates. Articles by the Editor:—

Botanical information, pp. 24–32, 58–64, 84–96, 115–28, 148–60, 185–92, 213–24, 252–6, 272–88, 312–20, 373–84.

On the Palmite of South Africa (*Prionium Palmita*, E. Mey.), p. 173, t. iv.

On *Asplenium nigripes*, Fée, and *Davallia? nodosa*, Hk., p. 265, t. ix, x.

Filices of Hong Kong, p. 353.

Concluding address by the Editor, p. 383.

1849. **Niger Flora,** or an Enumeration of the plants of Western tropical Africa collected by the late Theodore Vogel, Botanist to the Voyage of the Expedition sent by His Britannic Majesty to the river Niger, in 1841, under the command of Captain H. D. Trotter, R.N., including Specilegia Gorgonea by P.B. Webb, Esq., and Flora Nigritiana, by Dr. J. D. Hooker, R.N., F.R.S. and George Bentham, Esq., with a sketch of the life of Dr. Vogel. Edited by Sir W. J. Hooker, K.H., &c., one vol. 8vo, with two views, a map, and fifty plates (also published in Hooker's 'Icones Plantarum,' vol. viii). Preface and Desiderata by the Editor. Dedicated to Captain Trotter, R.N. Dr. Vogel's Journal of the Voyage, from May 12, 1841, to December 2, is also included in this work.

1851. **Victoria Regia,** or Illustrations of the Royal Water Lily, in a series of coloured figures, chiefly made from specimens flowering at Syon and at Kew, by W. Fitch; the descriptions by W. J. H. Plates, Elephant folio.

1852. **Description du Barclaya longifolia, Wall., de la Famille de Nymphaeacées.** Annales des Sciences Naturelles. Ser. III, vol. xvii (1852), pp. 301, t. 21. A detailed account. The figure is a copy of that in the 'Icones Plantarum,' t. 809, 810. The specific description is by Wallich.

1854. **A Century of Ferns,** being figures and descriptions of 100 new, rare, and imperfectly known species of Ferns, from various parts of the world, a selection from the author's 'Icones Plantarum,' large 8vo, with coloured plates. This is a reissue of vol. x of the 'Icones Plantarum,' which consisted wholly of Ferns, brought out by the publisher in a larger form with coloured plates for the use of pteridologists who were unable or indisposed to take the whole ten volumes of the work.

1855. **Museum of 'Economic Botany,'** or a Popular Guide to the Museum of the Royal Botanic Gardens of Kew; with pp. 80, 26 woodcuts of exhibits by W. Fitch, and descriptions of 560 objects most worth the visitor's inspection. See also Kew Gard. Misc., vols. v, vi, and vii.

1857. Report on Vegetable Products obtained without Cultivation, exhibited in the Paris Universal Exhibition of 1855, addressed by W. J. H. to the Right Honourable Lord Stanley of Alderley, President of Council of Board of Trade. Pp. 182, 8vo. The exhibits are arranged under countries.

1859. Filices Exoticae, or coloured figures and descriptions of Exotic Ferns, chiefly of such as are cultivated in the Royal Gardens of Kew, by W. J. H. The drawings executed by W. Fitch. 4to. Dedicated to the Right Honourable Lord John Manners, First Commissioner of Works. A beautiful work, with very full synonymy and copious dissertations. Only three species were previously undescribed. *Lycopodium*, *Selaginella*, and *Psilotum* are included. The drawings are masterpieces of the artist.

1861. A Second Century of Ferns, being figures with brief descriptions of one hundred new, rare, or imperfectly known species of Ferns, from various parts of the world, by W. J. H. One vol., imperial 8vo (1861), with plates coloured or uncoloured by W. Fitch. Dedicated to Dr. G. Mettenius of Leipsic. Of the species figured in this work forty were previously undescribed. The *Lycopodiaceae* (four species of *Selaginella*) and *Equisetaceae* (one species) are included.

—— **The British Ferns,** or coloured figures and descriptions, with the needful analyses of the fructification and venation, of the Ferns of Great Britain and Ireland, systematically arranged,' by W. J. Hooker. The drawings by Walter Fitch, F.L.S. One vol., royal 8vo, with sixty-six coloured plates. The *Filices* are subdivided into six sub-orders:—(1) *Polypodiaceae*, fourteen genera and thirty-nine species; (2) *Osmundeae*, one genus and species; (3) *Ophioglosseae*, two genera and two species; (4) *Lycopodieae*, one genus and six species; (5) *Isoeteae*, one genus and two species; (6) *Marsileae*, one genus and one species. In all twenty genera and 51 species. The synonymy is very fully given, and the discussions on critical species are generally very detailed. Thus for *Cystopteris fragilis*, Bernh., and its variant *dentata*, sixteen synonyms are given under twenty-nine citations. New Zealand is added to its known range of distribution (I believe that Australia is the only large area in which it has not been found). As showing the advances made in the study of *Filices* as understood at the date of the publication of 'The British Ferns,' it may be stated that in my latest work on this subject ('The Student's Flora of the British Islands,' 1884), the *Filices* of that work are grouped under four natural Orders:—(1) *Filices*, seventeen genera and thirty-eight species; (2) *Lycopodiaceae*, one genus and five species; (3) *Selaginellaceae*, two genera and three species; (4) *Marsileaceae*, one genus and species. In all twenty-one genera and forty-seven species. In the eighth edition (1890) of the 'London Catalogue of British Plants' fifty-nine are given.

1862. Garden Ferns, or coloured figures and descriptions, with the needful analyses of the fructification and venation, of a selection of Exotic Ferns adapted for cultivation in the Garden, Hothouse, and Conservatory, by W. J. Hooker. The drawings by Walter Fitch, F.L.S. One vol., royal 8vo, with sixty-four plates (1862). As in the case of the 'Filices Exoticae,' the plants figured in this work, the last completed by the Author, then in his seventy-seventh year, were for the most part cultivated in the Royal Gardens, Kew. It includes as Ferns a *Marsilea* and *Helminthostachys*; eight of the plates are devoted to *Trichomanes*, one, *T. pinnatum*, Hedw., with seventeen synonyms, and another, *T. javanicum*, with eighteen.

1863. Letter from Sir W. J. H. to the Secretary of State for the Colonies on the publication of Colonial Floras. See p. lxxxii.

1865. Synopsis Filicum, or a Synopsis of all known Ferns, including the *Osmundaceae*, *Schizaeaceae*, *Marattiaceae*, and *Ophioglossaceae* (chiefly derived from the Kew Herbarium). Accompanied by figures representing the essential characters of each genus, by the late Sir W. J. H., Director of the Royal Gardens, Kew, and John Gilbert Baker, F.L.S., Assistant-Curator of the Kew Herbarium. One vol., 8vo, with nine coloured plates containing analyses of seventy-five genera (1868). Upon this posthumous work my father was engaged up to a few days before his decease, and forty-eight pages of it in print were left on his desk, together with the Preface and much matter in manuscript. After full consideration it appeared to me that, with the material in hand, the aid of the 'Species Filicum' completed only three years earlier, and of the Fern Herbarium in perfect order, and named according to his views, a competent botanist should find no great difficulty in carrying on this work to its completion. Such a botanist I knew my friend Mr. Baker to be, and also that he had made a study of Ferns, and accepted my father's limitations of their genera and species. I therefore requested that gentleman to undertake the work, which to my great satisfaction he has done. The 'Synopsis Filicum' contains seventy-five genera and about 2,252 species, inclusive of *Osmundaceae*, *Schizaeaceae*, *Marattiaceae*, and *Ophioglossaceae* (fourteen genera and about 107 species), which are not included in the 'Species Filicum.' The total number of plates of Ferns published by my father is about 1,210, embracing 1,267 species; of which about 250 appeared under the joint authorship of Dr. Greville and himself.

APPENDIX B.

AN ATTEMPT TO CLASSIFY THE MORE IMPORTANT ARTICLES CONTAINED IN THE BOTANICAL JOURNALS EDITED BY SIR W. J. HOOKER, EXCLUSIVE OF CATALOGUES OF COLLECTIONS AND PURELY SYSTEMATIC AND DESCRIPTIVE ARTICLES, WHICH MAY BE SUPPOSED TO BE INCORPORATED IN LATER WORKS.

List of Botanical periodicals with dates, &c. :—

1. The Botanical Miscellany (Bot. Misc.). 3 vols. 152 plates. 1830–3.

2. The Journal of Botany (Journ. Bot.). Vol. i. 21 plates. 1834.

3. The Companion to the Botanical Magazine (Comp. Bot. Mag.). 2 vols. 34 plates. 1835–6.

4. Jardine's (or Taylor's) Annals of Natural History (Ann. Nat. Hist.). 4 vols. (vols. i–iv). 22 botanical plates. 1838–40.

5. The Journal of Botany continued (Journ. Bot.). Vols. ii–iv. 37 plates. 1840–2.

6. The London Journal of Botany (Lond. Journ. Bot.). 7 vols. 164 plates. 1842–8.

7. The Companion to the Botanical Magazine, New Series (Bot. Mag. Vol. xx, Comp.), consisting of Appendices to Vols. lxii–lxxxiv of that work. No plates. 1845–8.

8. The London Journal of Botany and Kew Garden Miscellany (Kew Gard. Misc.). 9 vols. 109 plates. 1849–57.

(In all 28 volumes, exclusive of the Appendices to Vols. lxxii–iv of the Botanical Magazine, and 556 Plates.)

B i. REVIEWS AND NOTICES OF BOTANICAL WORKS, HERBARIA, AND GARDENS; ALSO LETTERS FROM TRAVELLERS, COLLECTORS, AND BOTANISTS REFERABLE TO INDIVIDUAL COUNTRIES; ARRANGED GEOGRAPHICALLY.

I. EUROPE.

GREAT BRITAIN AND IRELAND.

Andrews (W.). Botany of Great Arran Island, Lond. Journ. Bot. iv, 569.

Arnott and Hooker. On Musci of the Dillenian Herbarium, Journ. Bot. i, 88.

Babington (C. C.). Flora Sarnica, Journ. Bot. ii, 185; Ann. Nat. Hist. iii, 341.

—— Botany of the Channel Islands, Ann. Nat. Hist. ii, 348.

—— Flora Bathoniensis, Journ. Bot. ii, 185.

Baker (J. G.). Geognostic Relations of British Plants, Kew Gard. Misc. viii, 157.

—— Hieracia of N. Yorkshire, &c., Kew Gard. Misc. vi, 57.

Ball (J.). A Botanical Tour in Ireland, Ann. Nat. Hist. ii, 28.

Banks (Sir J.). Herbarium of, Journ. Bot. iii, 363.

Baxter (W.). Stirp. Cryptog. Oxon., Journ. Bot. i, 158.

Bentham (G.). Herbarium of, Journ. Bot. iii, 365.

Berkeley (Rev. M. J.). Specimens of British Fungi, Comp. Bot. Mag. i, 282.

—— Gleanings of British Algae, Bot. Misc. iii, 367.

—— Notices of British Fungi, Ann. Nat. Hist. i, 198, 257.

Bloxam (Rev. A.). British Rubi, Lond. Journ. Bot. v, 660.

Bobarts (J.). Herbarium of, Kew Gard. Misc. vi, 248.

Bohler (J.). Lichenes Britannici, Comp. Bot. Mag. i, 19.

British Museum. Herbarium of, Journ. Bot. iii, 362.

Bromfield (W. A.). On Spartinae, Comp. Bot. Mag. ii, 254.

—— Flora of the Isle of Wight, Kew Gard. Misc. v, 256; viii, 281.

Cambridge. Bot. Garden of, Bot. Misc. i, 55.

Chalmers (J.)[1]. Algae Scoticae, Journ. Bot. i, 158.

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[1] This is the only allusion that I have met with to 'Fascicles of named Scotch Algae,' issued by a very intelligent man who acted for some years as a manipulator

Chelsea. Botanical Garden of, Bot. Misc. i, 67.

Croall (A.). Botany of Clova Mts., Kew Gard. Misc. v, 337, 389.

—— Plants of Braemar, Kew Gard. Misc. vi, 284.

Daubeny (C.). The Oxford Herbarium, Kew Gard. Misc. vi, 247, 279.

Dickie (G.). Altitudes of Aberdeenshire Plants, Lond. Journ. Bot. ii, 131, 355; vi, 197.

Dillenius. Herbarium of, Kew Gard. Misc. vi, 249.

Du Bois (F.). Herbarium of, Kew Gard. Misc. vi, 249.

Dublin College. Herbarium of, Lond. Journ. Bot. iii, 299.

Edmonstone (T.). Flora of Shetland, Lond. Journ. Bot. iii, 295.

Fielding (H. B.). Herbarium of, Kew Gard. Misc. vi, 279.

Francis (G. W.). The Little English Flora, Ann. Nat. Hist. iii, 187.

Gardiner (W.). Musci Angusiani, Comp. Bot. Mag. ii, 338.

—— Plants of Clova Mts., Lond. Journ. Bot. ii, 160; iii, 138.

—— Rambles in Braemar, Lond. Journ. Bot. iv, 208, 497.

—— Lessons on British Mosses, Lond. Journ. Bot. v, 244; Kew Gard. Misc. i, 288.

—— Flora of Forfarshire, Lond. Journ. Bot. vii, 387.

Gardner (G.). British Mosses, Comp. Bot. Mag. i, 3, 20.

Graham (R.). Herbarium, Sale of, Lond. Journ. Bot. v, 11.

Hartmann (H.). Scandinavian Plants in Linn. Herb., Kew Gard. Misc. iv, 217, 252; v, 25.

Harvey (W. H.). British Algae, Journ. Bot. i, 296; Lond. Journ. Bot. v, 245.

—— Sea-side Book, Kew Gard. Misc. i, 192.

—— Keeper of Herbarium of Dublin University College, Lond. Journ. Bot. iii, 299.

—— Professor of Botany, Royal Dublin Institution, Lond. Journ. Bot. vii, 163.

—— On Saxifraga Andrewsii, Harv., Lond. Journ. Bot. vii, 569.

Hassall (A. H.). British Fresh-water Algae, Lond. Journ. Bot. iii, 136.

Hobson (E.). Musci Britannici, Journ. Bot. i, 158.

Hooker (W. J.). Herbarium of, Journ. Bot. iii, 366.

—— Royal Bot. Gardens, Kew, Bot. Mag. lxxi, Comp. i.

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in my father's Herbarium at Glasgow (see p. xxxiv). There is no copy of his Fascicles in the Kew Library, but the specimens are incorporated in the Kew Herbarium.

Hooker (W. J.). Guide to Royal Bot. Gardens, Kew, Kew Gard. Misc. viii, 352.

—— Guide to Museums of Royal Bot. Gardens, Kew, Kew Gard. Misc. iv, 150; v, 329, 381; vi, 10; vii, 97, 129, 209, 245, 273; viii, 352.

—— Observations on British Plants, Comp. Bot. Mag. i, 188, 225.

—— British Flora, Bot. Misc. i, 353; Ann. Nat. Hist. ii, 476.

Horticultural Society. Gardens of, Bot. Misc. i, 65.

Ibbotson (H.). Plants of North England, Lond. Journ. Bot. iv, 496.

Irvine (A.). The London Flora, Ann. Nat. Hist. iii, 186.

Johnson (J.). Iter Plantarum, Lond. Journ. Bot. iii, 114.

—— Opuscula omnia, Lond. Journ. Bot. vii, 272.

Kew. Royal Gardens of, in 1824, Bot. Misc. i, 64.

Lambert (A. B.). Herbarium of, Bot. Misc. i, 62; Journ. Bot. iii, 365; Lond. Journ. Bot. i, 394.

Leefe (Rev. J. C.). British Willows, Lond. Journ. Bot. i, 418; ii, 156; iv, 219.

Lindley (J.). Works on British, &c., Plants, Comp. Bot. Mag. i, 186.

—— Herbarium of, Journ. Bot. iii, 365.

Lindsay (Lauder). Popular History of British Lichens, Kew Gard. Misc. viii, 256.

Linnaeus. Visit to Oxford, Bot. Misc. i, 59.

Linnean Society. Herbarium of, Bot. Misc. i, 61; Journ. Bot. iii, 354, 361; Kew Gard. Misc. iv, 217, 252; v, 25.

Loddiges (C.). Nursery Gardens of, Bot. Misc. i, 74.

London Catalogue of British Plants, Kew Gard. Misc. ix, 379.

Marshall (W.). On Anacharis Alsinastrum, Kew Gard. Misc. iv. 320.

McIvor (W. G.). Hepaticae Britannicae, Lond. Journ. Bot. vi, 327; vii. 55.

Menzies (A.). Herbarium of, &c., Bot. Misc. i, 69.

Mitten (W.). Plants new to British Flora, Lond. Journ. Bot. vii, 528, 556.

Moore (T.). Popular History of British Ferns, Kew Gard. Misc. i, 31; iv, 63.

—— Handbook of British Ferns, Kew Gard. Misc. v, 416.

Moore (T.). Ferns of Gt. Britain and Ireland, Kew Gard. Misc. vii, 286, 320, 350; viii, 28, 125, 285.

Morison (R.). Herbarium of, Kew Gard. Misc. vi, 248.

Murray (Alex.). The Northern Flora, Comp. Bot. Mag. ii, 78.

Oxford University. Herbarium of, Kew Gard. Misc. vi, 247, 279.

—— Botanical Gardens of, Bot. Misc. i, 57.

Packer (James). British Mosses, Kew Gard. Misc. vii, 128.

Ralfs (J.). British Desmidieae, Lond. Journ. Bot. vii, 392, 501.

—— British Phaenog. Plants and Ferns, Journ. Bot. ii, 183.

Salway (Rev. T.). On Conferva aegagropila, Lond. Journ. Bot. vii, 213.

Schultes (Dr.). A Botanical Visit to England in 1824, Bot. Misc. i, 48.

Shaw (Rev. T.). Herbarium of, Kew Gard. Misc. vi, 250.

Sherard (W.). Herbarium of, Kew Gard. Misc. vi, 248.

Sibthorp (J.). Herbarium of, Kew Gard. Misc. vi, 250.

Smith (Sir James). Herbarium of, Bot. Misc. i, 50; Journ. Bot. iii, 361.

Stevens (H. O.). On the Mycology of the neighbourhood of Bristol, Ann. Nat. Hist. iv, 246.

Taylor (T.). Herbarium and Library of, Lond. Journ. Bot. vii, 445.

Wallich (N.). Herbarium of, Journ. Bot. iii, 361.

Ward (N. B.). On Cases for Transport of Plants, Comp. Bot. Mag. i, 317; Kew Gard. Misc. v, 64.

Watson (H. Cottrell). Extension of Brit. Plants in Elevation and Distribution, Comp. Bot. Mag. i, 86.

—— Botanical Geography of Britain, Lond. Journ. Bot. iv, 199.

—— Characters of some Brit. Plants, Lond. Journ. Bot. iii, 62.

—— Cybele Britannica, Lond. Journ. Bot. vi, 260; Kew Gard. Misc. i, 383; iv. 223.

—— On Distinction of Species, Lond. Journ. Bot. ii, 613.

—— Geograph. Distrib. of Brit. Plants, Lond. Journ. Bot. ii, 154; iv, 199; Comp. Bot. Mag. i, 195.

—— On Murray's Encycl. of Geography, Comp. Bot. Mag. i, 228.

—— Proportions of Nat. Ord. of Brit. Plants at Different Elevations, Comp. Bot. Mag. i, 196.

—— Notices of Plants new to Brit. Flora, Lond. Journ. Bot. i, 76.

—— New Botanists' Guide, Comp. Bot. Mag. i, 195.

—— Observations on Brit. Plants, Journ. Bot. i, 258, 306.

Watson (H. Cottrell). Perthshire, Bot. Tour in the Highlands of, Kew Gard. Misc. ix, 381.

—— Plants of the Grampians, Lond. Journ. Bot. i, 50, 241.

—— Remarks on the English Flora, Bot. Misc. ii, 133, 406.

Webb (Rev. R. H.). Flora Hertfordiensis, Kew Gard. Misc. i, 31.

Wilson (W.). Observations on Brit. Plants of 'The English Flora,' Bot. Misc. i, 336; ii, 133, 406; iii, 109; Journ. Bot. i, 258, 306, 312; iii, 374.

—— Localities of rare Scotch Plants, Bot. Misc. i, 81.

—— Notes on British Muscology, Journ. Bot. iii, 374.

—— Bryologia Britannica, Kew Gard. Misc. vi, 255; vii, 155.

Woods (J.). The 'Tourist's' Flora, Kew Gard. Misc. ii, 256.

—— On the British Salicornias, Kew Gard. Misc. iii, 96.

—— Botany of the N. of England, Comp. Bot. Mag. i, 288.

Wyatt (Mary). Algae Damnonienses, Journ. Bot. i, 157; Comp. Bot. Mag. i, 325; ii, 246.

SCANDINAVIA.

Bentham (anonym.). Botany in Copenhagen, Lond. Journ. Bot. v, 525.

Blytt (A.). Plantae Novegicae rariores, Kew Gard. Misc. viii, 284.

Crowe (H. W.). Finland Bread, Kew Gard. Misc. ix, 279.

Fries (E.). Noviciae Florae Suecicae, Mant. l, Ann. Nat. Hist. iii, 256.

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B vi. CATALOGUE OF ARTICLES ON AND NOTICES OF THE MORE IMPORTANT[1] ECONOMIC PLANTS CONTAINED IN THE BOTANICAL JOURNALS; TO WHICH ARE ADDED REFERENCES TO FIGURES OF THOSE PUBLISHED BY THE EDITOR IN THE BOTANICAL MAGAZINE.

Achras Sapota, L., *see* Bulley-tree.

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Alligator Apple (Anona palustris, L.), Bot. Mag. t. 4226.

—— **Pear** (Persea gratissima, Gaertn.), Bot. Mag. t. 4580.

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[1] Notices of very many more Economic Plants will be found under their native names in the letters of travellers, but these being scientifically unidentifiable are not taken up here. See also under the heads of the Kew Museums and other articles for innumerable mentions of Economic Products.

Aloes, Cape, Kew Gard. Misc. iv, 238; ix, 126.
Andiroba Oil (Carapa guianensis, Aubl.), Kew Gard. Misc. vi, 335.
Antà (Phytelephas sp.), *see* Ivory Palm of Panama.
Apple, Water (Anona palustris, L.), Bot. Mag. t. 4226.
—— **Malay** (Jambosa malaccensis, D.C.), *see* Malay Apple.
—— **Star** (Chrysophyllum Cainito, L.), *see* Star Apple.
—— **Sugar** (Anona squamosa, L.), *see* Sweet Sop.
Arabia, Drugs of, Kew Gard. Misc. v, 124.
Arachis hypogaea, *see* Ground-nut.
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Araucaria imbricata, Pav., Comp. Bot. Mag. i, 351.
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Argan-tree of Morocco (Argania Sideroxylon, R. and S.), Kew Gard. Misc. vi, 97, t. iii, iv.
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Attalea funifera, Mart., *see* Coquilla-nut.
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Avocado Pear, *see* Alligator Pear.
Bahamas Islands, Fibres of, Kew Gard. Misc. vi, 237.
Balsam-bog (Bolax glebaris, Comm.), Kew Gard. Misc. viii, 74.
Balsam-trees of Scinde, Kew Gard. Misc. i, 257, t. viii, ix.
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Banyan-tree (Ficus indica, L.), Journ. Bot. iii, 284, 287, 351, t. xiii, xiv.
Barley, Tibetan, Lond. Journ. Bot. vii, 215.
Batatas dozes (Convolvulus edulis, Thunb.), Journ. Bot. i, 19.
Beeberu or Birbiru Tree (Nectandra Rodiaei, Schomb.), *see* Greenheart-tree.

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Bhang (Cannabis sativa, L.), Kew Gard. Misc. vi, 277.
Bitter Root (Lewisia rediviva, Pursh.), *see* Spatulum.
Black Pepper (Piper nigrum, L.), *see* Pepper.
Bonapartea, Fibre of, Kew Gard. Misc. viii, 369.
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Brayera anthelmintica, Kth., *see* Kosoo.
Bread of Finland (made of Lichens), Kew Gard. Misc. ix, 279.
—— **Native, of Tasmania** (Mylitta ?), Comp. Bot. Mag. ii, 40.
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Camphor-tree of Sumatra, Comp. Bot. Mag. i, 265; Kew Gard. Misc. iv, 33, 68, 200.
Canara, Drugs of, Kew Gard. Misc. vii, 314.
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Tea, Cultivation in Assam, Journ. Bot. ii, 169; iii, 137.
—— **Green, Manufacture of, in China,** Kew Gard. Misc. iv, 23.
—— **Introduction into France,** Journ. Bot. iii, 1.
—— **Paraquay** (Ilex paraguayensis, Lam.), *see* Mate.
—— **Varieties of, in Kew Economic Museum,** Kew Gard. Misc. vii, 130.
Teak, African (Oldfieldia africana, Benth. and Hook.), *see* African Oak.
—— **Forests of India** (Tectona grandis, L.), Kew Gard. Misc. v, 256.
Telfairia pedata, Hook., *see* Liana Lejoliff.
Thuja tetragona, Hook., *see* Alerse.
Tobacco, Congo (Cannabis sativa, L.), Kew Gard. Misc. iii, 9.
Toddy Palm (Cocos nucifera, L.), Kew Gard. Misc. ii, 23, t. i, ii.
Tonquin Bean (Dipterix oleifera, Hook.), *see* Eboe-nut.
Travancore, Drugs of, Kew Gard. Misc. vii, 314.
Tussac Grass (Dactylis caespitosa, Forst.), Lond. Journ. Bot. ii, 280, 293, t. ix, x; vi, 477.
Ucú-Uba, Oil tree (Myristica sebifera, Sw.), Kew Gard. Misc. ii, 66.
Ulluco (Ullucus tuberosus, Cald.), Bot. Mag. t. 4617.
Uncaria Gambir, Roxb., *see* Gambir.
Uncomo-como (Aspidium athamanticum, Kunze), Kew Gard. Misc. v, 311.
Upas-tree (Antiaris toxicaria, Vent.), Comp. Bot. Mag. i, 310, t. xvii; Ann. Nat. Hist. ii, 295.
Vanilla, Production of, in Europe, Ann. Nat. Hist. iii, 1.
Vateria indica, *see* Piney Resin.
Vegetable Ivory (Phytelephas macrocarpa, R. and S.), *see* Ivory Palm.
—— —— **of Panama** (Phytelephas sp.?), *see* Ivory Palm.
Vine, Disease of, Kew Gard. Misc. vi, 49.
Vinhatico (Laurus indica, L.), Journ. Bot. i, 18.

Visnaga (Echinocactus Visnaga, Hook.), Kew Gard. Misc. iv, 123; Bot. Mag. t. 4 59.

Vutsunab (Lagenandra toxicaria, Dalz.), Kew Gard. Misc. iv, 289.

Waccawai Nutmeg (Acrodiclidium Camara, Schomb.), *see* Camara.

Warburg's Fever Drops, *see* Greenheart-tree and Beeberu.

Ward's Cases, Comp. Bot. Mag. i, 317.

Wax Insect of China, *see* Insect Wax.

Zabucaya-nut (Lecythis Zabucajo, Aubl.), Kew Gard. Misc. i, 21.

Zapote blanco (Casimiroa edulis, Ll. and Lex.), Kew Gard. Misc. ii, 366.

Zizyphus Jujuba, Lam., Vars. of, *see* Jujubes.

B vii. OBITUARY NOTICES, MEMOIRS, ÉLOGES, AND PORTRAITS OF BOTANISTS.

Aucher, Eloi (1838). Lond. Journ. Bot. iii, 167. Ispahan.

Barclay, Robert (1830). Bot. Misc. ii, 122. Bury Hill.

Bartram, John (1777). Lond. Journ. Bot. i, 1; Kew Gard. Misc. ii, 62. Delaware.

Bauer, Ferdinand (1826). Lond. Journ. Bot. ii, 106. Vienna.

Bertero, M. D. Bot. Misc. iii, 303. Drowned at sea.

Bicheno, James E. (1851). Kew Gard. Misc. iii, 250. Hobarton.

Bidwill, John C. (1853). Kew Gard. Misc. v, 252. Tinana, New South Wales.

Bojer, Wenceslaus (1856). Kew Gard. Misc. viii, 312. Mauritius.

Bory de St. Vincent, Baron de (1846). Lond. Journ. Bot. vi, 262. Paris.

Bromfield, William A. (1851). Kew Gard. Misc. iii, 373. Damascus.

Brotero, Felix Avillar (1828). Bot. Mag. lxxi, Comp. 37. Lisbon.

Brown, Robert (1858), Éloge of. Kew Gard. Misc. ii, 61. London.

Candolle, A. P. de (1841). Journ. Bot. iv, 229. Geneva.

—— Bust of, in Geneva, Kew Gard. Misc. iv, 223.

Carmichael, Capt. D. (1827). Bot. Misc. ii, 1, 258; iii, 33. Appin, Argyleshire.

Chamisso, Adelb. von (1838). Lond. Journ. Bot. ii, 483. Berlin.

Coquebert de Montbret (1801). Comp. Bot. Mag. i, 306. Cairo. Journ. Bot. iii, 179. Paris.

Cunningham, Allan (1839). Journ. Bot. iv, 231; Lond. Journ. Bot. i, 107, 263. Sydney.

—— Monument to, Lond. Journ. Bot. v, 662 (Frontispiece).

—— **Richard** (1835). Comp. Bot. Mag. ii, 210. New South Wales.

Delessert, Baron B. (1847). Lond. Journ. Bot. vi, 206. Paris.

Dietrich, F. G. (1850). Kew Gard. Misc. iii, 190. Eisenach.

Douglas, David (1834). Comp. Bot. Mag. ii, 178. Hawaii.

—— Tribute to, by J. F. Schouw, Kew Gard. Misc. iv, 26.

—— Monument to, Kew Gard. Misc. viii, 111.

Drummond, T. (1835). Havana.

Endlicher, Stephen (1849). Kew Gard. Misc. i, 378. Vienna.

Fraser, Charles (1831). Comp. Bot. Mag. ii, 300. Sydney.

Gardner, George (1849). Kew Gard. Misc. i, 154. Ceylon.

Gaudichaud-Beaupré, C. (1864). Kew Gard. Misc. vi. 307. Paris.

Geyer, Charles Andreas (1853). Kew Gard. Misc. vii, 181. Meissen, near Dresden.

Goudot, August (1847). Kew Gard. Misc. iii, 286. New Grenada.

Graham, John (1839). Journ. Bot. iii, 301. Khandalla, Bombay.

Griffith, William (1845). Lond. Journ. Bot. iv, 371. Malacca.

Guillemin, A. (1842). Lond. Journ. Bot. i, 411. Montpellier.

Hornschuch, C. F. (1850). Kew Gard. Misc. iii, 190. Greifswald.

Jack, William (1822). Comp. Bot. Mag. i, 121. Indian Ocean.

Jussieu, Adr. de (1853). Kew Gard. Misc. v, 251; vii, 138, 172. Paris.

—— **Ant. Laur.** (1836), Éloge of. Journ. Bot. iii, 47. Paris.

Knight, T. A. (1838). Ann. Nat. Hist. i, 411. Herefordshire.

Koch, W. D. (1850). Kew Gard. Misc. ii, 94. Erlangen.

Kunth, C. S. (1850). Kew Gard. Misc. iii, 190. Berlin.

Kunze, G. (1851). Kew Gard. Misc. iii, 190. Leipzig.

Ledebour, C. F. von (1851). Kew Gard. Misc. iv, 65. Munich.

Lemann, C. (1854). Kew Gard. Misc. iii, 307. London.

Link, H. F. (1851). Kew Gard. Misc. iii, 60. Berlin.

Marshall, Humphrey (1801). Kew Gard. Misc. ii, 62. Pennsylvania.

Martíus, C. F. von (1868). Kew Gard. Misc. viii, 362; ix, 6, 41. Munich.

Matthews, A. (1841). Lond. Journ. Bot. i, 392. Chachapoyas, Peru.

Michaux, A. (1802). Lond. Journ. Bot. i, 2. Madagascar.

Moretti, J. (1853). Kew Gard. Misc. vi, 59. Pavia.
Nestler, C. G. (1832). Journ. Bot. i, 158. Strassburg.
Nuttall, T. (1859). Kew Gard. Misc. ii, 94. Nuthill, Lancashire.
Prescott, J. D. (1847). Comp. Bot. Mag. ii, 342. St. Petersburg.
Purdie, W. (1857). Kew Gard. Misc. ix, 374. Trinidad.
Reinwardt, C. G. C. (1854). Kew Gard. Misc. vi, 126; vii, 21; ix, 29. Leyden.
Requien, E. (1851). Kew Gard. Misc. iii, 250. Corsica.
Richard, L. C. (1821). Journ. Bot. iv, 423. Paris.
—— **Achille** (1852). Kew Gard. Misc. vi, 307. Paris.
Röttler, Rev. J. (1836). Kew Gard. Misc. iii, 67. Madras.
Schaerer, L. E. (1853). Kew Gard. Misc. v, 307. Bern.
Schouw, J. F. (1852). Kew Gard. Misc. iv, 156. Copenhagen.
Schrank, F. von (1835). Kew Gard. Misc. iii, 70. Munich.
Schreber, J. C. von (1810). Kew Gard. Misc. ii, 118; iii, 65. Erlangen.
Schwaegrichen, C. F. (1853). Kew Gard. Misc. vi, 307. Leipzig.
Schweinitz, L. D. von (1834). Comp. Bot. Mag. i, 16. Philadelphia.
Sprengel, A. (1851). Kew Gard. Misc. iii, 190. Rendsburg.
St. Hilaire, Aug. de (1853). Kew Gard. Misc. vi, 307. Orleans.
Sternberg, C. von (1838). Ann. Nat. Hist. iii, 457. Brezina, Prague.
Stocks, John E. (1854). Kew Gard. Misc. vi, 308. Cottingham, Hull.
Swartz, Olof (1818). Journ. Bot. ii, 382. Stockholm.
Taylor, Thomas (1848). Lond. Journ. Bot. vii, 162, 445. Kerry.
Telfair, Charles (1833). Journ. Bot. i, 150. Mauritius.
Trattinick, L. (1849). Kew Gard. Misc. i, 219. Vienna.
Vogel, Theod. (1841). Lond. Journ. Bot. v, 600, 621. Fernando Po.
Wahlenberg, G. (1851). Kew Gard. Misc. iii, 190. Upsala.
Wallich, N. (1854). Kew Gard. Misc. vi, 185. London.
Walpers, W. G. (1853). Kew Gard. Misc. v, 252. Berlin.
Webb, Philip B. (1854). Kew Gard. Misc. vi, 310. Paris.
Winch, N. (1838). Ann. Nat. Hist. i, 415. Newcastle.
Winterbottom, J. E. (1854). Kew Gard. Misc. vi, 307, 345. Rhodes.
Zuccarini, J. G. (1848). Kew Gard. Misc. i, 180; ii, 71. Munich.

PORTRAITS.

Allan Cunningham. Journ. Bot. iv.
—— Monument to. Lond. Journ. Bot. v.
Richard Cunningham. Comp. Bot. Mag. ii.
David Douglas. Comp. Bot. Mag. ii.
Charles Fraser. Comp. Bot. Mag. ii.
A. de Jussieu. Journ. Bot. iii.
Claude Richard. Journ. Bot. iv.
Olof Swartz. Journ. Bot. ii.
Robert Wight. Journ. Bot. ii.

APPENDIX C.

LIST OF SOME OF SIR W. J. HOOKER'S CHIEF CORRESPONDENTS (1808–65).

THE following selection of the names of Botanists, and of others who in various ways materially aided my father in his life-long labours (with the number of letters from each), is made from the volumes of letters from his correspondents, which are deposited in the Herbarium of the Royal Gardens of Kew. It has been drawn up at the request of the Editors of the Annals, as a contribution to the history of Botany during the first half of the nineteenth century.

The letters, of which there are about 29,000 from 4,420 individuals, are bound up in seventy-eight quarto volumes. They date from 1808 to 1865, and almost exclusively refer, directly or indirectly, to the recipient's work as a botanist, as founder of the Herbarium, Library and Museum, Kew, and as reformer of the Royal Botanic Garden, or to his authorship. Unfortunately, few of them date from the years between 1808 and 1820, a period during which, as his works and collections abundantly prove, he was in active correspondence with British, Continental, and American botanists. It appears to me to be probable, that many such letters contributed to swell the bulk of his father-in-law's Mr. Dawson Turner's monumental collection of Autographs, which was dispersed by sale[1] in 1859.

In selecting the 1,612 names here given, from the 4,420 correspondents, I have been guided by the following considerations:—

(1) Botanists, travellers, and collectors of eminence, whether of world-wide or more restricted reputation, the latter especially in connexion with British botany, many of whom will be found, with particulars of their lives and labours, in Britten and Boulger's valuable 'Bio-

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[1] See 'Catalogue of the Manuscript Library of the late Dawson Turner, Esq., M.A., F.R.S., &c., formerly of Yarmouth, comprising the matchless collection of upwards of 40,000 autograph letters, &c., which will be sold by auction by Messrs. Puttick and Simpson, No. 47 Leicester Square, on June 6, 1859, and four following days.' One vol., 8vo, pp. xix and 308, lots 719. (The sale realized £6,558 8*s*.)

graphic Index of British and Irish Botanists.' Others I include with the view of rescuing their names and disinterested labours from total oblivion, a few from their writer's great learning or distinction.

(2) Individuals who have materially aided my father otherwise than strictly scientifically in his various efforts for the advancement of botany, and especially by the development of Kew as a National Establishment. Such were many merchants and manufacturers, who urged their foreign agents or correspondents to respond to my father's requests for information and specimens. Many of them transmitted freight free all consignments of specimens to and from the Royal Gardens, Kew.

(3) Government officials, who, to use a common expression, 'went out of their way' to carry out my father's views and wishes. It is impossible to exaggerate the services rendered officially or semi-officially by the Secretaries and other employés of the Admiralty (especially its Hydrographers), the Foreign and Colonial Offices, the Board of Trade, the East India Company and the Hudson's Bay Company, and by the Governors and Secretaries of our Colonies all over the globe.

(4) Directors and owners of Horticultural Establishments, Imperial, Royal and Commercial, including many of the leading Nurserymen of Great Britain and Ireland, France, Belgium, Holland and Germany, who by gifts and exchanges lavishly enriched the Gardens of Kew.

I regret that it is impossible to give more information regarding the 1,612 individuals catalogued, than their names, the number of their letters which have been preserved (more than 21,500), the years over which their correspondence extended, and very vaguely and unsystematically the localities where they resided, or from which they wrote. In very many instances they wrote from many localities, in which case I have selected a prominent one.

Of my father's letters to these correspondents I have seen comparatively few. There are preserved in the Kew Herbarium those addressed to Mr. Bentham, 610 (1825 to 1865), to Sir John Richardson, 87 (1819–1843), to Dr. Harvey, 247 (1832–1868), and some others. I have those addressed to Mr. Dawson Turner, 728 (1805–1851), and Mr. Turner's addressed to Mr. Borrer, 135 (1806–1819). To the last two series I am indebted for many particulars of the life of my father, who, except sometimes when travelling, kept no diary or journal of any kind.

1. **Abel** (**Clark**), Calcutta, 1824.
4. **Adamson** (**Fredk.**), Melbourne, Victoria, 1837.
6. **Adamson** (**O. G.**), Brazil, &c., 1834–57.
9. **Agardh** (**C. A.**), Lima, 1820–36.
4. **Agardh** (**J. G.**), Lima, 1836–49.
2. **Agassiz** (**L.**), Neufchâtel, 1837.
1. **Airy** (**G. B.**), Greenwich, 1845.
8. **Aiton** (**J. T.**), Kensington Palace, 1831–49.
23. **Alcard** (**J.**), London, &c., 1834–43.
18. **Alcock** (**Sir Rutherford**), Japan, &c., 1851–64.
9. **Aldridge** (**J.**), Dublin, 1840–2.
Alexander (**R. C.**). *See* **Prior.**
5. **Anderson** (**J.**), Calcutta, 1861–5.
12. **Anderson** (**N. J.**), Stockholm, 1855–60.
2. **Anderson** (**W.**), Chelsea, 1843–44.
6. **Andrews** (**W.**), Dublin, 1841–44.
9. **Ansell** (**J.**), W. Africa, 1841–7.
4. **Appun** (**C. F.**), Demerara, 1861–4.
25. **Archer** (**J. H.**), China, Jamaica, 1856–65.
17. **Archer** (**Thos. C.**), Liverpool, 1853–65.
11. **Archer** (**W.**), Tasmania, &c., 1854–65.
7. **Argyll** (**John, Duke of**), Inverary, &c., 1839–60.
7. **Armstrong** (**John**), Timor, &c., 1830–45.
5. **Arnot** (**David**), Colesberg, 1860–3.
406. **Arnott** (**G. A. W.**), Arlary, &c., 1825–64.
11. **Atherstone** (**W. G.**), Grahamstown, 1847–60.
34. **Auckland** (**Lord**), Admiralty, &c., 1847–8.
10. **Ayres** (**P. B.**), Mauritius, 1855–60.
25. **Babington** (**C. C.**), Cambridge, 1834–51.
19. **Babington** (**Rev. Churchill**), Cambridge, 1839–60.
65. **Backhouse** (**James**), York, &c., 1820–63.
37. **Baikie** (**W. B.**), West Africa, 1852–63.
8. **Baines** (**T.**), South Africa, 1854–65.
2. **Baird** (**J.**), Buenos Ayres, 1829–30.
3. **Balansa** (**J. G.**), Paris, 1855–6.
42. **Balfour** (**J. H.**), Edinburgh, &c., 1835–59.
2. **Ball** (**R.**), Dublin, 1836–7.
28. **Ball** (**J.**), Dublin and Colonial Office, 1842–55.
4. **Banks** (**G.**), Devonport, 1830–1.

14. **Banks (Sir Joseph)**, London, &c., 1809–20.
7. **Barber (E.)**, Cannon Row, 1849–58.
2. **Barber (E. S.)**, Labuan, 1853–4.
1. **Barber (Mrs. M. E.)**, Grahamstown, 1860.
14. **Barclay (A.)**, Hudson's Bay House, 1843–51.
26. **Barclay (Chas.)**, Bury Hill, 1830–50.
8. **Barclay (G. W.)**, 1843–51.
34. **Barkly (Sir H.)**, Hong Kong, &c., 1852–65.
13. **Barnard (Capt. F. L.)**, Ascension Isld., 1863–5.
1. **Barnéoud (F. M.)**, Hyères, 1849.
39. **Barrow (Sir John)**, Admiralty, 1831–48.
10. **Barry (Dr. Martin)**, Edinburgh, 1831–7.
17. **Barter (Ch.)**, Niger, &c., 1837–9.
2. **Bartling (S. G.)**, Göttingen, 1839–52.
43. **Bateman (J.)**, Biddulph Grange, &c., 1837–65.
8. **Bauer (Franz)**, Kew, 1832–7.
2. **Baxter (W.)**, Oxford, 1829–47.
76. **Beaufort (Capt. Sir F.)**, Admiralty, 1829–57.
3. **Beck (L. C.)**, New York, 1836.
8. **Beddome (R. H.)**, Ootacamund, 1862–4.
193. **Bedford (John, Duke of)**, Woburn, &c., 1830–9.
21. **Bedford (Francis, Duke of)**, Woburn, &c., 1840–56.
7. **Bedford (Georgiana, Countess of)**, Campden Hill, &c.
28. **Beecher (Capt. A. B.)**, Admiralty, 1836–63.
53. **Beechey (Capt. F. W.)**, London, &c., 1828–43.
9. **Belanger (C. S.)**, Martinique, &c., 1852–6.
15. **Belcher (Capt. Sir E.)**, London, &c., 1843–63.
8. **Bell (Jacob)**, London, 1847–52.
14. **Bell (Thos.)**, London, 1842–61.
13. **Bennett (G.)**, Sydney, &c., 1853–64.
5. **Bennett (G. B.)**, St. Helena, 1843–8.
20. **Bennett (J. J.)**, British Museum, 1841–59.
7. **Benson (Genl. R.)**, Moulmein, &c., 1863–5.
610. **Bentham (G.)**, London, &c., 1823–57.
13. **Berg (A. de)**, London, &c., 1844–63.
2. **Berghaus (Prof.)**, Potsdam, 1849–51.
143. **Berkeley (Revd. M. J.)**, Kingscliff, &c., 1832–65.
3. **Bertero (C.)**, Valparaiso, 1830.
2. **Bertoloni (Ant.)**, Bologna, 1836.

20.	**Besser** (**W.**), Kief, &c., 1822–37.
1.	**Bibra** (**E.**), Nürnberg, 1855.
5.	**Bicheno** (**J. C.**), London, 1820–42.
25.	**Bidwill** (**J. C.**), Sydney, &c., 1843–50.
1.	**Bigelow** (**J.**), Boston, U. S., 1820.
2.	**Billberg** (**G.**), Stockholm, 1828–34.
3.	**Binnendyck** (**J.**), Buitenzorg, 1859–62.
1.	**Birchall** (**H.**), Bogota, 1859.
3.	**Birdwood** (**Sir G.**), Bombay, 1862.
4.	**Black** (**Allan**), Bangalore, 1853–64.
4.	**Blakiston** (**T.**), London, 1857–62.
2.	**Blechynden** (**A. H.**), Calcutta, 1853–4.
11.	**Bloxam** (**Revd. A.**), Atherstone, 1839–56.
6.	**Blume** (**C. L.**), Leyden, 1833–53.
2.	**Blytt** (**Axel**), Christiania, 1843–62.
14.	**Boissier** (**E.**), Geneva, 1839–55.
18.	**Bojer** (**W.**), Mauritius, 1826–53.
1.	**Bolander** (**H.**), San Francisco, 1861.
2.	**Bolle** (**C.**), Berlin, &c., 1851–63.
2.	**Bolton** (**D.**), Grahamstown, 1857–8.
1.	**Bolton** (**W.**), Auckland, 1852.
4.	**Bongard** (**H. G.**), St. Petersburg, 1835–8.
2.	**Bonjean** (**J.**), Chambéry, 1827.
3.	**Boog** (**W.**), Rio de Janeiro, 1823–5.
5.	**Booth** (**G. & J.**), Hamburg, 1839–50.
230.	**Boott** (**F.**), London, 1818–64.
145.	**Borrer** (**W.**), Henfield, 1823–63.
6.	**Bory de St. Vincent** (**B. M.**), Paris, 1821–44.
11.	**Bosch** (**R. B. Van den**), Zealand, 1854–61.
5.	**Bossey** (**F.**), Woolwich, 1858.
8.	**Boughton** (**E. G.**), British Guiana, 1848–65.
33.	**Bourgeau** (**E.**), Paris, &c., 1846–63.
23.	**Bouton** (**L.**), Mauritius, 1830–60.
1.	**Bowerbank** (**J. S.**), Brighton, 1855.
3.	**Bowie** (**J.**), South Africa, 1826–42.
3.	**Bowker** (**J. H.**), South Africa, 1853.
19.	**Bowman** (**J. E.**), Wrexham, 1830–41.
26.	**Bowman** (**R. B.**), Newcastle, 1831–40.
6.	**Bowman** (**Sir W.**), London, 1842–58.

31. **Bowring (Sir J.)**, Hong Kong, &c., 1844–63.
3. **Brackenridge (W. D.)**, Baltimore, 1855–6.
15. **Braine (C. G.)**, Hong Kong, 1849–50.
7. **Brand (W.)**, Edinburgh, 1832–46.
1. **Brandis (Sir D.)**, London.
1. **Brandt (J. T.)**, St. Petersburg, 1837.
12. **Braun (Alex.)**, Berlin, &c., 1828–63.
2. **Bree (Revd. W. T.)**, Coventry, 1831–8.
16. **Brenton (Mary E.)**, Newfoundland, 1830–6.
5. **Brewer (W.)**, California, 1861–5.
2. **Brewster (Sir D.)**, Edinburgh, 1836.
25. **Bridges (T.)**, Chili, 1829–46.
1. **Brightwell (T.)**, Norwich, 1852.
39. **Bromfield (Eliza)**, Ryde, 1852–64.
45. **Bromfield (W. A.)**, Ryde, United States, &c., 1836–50.
8. **Brongniart (A.)**, Paris, 1826–62.
3. **Brooke (Sir J., Rajah)**, Sarawak, 1853–5.
4. **Broome (C. E.)**, Clifton, &c., 1844–50.
9. **Brown (J. C.)**, South Africa, &c., 1863–5.
46. **Brown (Robert)**, Soho Square, &c., 1820–53.
4. **Brunner (S. H.)** (Lacosta), Paris, 1857.
9. **Brydges (Sir Harford)**, Boultibrooke, 1832–52.
17. **Buckland (Revd. W.)**, Oxford, 1832.
9. **Buckle (C. C. F.)**, Deptford, 1858–60.
14. **Bunbury (Sir C.)**, Mildenhall, 1831–51.
13. **Bunge (A.)**, Dorpat, 1836–59.
12. **Burchell (W: J.)**, Fulham, &c., 1819–47.
6. **Burges (W.)**, West Australia, 1858–61.
3. **Burke (Fr.)**, Montserrat, 1853–4.
18. **Burke (J.)**, Canada, &c., 1843–7.
26. **Burnett (Sir W.)**, Admiralty, 1853–4.
72. **Burton (Decimus)**, London, 1844–64.
4. **Burton (Sir Richard F.)**, West Africa, &c., 1862.
10. **Bushnan (J. S.)**, Dumfries, 1831–49.
19. **Calddeugh (A.)**, Chili, &c., 1829–51.
5. **Callcott (Lady Maria)**, *see* Graham (Maria).
6. **Calvert (H. H.)**, Erzerum, 1854–5.
8. **Cameron (D.)**, Birmingham, 1840–51.
23. **Campbell (W. H.)**, Demerara, 1836–65.

24. **Candolle (A. P. de)**, Geneva, &c., 1820–38.
25. **Candolle (Alph. de)**, Geneva, 1828–64.
12. **Capanema (S. de)**, Rio de Janeiro, 1855–61.
11. **Cardwell (Lord)**, Whitehall Gardens, 1845–64.
8. **Carey (Revd. W.)**, Serampore, 1825–34.
17. **Carlisle (Earl of)**, Naworth, 1849–55.
13. **Carmichael (Capt. D.)**, Appin, 1821–5.
2. **Carrington (B.)**, Leeds, 1859–60.
10. **Caspary (R.)**, Berlin, &c., 1849–57.
8. **Cathcart (Lady Mary)**, Cathcart, 1837–57.
1. **Chalmers (Th.)**, St. Andrews, 1826.
2. **Chamisso (Adelb. von)**, Berlin, 1828–31.
57. **Champion (Major J. G.)**, Ceylon, &c., 1837–52.
25. **Chapman (H. S.)**, New Zealand, 1841–5.
18. **Children (J. G.)**, British Museum, 1831–51.
3. **Choisy (E.)**, Geneva, 1829–43.
15. **Christison (Sir R.)**, Edinburgh, 1836–56.
34. **Christy (Henry)**, London, &c., 1841–63.
38. **Christy (W. D.)**, Argentine, &c., 1848–59.
53. **Christy (W. J.)**, London, &c., 1829–39.
30. **Clarke (B.)**, Hampstead and Chelsea, 1851–64.
8. **Cleghorn (H.)**, Madras, 1854–7.
7. **Clifton (G.)**, Fremantle, 1857–62.
15. **Clowes (Revd. J.)**, Broughton Hall, 1841–6.
21. **Cole (Sir H.)**, South Kensington, &c., 1829–55.
Colenso (Revd. J. W.). *See* Natal, Bishop of.
17. **Colenso (Revd. W.)**, New Zealand, 1840–2.
2. **Collie (A.)**, Chatham, 1828.
48. **Conyngham (G. Lennox)**, Foreign Office, 1845–62.
20. **Cooper (Sir D.)**, London, 1861–4.
3. **Cope (Caleb)**, Philadelphia, 1850–1.
3. **Cosson (E.)**, Paris, 1857–8.
1. **Cresson (Ph.)**, Gand, 1865.
43. **Croall (A.)**, Montrose, 1844–62.
43. **Croker (T.)**, Admiralty, 1843–7.
26. **Cruckshanks (A.)**, Edinburgh, 1825–50.
32. **Cruger (H.)**, Trinidad, 1858–62.
2. **Cullum (Sir T.)**, Hardwick House, 1845.
33. **Cuming (Hugh)**, London, &c., 1832–58.

64. **Cunningham (Allan)**, Kew, &c., 1824–49.
45. **Cunningham (Richd.)**, Kew, &c., 1819–35.
3. **Currey (F.)**, Lincoln's Inn, 1856–7.
7. **Curror (A. B.)**, London, &c., 1843–4.
6. **Curtis (Saml.)**, Jersey, 1842–57.
8. **Dalhousie (Countess of)**, Dalhousie, &c., 1826–33.
32. **Dalton (Revd. J.)**, Croft, 1828–42.
44. **Dalzell (N. A.)**, Bombay, &c., 1847–63.
6. **Daniell (W. T.)**, West Africa, &c., 1845–7.
31. **Darlington (W.)**, Pennsylvania, 1830–62.
5. **Darwall (Revd. L.)**, Salop, 1852–62.
7. **Darwin (C.)**, Down.
55. **Daubeny (C. G.)**, Oxford, 1837–64.
10. **Deakin (R.)**, Attercliffe, 1835–8.
24. **Decaisne (J.)**, Jardin des Plantes, 1835–63.
18. **Delessert (Baron B.)**, Paris, 1826–60.
4. **Delile (A. R.)**, Montpellier, 1824–6.
16. **Denham (Capt.)**, H.M.S. *Herald*, 1852–8.
43. **Denison (Sir W.)**, Madras, &c., 1847–65.
135. **Derby (Earl of)**, Knowsley, 1843–53.
26. **Desjardin (J.)**, Mauritius, 1830–3.
14. **Devonshire (Duke of)**, Chatsworth, 1834–49.
13. **Dewar (A.)**, Dunfermline, 1834–46.
12. **Dickie (G.)**, Aberdeen, &c., 1837–63.
5. **Dickins (F.)**, Japan, 1865.
6. **Dieffenbach (E.)**, London, 1842–4.
32. **Dillwyn (L. W.)**, Swansea, 1829–51.
6. **Distin (H.)**, Jamaica, 1830–40.
8. **Don (David)**, Linnean Society, 1823–40.
27. **Doneraile (Lady)**, Doneraile, 1854–63.
2. **Doubleday (E.)**, Brit. Museum, 1843.
28. **Douglas (D.)**, British Columbia, &c., 1825–34.
1. **Drege (J. H.)**, Hamburg, 1842.
73. **Drummond (J.)**, West Australia, 1839–60.
46. **Drummond (Thos.)**, North America, 1826–35.
6. **Dunal (F.)**, Montpellier, 1829–49.
33. **Duncan (Jas.)**, Mauritius, 1849–62.
11. **D'Urban (W.)**, Exeter, 1861–3.
2. **Durieu (M. E. de Maisonneuve)**, Bordeaux, 1835.

6. **Duvau (A.)**, Paris, 1824–7.
5. **Dyck (Pr. Salm)**, Dyck, 1844–50.
7. **Eagle (F. K.)**, Bury, 1831–46.
1. **Eaton (Amos)**, Troy, U.S.A., 1836.
15. **Eaton (Dan.)**, Newhaven, U.S.A., 1855–65.
3. **Ecklon (C. F.)**, Hamburg, 1828–61.
4. **Edgerley (J.)**, New Zealand, 1842.
24. **Edgeworth (P.)**, Mooltan, &c., 1841–51.
8. **Edmonstone (L.)**, Shetland Islands, 1837–51.
14. **Edmonstone (Thos.)**, Aberdeen, &c., 1837–45.
10. **Edwards (W.)**, Manchester, 1839–41.
16. **Edye (J.)**, Somerset House, 1842–50.
15. **Ellice (A.)**, Southampton, 1843–5.
7. **Elliott (Admiral Sir C.)**, St. Helena, 1864–5.
30. **Elliott (Sir Fredk.)**, Colonial Office, 1859–63.
4. **Elliott (Steph.)**, South Carolina, 1823–8.
9. **Ellis (Sir H.)**, British Museum, 1847–55.
24. **Ellis (Revd. W.)**, Hoddesden, 1850–62.
16. **Elsey (J. R.)**, St. Kitts, &c., 1857.
5. **Enderby (Ch.)**, London, 1846–53.
25. **Engelmann (G.)**, St. Louis, 1843–64.
22. **Evans (J.)**, Delaware, &c., 1849–55.
8. **Exeter (Bishop of)**, Torquay, 1848–63.
8. **Eyre (Lt. Col. J.)**, Hong Kong, 1850–2.
2. **Fabroni (Pelli)**, Florence, 1830.
40. **Falconer (H.)**, Calcutta, &c., 1837–49.
6. **Fanning (D.)**, Caracas, 1829–31.
3. **Fendler (Aug.)**, Venezuela, 1856–7.
4. **Fenzl (M. Aug.)**, Vienna, 1840–52.
16. **Ferguson (D.)**, Belfast, 1838–43.
12. **Ferguson (W.)**, Ceylon, &c., 1850–61.
122. **Fielding (H. B.)**, Lancashire, 1834–53.
6. **Finch (H.)**, Mexico, 1846–8.
8. **Finlay (K.)**, Trinidad, 1837–65.
109. **Fischer (F. von)**, St. Petersburg, 1824–53.
6. **Fitt (G.)**, Yarmouth, 1844–9.
16. **Fitzwilliam (Earl)**, Wentworth, 1834–56.
2. **Fleming (Revd. J.)**, Aberdeen, 1835–6.
6. **Forbes (E.)**, Geolog. Survey, 1847–8.

69. **Forbes (J.)**, Woburn Abbey, 1830–42.
2. **Forchammer (G.)**, Copenhagen, 1850-3.
11. **Forster (Ed.)**, London, 1831–46.
8. **Fortune (R.)**, China, &c., 1843–50.
7. **Foulkes (Revd. T.)**, India, 1855–60.
2. **Fox (G. C.)**, Falmouth, 1835–7.
19. **Francis (G.)**, Adelaide, &c., 1835–65.
5. **Franklin (Capt. Sir J.)**, Tasmania, &c., 1827–41.
15. **Fraser (C.)**, Sydney, 1824–31.
5. **Freeman (Rev. J.)**, Madagascar, 1830–2.
20. **Frere (G. E.)**, Roydon Hall, 1849-64.
9. **Frere (W. E.)**, Bombay, 1858–64.
4. **Fries (Elias)**, Upsala, 1847–57.
18. **Gairdner (G.)**, Downing Street, 1853–60.
7. **Gairdner (M.)**, Vancouver Island, &c., 1832–5.
12. **Galeotti (H.)**, Brussels, 1840–6.
16. **Garden (Major R. J.)**, Erzerum, &c., 1854–62.
26. **Gardener (W.)**, Dundee, 1835–50.
130. **Gardner (G.)**, Brazil, Ceylon, &c., 1836–49.
10. **Garry (N.)**, Hudson's Bay Co., 1828–31.
1. **Gasparrini (G.)**, Naples, 1839.
1. **Gaudin (F.)**, Lausanne, 1861.
15. **Gay (J.)**, Paris, 1824–54.
4. **Gerrard (W. T.)**, Port Natal, 1865.
18. **Geyer (C. A.)**, Dresden, &c., 1845–7.
3. **Gibert (C.)**, Monte Video, 1858.
31. **Gibson (Alex.)**, Bombay, 1841–60.
2. **Giesecke (C. L.)**, London, 1817–26.
5. **Giffard (J.)**, Vera Cruz, 1841–4.
50. **Gillies (J.)**, Mendoza, &c., 1823–34.
2. **Glendinning (R.)**, Chiswick, 1844–57.
28. **Glover (Thos.)**, Manchester, 1833–65.
2. **Goeppert (J. H.)**, Breslau, 1851–4.
2. **Goldie (J.)**, Canada, 1837–51.
6. **Gordon (Alex.)**, Alabama, &c., 1844–5.
6. **Gordon (Revd. G.)**, Elgin, 1829–43.
43. **Gore (The Honble. C.)**, O. of Works, 1838–63.
8. **Gosse (P. H.)**, Torquay, 1851–62.
1. **Gottsche (C. M.)**, Altona, 1843.

3. **Gould** (**J.**), London, 1843–4.
20. **Gourlie** (**W.**), Glasgow, 1840–50.
22. **Gowen** (**J. R.**), London, 1843–53.
3. **Grabowski** (**H.**), Breslau, 1842.
4. **Graham** (**Cyril**), 1859.
1. **Graham** (**John**), Bombay, 1834.
5. **Graham** (**Maria**), London, 1825–6.
196. **Graham** (**Robt.**), Edinburgh, 1831–45.
4. **Graham** (**Thos.**), Glasgow, 1845–7.
10. **Grant** (**J. W.**), Calcutta, 1846–63.
181. **Gray** (**Asa**), Cambridge, U.S.A., 1835–65.
47. **Gray** (**J. E.**), British Museum, 1826–65.
22. **Greene** (**B. D.**), New York, 1831–47.
59. **Greville** (**R. K.**), Edinburgh, 1820–56.
10. **Grey** (**Sir G.**), Capetown & New Zealand, 1858–63.
5. **Griffith** (**Phil.**), Bogota, 1859–60.
12. **Griffith** (**W.**), India, 1840–4.
77. **Griffiths** (**Amelia**), Torquay, 1826–55.
2. **Grindon** (**Leo**), Manchester, 1864.
42. **Grisebach** (**A.**), Göttingen, 1835–63.
18. **Guilding** (**Revd. L.**), St. Vincent, 1823–31.
6. **Guillemin** (**J. B.**), Paris, 1832–9.
44. **Gunn** (**R.**), Tasmania, 1832–49.
112. **Gurney** (**Anna**), Cromer, 1836–56.
11. **Gurney** (**Hudson**), London, 1846–61.
10. **Gurney** (**J. Henry**), Earlham, &c., 1838–63.
2. **Gussone** (**Giov.**), Naples, 1834–6.
3. **Haast** (**J.**), New Zealand, 1861–2.
1. **Haidinger** (**W.**), Vienna, 1862.
47. **Halkett** (**J.**), Hudson's Bay Company, 1842–51.
46. **Hall** (**Sir B.**), Office of Works, 1855–8.
1. **Hall** (**Col. J.**), Quito, 1833.
1. **Hamilton** (**Duke of**), Hamilton Palace, 1850.
1. **Hamilton** (**F. Buchanan H.**), Glasgow, 1825.
4. **Hamilton** (**G. A.**), Treasury, 1842.
34. **Hamilton** (**W.**), Plymouth, 1828–38.
3. **Hampe** (**Ernst**), Harz, 1846.
90. **Hanbury** (**D.**), London, 1848–65.
10. **Hanbury** (**R.**), Ware, 1850–8.

36.	**Hance (H. F.)**, China, 1845–65.
4.	**Hancock (Albany)**, Newcastle, 1834–40.
1.	**Hanstein (J.)**, Berlin, 1854.
4.	**Hardi (A. O.)**, Algiers, 1855–62.
8.	**Harland (W. A.)**, London, &c., 1857–8.
9.	**Harris (Lord)**, Madras, Trinidad, 1847–52.
1.	**Hartman (C. F.)**, Sweden, 1849.
5.	**Hartweg (Th.)**, Hort. Soc., 1845–8.
470.	**Harvey (W. H.)**, Dublin, &c., 1831–65.
11.	**Hassall (A. H.)**, London, 1842–5.
4.	**Hasskaarl (J. K.)**, Java, &c., 1825–56.
6.	**Haughton (J.)**, St. Helena, 1863–5.
9.	**Hawes (Sir B.)**, Colonial Office, &c., 1849–59.
2.	**Hay (Sir John D.)**, Tangier, 1854.
8.	**Hayes (Sutton)**, Panama, 1861–2.
4.	**Hearsey (Major-Genl.)**, India, 1844–50.
8.	**Hector (Sir J.)**, London, &c., 1857–60.
4.	**Heldreich (Th. von)**, Athens, 1855–61.
2.	**Henfrey (A.)**, London, 1849.
1.	**Henschel (W.)**, Breslau, 1846.
233.	**Henslow (Rev. J. S.)**, Cambridge, 1826–57.
122.	**Herbert (The Honble. & Revd.)**, Spofforth, 1834–59.
3.	**Herbst & Rossiter**, Rio de Janeiro, 1858–9.
14.	**Herschel (Sir J.)**, Collingwood, 1843–8.
46.	**Heward (R.)**, Kensington, 1839–63.
4.	**Hewitson (H.)**, Seaton Burn, 1834–5.
9.	**Heysham (T. C.)**, Carlisle, 1835–42.
76.	**Higgins (W. F.)**, Colonial Office, 1849–62.
4.	**Hill (Walter)**, Brisbane, 1859–65.
12.	**Hillebrand (W.)**, Honolulu, 1857–65.
12.	**Hincks (Revd. W.)**, York, &c., 1833–61.
11.	**Hinds (R. B.)**, London, 1842–4.
3.	**Hitchin (T.)**, Norwich, 1826–38.
12.	**Hobler (F.)**, Canonbury, 1856–63.
1.	**Hobson (E.)**, Manchester, 1827.
16.	**Hochstetter (C. F.)**, Stuttgart, 1829–45.
11.	**Hodgson (B. H.)**, Darjeeling, 1848–9.
12.	**Hodgson (P.)**, Hakodadi, 1853–62.
4.	**Hoey (H.)**, Japan, 1853–62.

2. **Hoffmansegg (J. Graf von)**, Dresden, 1837.
1. **Hofmeister (F.)**, Leipzig, 1851.
16. **Hogg (J.)**, Temple Bar, 1833–59.
22. **Hohenacker (R. F.)**, Stuttgart, 1842–63.
13. **Holmes (W. H.)**, Demerara, 1856–64.
5. **Holmes (W. R.)**, Diarbekir, 1858–9.
27. **Home (Capt. Sir E.)**, London, &c., 1846–53.
5. **Hope (Beresford)**, Cranbrook, 1856–64.
14. **Hore (Revd. W. S.)**, Devonport, 1840–5.
4. **Horne (Chas.)**, Trinidad, 1862–4.
10. **Hornemann (J. W.)**, Copenhagen, 1818–36.
8. **Horner (Leonard)**, London, 1838–58.
1. **Hornschuch (C. F.)**, Greifswald, 1829.
15. **Horsfall (Ch.)**, Liverpool, 1833–43.
3. **Horsfield (T.)**, India House, 1842–5.
13. **Hostmann (F. W.)**, Surinam, 1838–41.
12. **Houlton (Sir V.)**, Malta, 1856–60.
4. **Houtte (J. van)**, Ghent, 1844–63.
15. **Howard (J. E.)**, London, 1856–65.
4. **Howitt (W.)**, Kentish-town, 1854.
7. **Hudson (J.)**, Rl. Agric. Soc., 1830–63.
9. **Hudson (R.)**, Clapton, 1844–63.
21. **Hugel (Baron C.)**, Vienna, 1840–6.
10. **Humboldt (A. von)**, Berlin, 1840–57.
9. **Hume (Joseph)**, London, 1840–53.
188. **Hunnemann (J.)**, London, 1829–39.
8. **Hunt (R.)**, Geolog. Survey, 1846–9.
3. **Hunter (A.)**, Madras, 1857–61.
21. **Huntley (J. T.)**, Kimbolton, 1829–34.
38. **Hutchinson (Thos.)**, Fernando Po, 1854–61.
5. **Hutt (J.)**, London, 1867.
14. **Hutt (J. jr.)**, Gateshead, &c., 1840–9.
27. **Hutton (H.)**, Grahamstown, 1837–65.
9. **Hutton (W.)**, Newcastle, 1837–9.
1. **Huxley (T.)**, London, 1856.
3. **Hyslop (J. H.)**, Bagdad, 1853–4.
5. **Ibbotson (H.)**, Gawthorpe, 1845.
9. **Ilchester (Earl of)**, Abbotsbury, 1859–62.
7. **Iliff (W. A.)**, Newington, 1841–53.

54. **Imray (J.)**, Dominica, 1837–60.
6. **Inchbald (P.)**, Huddersford, 1850–60.
6. **Ingle (Thos.)**, Emworth, 1865.
18. **Inglis (Sir R.)**, Bedford Square, 1829–48.
3. **Irving (G. E.)**, Abbeokuta, 1854–5.
7. **Jackson (J. W. B.)**, Geograph. Soc., 1842–6.
2. **Jacquin (J. P.)**, Vienna, 1825–36.
21. **James (T. P.)**, Philadelphia, 1850–63.
3. **Jameson (R.)**, Edinburgh.
10. **Jameson (R.)**, Liverpool, 1833–47.
95. **Jameson (W.)**, Quito, 1827–59.
14. **Jardine (Sir W.)**, Jardine Hall, 1830–51.
4. **Jaubert (Count H.)**, Paris, 1844–58.
10. **Jenkins (Col. F.)**, Assam, 1843–54.
21. **Jenkinson (R. W.)**, Norbury, 1849–53.
10. **Jennings (J.)**, Knowsley, 1838–62.
3. **Jenyns (G.)**, Bottisham Hall, 1849.
1. **Jenyns (Revd. L.)**, Bath, 1854.
6. **Jerdan (W.)** (Lit. Gazette), 1848–9.
21. **Jesse (E.)**, Windsor, 1843–50.
8. **Jeune (Rev. F.)**, Jersey, 1843–7.
6. **Jocelyn (Lord)**, Windsor, &c., 1848–9.
31. **Johns (Revd. C. A.)**, Plymouth, 1834–48.
7. **Johnson (Revd. E.)**, South India, &c., 1852–60
14. **Johnson (G.)**, Berwick-on-Tweed, 1830–5.
3. **Johnson (J. Yate)**, Madeira, 1851–7.
5. **Jones (H. Bence)**, London, 1846–52.
2. **Jordan (Alexis)**, Lyon, 1851–2.
4. **Jorgensen (Jorgen)**, Tasmania, 1834–40.
4. **Jussieu (Adr. de)**, Paris, 1832–44.
1. **Karelin (Greg.)**, St. Petersburg, 1835.
3. **Karsten (H. G.)**, Caracas, 1845–6.
1. **Kaulfuss (G. F.)**, Halle, 1826.
10. **Keats (R. W.)**, Trinidad, &c., 1849–64.
5. **Kelaart (E. F.)**, Ceylon, &c., 1841–59.
13. **Kellett (Capt. W.)**, Panama, &c., 1842–9.
6. **Kendall (Capt. S.)**, Southampton, 1839–43.
3. **Kent (J. C.)**, Upton-on-Severn, 1852–3.
7. **Ker (H. Bellenden)**, Lincoln's Inn, 1837–42.

3. **Kidd (J.)**, Sydney, 1845–6.
20. **King (Capt. P.)**, New South Wales, 1840-52.
6. **King (Robt. L.)**, Cambridge, &c., 1844–7.
34. **Kingeman (C.)**, London, 1847–62.
3. **Kippist (R.)**, Linn. Soc., 1858–64.
1. **Kirby (Revd. W.)**, Barham, 1834.
33. **Kirk (Sir J.)**, East Africa, &c., 1857–63.
31. **Klotzsch (F.)**, Berlin, 1832–49.
72. **Knesebeck (Baron P.)**, Kew, 1844–59.
5. **Knight (C.)**, New Zealand, 1852–63.
5. **Knight (J.)**, Exotic Nurseries, 1841–8.
8. **Knighton (W. M.)**, Horndean, 1857–9.
3. **Koch (Karl)**, Berlin, 1845–60.
7. **Kralik (L.)**, Paris, 1849–59.
5. **Krauss (Ferd.)**, Stuttgart, 1840–7.
1. **Krebs (H.)**, St. Thomas, 1847.
14. **Kreuter (F.)**, Vienna, 1855–61.
5. **Kunth (C.)**, Paris, 1821–30.
8. **Kuntze (G.)**, Leipzig, 1837–47.
1. **Kurr (G.)**, Stuttgart, 1833.
1. **Kuster (C. von)**, St. Petersburg, 1856.
1. **Kützing (J.)**, Nordhausen, 1847.
1. **Lagasca (M.)**, Madrid, 1824.
8. **Laird (McGregor)**, London, 1858–60.
20. **Lambert (A. B.)**, Boyton, 1832–41.
4. **Lamoureux (J. P.)**, Caen, 1822.
3. **Landsborough (Revd. D.)**, Stevenston, 1856–9.
1. **Langsdorff (G. von)**, Brazil, 1824.
3. **Lankester (E.)**, London.
7. **Lapham (J. A.)**, Wisconsin, 1832–57.
2. **Lardner (Dem.)**, London, 1833.
4. **Lasègue (Ant.)**, Paris, 1842–4.
21. **Latrobe (C. J.)**, London, 1825–59.
37. **Law (J. S.)**, Tanna, Bombay, 1842–56.
28. **Lawrence (Lady)**, Ealing, 1842–54.
15. **Lawrence (R. W.)**, Tasmania, 1830-3.
6. **Lawson (Peter)**, Edinburgh, 1844–52.
3. **Lawson (S.)**, Canada, 1861–4.
2. **Lay (G. Tradesc.)**, London, 1829.

1. **Layard (Sir H. A.),** Foreign Office, 1864.
2. **Lea (Isaac),** Philadelphia, 1840–2.
5. **Lea (Thos.),** Cincinnati, 1838–42.
37. **Leach (B. Auber),** India Office, 1846–54.
1. **Ledbeater (B.),** London, 1832.
27. **Ledebour (K. F. von),** Dorpat, 1827–61.
8. **Lee (J.),** Edinburgh, 1845–9.
11. **Leeds (Ed.),** Manchester, 1839–58.
13. **Leefe (Revd. J. L.),** Audley End, &c., 1842–62.
1. **Lees (Edwin),** Leominster, 1831.
2. **Lees (J. E.),** Nassau, 1845.
18. **Lefroy (Genl. Sir J. H.),** Woolwich, &c., 1842–64.
49. **Lehmann (A.),** St. Thomas, 1856.
Lehmann (J. G. C.), Hamburg, 1824–53.
3. **Leichardt (L.),** Sydney, 1842–6.
6. **Leighton (Revd. W. A.),** Shrewsbury, 1835-64.
4. **Le Jolis (Aug.),** Cherbourg, 1848–64.
3. **Lemaire (Ch.),** Gand, 1854.
103. **Lemann (C.),** London, 1838–50.
22. **Lemon (Sir Chas.),** Cardow.
24. **Lenormand (René),** Vire, 1842–65.
2. **Leobold (F.),** Sweden, 1845–7.
2. **Leroy (André),** Angers, 1863.
1. **Lessing (C. F.),** Berlin, 1829.
5. **Lettsom (W. G.),** Mexico, &c., 1856–62.
1. **Leybold (F.),** Santiago, 1862.
4. **Leycester (A. A.),** Australia, 1859–61.
5. **Leycester (H. H.),** Burnham, 1851–60.
2. **Leyland (R.),** Halifax, 1840–1.
3. **L'Herminier (F.),** Guadeloupe, 1846–7.
15. **Lhotsky (J.),** London, 1842–8.
6. **Liebman (F.),** Copenhagen, 1853–6.
11. **Linden (J.),** Brussels, 1843–61.
1. **Lindenberg (J. B.),** Bergedorf, 1825.
231. **Lindley (J.),** London, 1820–59.
7. **Lindsay (Lauder),** Edinburgh, 1856–61.
3. **Link (H.),** Berlin, 1835–50.
7. **Lippold (J. F.),** Madeira, 1837–40.
6. **Livingstone (D.),** South Africa, &c., 1857–64.

5. **Livingstone (J.)**, Edinburgh, 1823–8.
20. **Llewellyn (J. D.)**, Penllergaer, 1836–55.
14. **Lloyd (G.)**, Leamington, 1831–52.
1. **Lobb (T.)**, Perran Wharf, 1854.
2. **Lobb (W.)**, San Francisco, 1843–58.
6. **Lockhart (D.)**, Trinidad, 1829–42.
8. **Lockhart (John)**, Trinidad, 1832–44.
15. **Loddiges and Sons**, Hackney, 1831–50.
17. **Loftus (W. K.)**, Constantinople, 1853–6.
2. **Logan (N. E.)**, Montreal, &c., 1856–7.
2. **Logier (F.)**, Cape of Good Hope, 1861–4.
12. **Longman (T.)**, Paternoster Row, 1841–9.
18. **Longman (W.)**, Paternoster Row, 1841–58.
9. **Loring (W.)**, Southampton, 1852.
17. **Loudon (J. C.)**, Bayswater, 1836–43.
18. **Low (Hugh and Co.)**, Clapton, 1840–63.
6. **Lowe (E. J.)**, Nottingham, 1855–8.
62. **Lowe (Revd. R. T.)**, Madeira, 1827–65.
1. **Luckie (G.)**, Demerara, 1852.
6. **Lucombe and Pince**, Exeter, 1841–3.
10. **Ludwig (C. F. von)**, Capetown, 1833–40.
32. **Luscombe (J.)**, Combe Royal, 1851–65.
16. **Lyall (D.)**, Vancouver, 1848–61.
2. **Lyall (R.)**, Mauritius, 1830.
135. **Lyell (C.)**, Kinnordy, 1828–45.
27. **Lyons (J.)**, Mullingar, 1839–50.
6. **McAdam (Capt. D.)**, Plymouth, 1838–46.
4. **McAdam (J. J.)**, Belfast, 1849–51.
10. **Macarthur (Sir W.)**, New South Wales, 1844–63.
4. **McCalla (W.)**, Dublin, 1841.
5. **MacCarthy (Lady)**, Ceylon, 1849–53.
6. **McClelland (J.)**, Calcutta, 1845–53.
6. **MacCulloch (J.)**, Aberdeen, &c., 1831–3.
5. **MacCulloch (J. R.)**, London, 1833–5.
6. **McDonald (Arch.)**, British Columbia, 1835–43.
13. **McDonald (J.)**, Abbotsbury, 1844.
35. **McFadyen (J.)**, Jamaica, 1826–50.
4. **McGibbon (J.)**, Cape of Good Hope, 1856–64.
11. **McGillivray (J.)**, Pacific, &c., 1848–54.

24. **Macintosh (Ch. and G.)**, Antimony and Dunchattan, 1828–48.
4. **McIvor (W. J.)**, Ootacamund, 1847–63.
51. **MacKay (J. T.)**, Dublin, 1830–50.
10. **McKen (M. F.)**, Jamaica, Natal, 1847–50.
4. **McKenzie (C.)**, Mexico, 1824–8.
6. **McKenzie (Sir George)**, Coul, 1810–11.
4. **Mackie (A. and F.)**, Norwich, 1836–9.
2. **Maclagan (Dougl.)**, Edinburgh, 1842.
85. **Maclean (J.)**, Lima, &c., 1832–55.
3. **Macleay (Alex.)**, Sydney, 1843–6.
13. **Macleay (Sir G.)**, London, 1859–64.
6. **McLeod (Sir H.)**, Trinidad, 1845–6.
1. **McNab (A.)**, Caled. Hort. Soc., 1843.
1. **McNab (D.)**, Buenos Ayres, 1827.
8. **McNab (Gilb.)**, Jamaica, 1835–47.
4. **McNab (J.)**, Bot. Gard. Edinb., 1833–9.
2. **McNab (W.)**, Bot. Gard., Edinb., 1847.
3. **Macoun (J.)**, Canada, 1863–4.
3. **Macrae (A.)**, Calcutta, 1849.
3. **MacTier (A. W.)**, Durris, 1856–8.
22. **McWilliam (I. O.)**, Tower Hill, 1844–57.
14. **Madden (Capt. E.)**, Kumaon, 1845–54.
4. **Madden (Sir F.)**, British Museum, 1853.
7. **Main (R.)**, Greenock, 1858–9.
1. **Maingay (A. C.)**, Co. Down, 1858.
2. **Malakoff (Duke of)**, Algiers, 1858–62.
2. **Malet (J.)**, Bermuda, 1843.
3. **Malle (Dureau de la)**, Paris, 1852–5.
16. **Malleson (F. A.)**, Pulborough, 1843–55.
10. **Malortie (Baron)**, Hanover, 1853–9.
2. **Manderville (H.)**, Buenos Ayres, 1844.
6. **Mandon (G.)**, Paris, &c., 1863–4.
2. **Mangles and Co.**, London, 1864.
6. **Mangles (Jas.)**, London, 1841–3.
5. **Mangles (R. M.)**, Sunninghill, 1836–48.
58. **Mann (Gustav)**, West Africa and Assam, 1859–65.
6. **Manners (Ld. John)**, London, 1858–62.
2. **Mantell (G. A.)**, Chester Square, 1850.

1. **Marchand (And.)**, Paris, 1860.
2. **Marjoribanks (Chas.)**, Canton, 1824–5.
10. **Mark (E. W.)**, Bogota, 1844–63.
86. **Markham (Sir C.)**, Eccleston Sq., 1859–64.
5. **Marlay (B.)**, O. of Works, 1858–9.
5. **Marnock (R.)**, Britton Hall, 1830–44.
11. **Marryat (Charlotte)**, Wimbledon House, 1845–56.
3. **Marryat (Chas.)**, London, 1845–56.
6. **Marryat (Ellen)**, Wimbledon House, 1845–56.
6. **Marsh (M. N.)**, Ramridge Park, 1861–2.
54. **Marsh (W. T.)**, Jamaica, 1853–63.
4. **Marsham (A.)**, Norwich, 1850–3.
12. **Martin (J.)**, Woburn Abbey, 1839–45.
16. **Martius (C. von)**, Munich, 1829–60.
5. **Maskelyne (N. S.)**, Oxford, 1854–5.
21. **Mason (Nath.)**, Madeira, &c., 1855–62.
2. **Masters (Maxw.)**, King's College.
10. **Masters (W.)**, Canterbury, 1846–60.
4. **Matheson (Sir J.)**, Dingwall, &c., 1847–64.
32. **Mathews (Anth.)**, Peru, 1829–42.
1. **Maxwell (G.)**, K. G. Sound, 1861.
14. **Medland (Revd. T.)**, Steyning, 1848–62.
6. **Meissner (C. J.)**, Basle, 1850–63.
16. **Meller (C.)**, Zambesi, &c., 1861–5.
20. **Melliss (H.)**, St. Helena, 1862–5.
7. **Melly (A.)**, Liverpool, 1835–45.
3. **Meneville (Guerin)**, Paris, 1861.
4. **Menzies (Arch.)**, London, 1826–40.
11. **Merrivale (H.)**, Colonial and India Offices, 1833–63.
3. **Mertens (C.)**, Bremen, 1801–16.
12. **Mettenius (G.)**, Leipzig, 1856–65.
5. **Meyer (C. A.)**, St. Petersburg, 1836–53.
4. **Meyer (Ernst)**, Königsberg, 1844–5.
10. **Middleton (Sir W.)**, Shrublands.
50. **Miers (J.)**, Hammersmith, 1826–57.
4. **Milde (J.)**, Breslau, 1864–5.
3. **Mill (J. S.)**, India House, 1830–1.
6. **Miller (Thos.)**, Capetown, 1825–61.
9. **Millet (C.)**, China, 1825–31.

2. **Milligan (J.)**, Hobarton, 1869.
52. **Milne (A. O.)**, O. Woods and For., 1841–50.
23. **Milne (W.)**, Pacific, &c., 1852–8.
12. **Minto (Lord)**, Admiralty, &c., 1841–9.
30. **Miquel (F. A. W.)**, Holland, 1844–65.
2. **Mirbel (A.)**, Jardin des Plantes, Paris, 1842.
5. **Mitchell (D. W.)**, Zoological Society, 1849–52.
9. **Mitchell (J. B.)**, Syria, Egypt, 1841–3.
3. **Mitchell (Sir Thos.)**, London, 1840–6.
38. **Mitten (W.)**, Hurstpierpoint, 1846–62.
2. **Mohr (B. A.)**, Amsterdam, 1843.
15. **Molesworth (Caroline)**, Cobham, 1848–60.
4. **Molesworth (Sir W.)**, O. of Works, 1843–9.
1. **Molina (F.)**, London, 1850.
1. **Molkenboer (J. H.)**, Leyden, 1843.
1. **Monck (Lord)**, Quebec, 1862.
3. **Monro (D.)**, New Zealand, 1852–4.
9. **Montagne (C.)**, Paris, 1835–44.
14. **Monteagle (Lord)**, London, 1838–61.
1. **Monteiro (J. P.)**, Pentonville, 1851.
3. **Montrose (Duke of)**, Buchanan, 1830–52.
7. **Moody (Lt.-Col.)**, London, Falkland Islands, 1842–6.
29. **Moore (Ch.)**, Regent's Park, Sydney, 1842–65.
63. **Moore (D.)**, Belfast, Glasnevin, 1834–55.
15. **Moore (Thos.)**, Chelsea, &c., 1841–65.
9. **Moricand (Stef.)**, Geneva, 1836–53.
12. **Morice (G. T.)**, New Cross, &c., 1857–9.
2. **Morison (R.)**, Newfoundland, 1824–5.
2. **Moritzi (A.)**, Switzerland, 1843–5.
14. **Mornay (Ed. de)**, London, &c., 1854–9.

Morpeth (Visct.). *See* **Carlisle, Earl of.**

3. **Morren (Ch.)**, Liège, 1846–50.
55. **Morris (J.)**, Great Ormond Street, 1851–65.
1. **Mortellat (G.)**, Geneva, 1852.
1. **Moseley (H.)**, Wandsworth, 1853.
6. **Moss (John)**, Otterspool, 1838–42.
12. **Motley (J.)**, Borneo, &c., 1852–9.
12. **Mougeot (J. B.)**, Vosges, 1823–58.
8. **Moxon (J. E.)**, Leyton, 1847–56.

139. **Mueller (Ferd.)**, Australia, 1850–65.
4. **Mueller (J. Argan)**, Geneva, 1857–64.
8. **Munby (Giles)**, Algiers, 1845–63.
3. **Mund (L.)**, South Africa, 1827–9.
25. **Munro (Col. W.)**, Druidstoke, 1847–65.
22. **Murchison (Sir R.)**, Belgrave Square, 1840–64.
1. **Murie (J.)**, Gondokoro, 1863.
2. **Murray (Alexr.)**, Aberdeen, 1835–6.
17. **Murray (And.)**, Edinburgh and S. Kensington, 1852–64.
6. **Murray (The Hon. C. A.)**, Cairo, &c., 1841–55.
1. **Murray (Hugh)**, London, 1846.
10. **Murray (J.)**, Albemarle Street.
24. **Murray (J.)**, Hull, &c., 1834–47.
6. **Murray (J. Craigie)**, Sierra Leone, 1846–9.
4. **Murray (Stewart)**, Glasgow, 1841–4.
2. **Myburg (F. G.)**, Nagasaki, 1862.
8. **Mylne (W. C.)**, Woburn, 1832–5.
3. **Napoleon (Prince)**, Paris, 1855–7.
15. **Nasmyth (Sir J. M.)**, Wimbledon, &c., 1850–64.
5. **Natal, Bp. (Colenso)** of, London, 1854–8.
4. **Nation (W.)**, Lima, 1853–65.
2. **Naudin (C.)**, Paris, 1858–9.
28. **Nees von Esenbeck**, Breslau, 1826–55.
33. **Neill (Patrick)**, Edinburgh, 1830–64.
1. **Nelson and Bronté (Visct.)**, London, 1858.
29. **Nesfield (W. A.)**, Eton, 1844–59.
4. **Nestler (C. G.)**, Strassburg, 1823–30.
4. **Neumann**, Jardin des Plantes, Paris, 1846–9.
4. **Neumann (Baron de)**, Chandos House, 1843–4.
38. **Nevill (Lady Dorothy)**, Dangstein.
1. **New (W.)**, Bangalore, 1858.
3. **Newman (E.)**, Wellclose Square, 1841–4.
4. **Newman (J.)**, Botanical Gardens, Mauritius, 1826–33.
13. **Newton (Alf.)**, Melford, &c., 1860–5.
4. **Nicholson (J.)**, Sheffield, 1835–43.
10. **Nicholson (Thos.)**, Antigua, 1829–35.
7. **Nightingale (F.)**, Embly.
8. **Nimmo (Jos.)**, Bombay, 1834–46.
6. **Nimmo (W.)**, Demerara, 1835–7.

10. **Niven (N.)**, Glasnevin, Dublin, 1836–53.
3. **Noé (Vicomte de)**, Paris, 1849–54.
2. **Nordenskiold (Nit.)**, Helsingfors, 1857–9.
11. **Northumberland (Duchess of)**, Syon, 1853.
30. **Northumberland (Duke of)**, Syon, 1843–54.
8. **Norwich (Bishop of)**, Norwich, 1840–9.
1. **Notaris (J. de)**, Milan, 1833.
78. **Nuttall (T.)**, Rainhill, &c., 1825–58.
1. **Nylander (W.)**, Paris, 1856.
6. **O'Connor**, Gambia, &c., 1854–61.
7. **O'Leary (D. F.)**, Bogota, 1846–51.
1. **Oakes (W.)**, Boston, U. S., 1841.
2. **Ocampo (Mich.)**, Mexico, 1842.
1. **Oersted (A. S.)**, Copenhagen, 1853.
6. **Ogilvie (R. A.)**, Custom House, 1856–9.
3. **Ogle (J. W.)**, London, 1863.
11. **Oldfield (Aug.)**, Tasmania, 1850–63.
9. **Oldfield (R. A.)**, Sierra Leone, 1851–7.
51. **Oldham (R.)**, China, Japan, 1861–4.
1. **Oliphant (L.)**, London.
6. **Oliver (D.)**, Newcastle, 1852–60.
4. **Oman (G.)**, H.M.S. *Wellesley*, 1837–9.
3. **Opie (Amelia)**, Norwich, 1834–42.
4. **Opie (C. Knox)**, South Africa, 1859.
9. **Orde (B. J.)**, Kilmory, 1835–56.
7. **Otto (F.)**, Berlin, 1827–42.
5. **Ouseley (Sir W. Gore)**, Assumption, 1854–7.
18. **Owen (Sir R.)**, London, &c., 1839–63.
2. **Oxford (Bishop of)**, Fulham, &c., 1854–5.
6. **Oxley (T.)**, Singapore, 1847–52.
6. **Paget (Sir J.)**, London, &c., 1833–60.
12. **Palgrave (Sir F.)**, Hampstead, 1831–52.
3. **Palgrave (W. G.)**, Hampstead, 1836–48.
7. **Palliser (Capt. J.)**, London, &c., 1857–9.
12. **Pamplin (W.)**, Soho, 1842–58.
2. **Panizzi (A.)**, British Museum, 1858–63.
7. **Pappe (Ludw.)**, Capetown, 1845–62.
70. **Parish (Rev. C.)**, Moulmein, 1855–65
90. **Parker (C. S.)** Demerara, &c., 1823–58.

5. **Parkinson (Col. C. T.)**, Durham, 1856–9.
58. **Parkinson (J.)**, Mexico, &c., 1839–45.
1. **Parkyns (Mansfield)**, Woodborough Hall.
22. **Parlatore (Ph.)**, Florence, 1841–60.
2. **Parnell (R.)**, Edinburgh, 1834.
2. **Parreyiss (L.)**, Vienna, 1834.
26. **Parry (Adml. Sir E.)**, Admiralty, &c., 1823–50.
7. **Pascoe (Capt. F. P.)**, Australia, &c., 1844–6.
6. **Pavia (Baron de Castell)**, Lisbon, 1861–2.
16. **Pavillon (Huet de)**, Geneva, 1854–7.
22. **Paxton (Sir J.)**, Chatsworth, 1837–62.
2. **Payer (J.)**, Paris, 1834.
5. **Peel (Sir Lawr.)**, Calcutta, 1848–54.
5. **Peel (Sir R.)**, Whitehall, 1844–5.
2. **Pelly (Sir J. H.)**, Hudson's Bay, 1843.
1. **Pengelly (W.)**, London, 1862.
26. **Pentland (J. B.)**, Bath, &c., 1847–9.
6. **Perceval (Anne Mary)**, London, &c., 1825–65.
23. **Pereira (J.)**, Finsbury Square, 1841–51.
7. **Perry (T. A.)**, Chelsea, 1842–4.
3. **Perry (W.)**, Penzance, 1846–7.
1. **Persoon (C. H.)**, Paris, 1840.
4. **Pettigrew (J.)**, London, 1838–50.
5. **Phelps (J. F.)**, Westminster, &c., 1841–2.
3. **Philippi (R. A.)**, Chili, 1860–3.
197. **Philipps (T. W.)**, O. of Works, 1844–55.
10. **Phillips (J.)**, York Mus., 1840–53.
42. **Phipps (Lt.-Col.)**, Osborne, &c., 1848–61.
3. **Pickering (C.)**, Philadelphia, 1828–43.
2. **Piddington (H.)**, Calcutta, 1856–7.
42. **Pince, Luccombe & Co.**, Exeter, 1842–4.
7. **Planchon (J. G.)**, Montpellier, 1847–59.
4. **Plant (R. W.)**, Natal, 1856–8.
7. **Playfair (Sir L.)**, South Kensington, 1850–62.
6. **Playfair (R. L.)**, Aden, 1862–5.
9. **Poeppig (E.)**, Leipzig, 1834–41.
2. **Pollexfen (Revd. J. H.)**, Edinburgh, &c., 1840.
6. **Porter (Sir R. K.)**, Caracas, 1836–59.
2. **Potts (J.)**, Mexico, 1850–7.

8. **Powell (Revd. T.)**, Samoa, 1861–4
8. **Preiss (L.)**, London, 1839–42.
2. **Prescott (J. D.)**, St. Petersburg, 1828–9.
1. **Presl (C. B.)**, Prague, 1832.
1. **Presl (E.)**, Brunswick, 1860.
7. **Prestoe (H.)**, Trinidad, 1864–5.
6. **Prevost (E.)**, Vancouver, 1859.
29. **Prior (R. C. Alex.)**, Taunton, &c., 1844–64.
4. **Pückler-Muskau (Prince)**, Dresden, &c., 1857–62.
10. **Pullen (Capt. W., R.N.)**, Suez, &c., 1851–9.
44. **Purdie (W.)**, New Grenada, Jamaica, 1843–55.
10. **Purton (T.)**, Alcester, 1830–2.
2. **Pusey (E. B.)**, Ch. Ch., Oxford.
4. **Raddi (J.)**, Florence, 1819–25.
2. **Radlkofer (L.)**, London, 1856.
3. **Rae (J.)**, Fort Simpson, &c., 1848–65.
1. **Raffles (Sir Stamf.)**, London, 1826.
1. **Rafinesque (L. S.)**, Philadelphia, 1831.
17. **Ralfs (J.)**, Penzance, 1838–54.
2. **Ramsay (Revd. E. B. R., Dean)**, Edinburgh, 1849.
5. **Ransome (G.)**, Ipswich, 1847–51.
3. **Rathbone (W.)**, Liverpool, 1855–7.
41. **Rawson (Sir E. R.)**, Capetown, &c., 1849–64.
11. **Reeves (J.)**, China, Clapham, 1829–?.
8. **Regel (E.)**, St. Petersburg, 1857–60.
23. **Reichenbach (H. G.)**, Leipzig, &c., 1846–65.
5. **Reichenbach (Ludwig)**, Dresden, 1826–60.
12. **Reid (Sir W.)**, Bermuda, &c., 1843–51.
1. **Reinwardt (C. G.)**, Leyden, 1831.
4. **Rennie (G.)**, Falkland Islands, 1854–6.
5. **Rensselaer (Jer. van)**, New York, 1824–6.
6. **Repper (B.)**, Real del Monte, 1845–8.
6. **Requien (Esprit)**, Avignon, 1829–50.
2. **Requina (Pedro)**, Mexico, 1857–65.
2. **Reuter (G. F.)**, Geneva, 1847–8.
7. **Ribedro (Chas. de)**, London, 1852–4.
8. **Richard (Achille)**, Paris, 1829–51.
7. **Richards (B. C.)**, Admiralty, 1858–65.
4. **Richards (Capt. G., R.N.)**, Vancouver, &c., 1856–7.

140. **Richardson (Sir J.)**, Chatham, &c., 1819–65.
1. **Richter (Alex.)**, Moscow, 1846.
1. **Riddell (J. L.)**, New Orleans, 1838.
2. **Ridolfi (Marchese Casimo)**, Florence, 1856.
14. **Rigby (Ed.)**, London, 1832–57.
1. **Rink (H.)**, Greenland, 1853.
3. **Rivière (T.)**, Paris, 1855.
4. **Robb (Jas.)**, New Brunswick, 1836–40.
8. **Roberts (G.)**, Hudson's Bay Ho., 1844–56.
13. **Roberts (Henry)**, London, 1852–7.
6. **Roberts (Revd. J.)**, Heligan, 1836–48.
27. **Robinson (Sir Herc.)**, West Indies, &c., 1857–61.
1. **Rodie (Hugh)**, Guiana, 1852.
1. **Roe (J. S.)**, Swan River, 1853.
1. **Roget (P. M.)**, Royal Society, 1831.
11. **Rolle (Lady)**, Bicton, 1844–58.
2. **Rollison (W. & Sons)**, Tooting, 1842–3.
9. **Romaine (W. G.)**, Admiralty, 1858–62.
4. **Rondot (Nat.)**, Paris, 1857–8.
5. **Rooper (Revd. Thos.)**, Brighton, 1850.
3. **Rooper (Revd. W. H.)**, Repton Rectory, 1853.
2. **Roscoe (L.)**, Liverpool, 1832–8.
Rosmead (Lord). *See* Robinson, Sir H.
14. **Ross (Adm. Sir Jas.)**, London, &c., 1826–44.
7. **Rosse (Earl of)**, Parsonstown, 1852–6.
35. **Rothery (C.)**, Stratford Place, 1845–65.
9. **Rothschild (Baroness)**, Gunnersbury.
4. **Roupell (J. H.)**, Welbeck Street, 1848–51.
7. **Routledge (Thos.)**, Oxford, &c., 1852–62.
6. **Roxburgh (Capt. B.)**, London, &c., 1842–4.
100. **Royle (J. F.)**, India House, &c., 1829–57.
1. **Rucker (Sigism.)**, Wandsworth, 1863.
1. **Rudge (E.)**, London, 1842.
2. **Ruprecht (F.)**, St. Petersburg, 1838–51.
123. **Russell (G.)**, O. of Works, 1857–65.
18. **Russell (Lady J.)**, Pembroke Lodge, 1841–54.
6. **Russell (Lord John)**, London, &c., 1841–59.
3. **Rutherford (Andr.)**, Edinburgh, 1846–52.
4. **Rylands (J. jun.)**, Warrington, 1840–51.

26\. **Sabine (Sir E.)**, Woolwich, &c., 1832–49.
14\. **Sabine (Joseph)**, Hort. Soc., 1825–36.
1\. **Sagot (Alph.)**, Paris, 1861.
3\. **Sagot (P.)**, Coulanges, 1860–5.
2\. **Sagra (Ramon de)**, Paris, 1851–5.
2\. **St. Hilaire (Aug. de)**, Paris, 1831.
2\. **St. Hilaire (J. Geoff.)**, Paris, 1861.
St. Vincent. *See* Bory de.
Salm-Dyck (Prince of). *See* Dyck.
11\. **Salter (T. Bell-)**, Ryde, 1845–56.
3\. **Salvin (O.)**, London, 1860–1.
6\. **Salwey (Revd. T.)**, Oswestry, 1833–59.
27\. **Sandbach (H. R.)**, Liverpool, 1833–52.
15\. **Sanderson (J.)**, Natal, 1852–65.
82\. **Saunders (W. W.)**, Lloyd's, 1843–64.
1\. **Savi (Gaetano)**, Pisa, 1830.
1\. **Savi (G. N.)**, Vicenza, 1851.
6\. **Savory (Revd. E.)**, Binfield, 1857–62.
4\. **Schach (Baron de)**, Trinidad, 1822–4.
6\. **Schaerer (L. E.)**, Berne, 1826–35.
3\. **Schaffner (J. G.)**, Port Zatlan, 1856–7.
2\. **Schauer (J. C.)**, Breslau, 1834–7.
34\. **Scheer (F.)**, Kew, 1842–57.
6\. **Schimper (W. P.)**, Strassburg, 1838–62.
7\. **Schirges (H.)**, Ecuador Land Co., 1857–9.
3\. **Schlagintweit (Ad.)**, London, 1850–1.
24\. **Schmid (Revd. B.)**, Nilghiris, 1845–57.
62\. **Schomburgk (R. H.)**, Guiana, &c., 1833–64.
10\. **Schott (H. W.)**, Schoenbrunn, 1855–62.
7\. **Schouw (J. F.)**, Copenhagen, 1842–9.
4\. **Schultz (C. H., Bipont)**, Deidesheim, 1842–4.
1\. **Schultzess (Ld.)**, Zurich, 1825.
12\. **Schwaegrichen (C. F.)**, Leipzig, 1818–39.
5\. **Schweinitz (L. de)**, Pennsylvania, 1823–8.
4\. **Sclater (P. L.)**, Zoolog. Soc., 1859–60.
8\. **Scott (Col. H.)**, South Kensington, 1862–5.
3\. **Scott (Thos.)**, Tasmania, 1827–32.
48\. **Scouler (J.)**, Dublin, &c., 1833–52.
47\. **Seemann (B.)**, Panama, &c., 1846–60.

1.	**Selby (Prid. J.)**, Twizel House, 1842.
1.	**Sendtner (Otto)**, Munich, 1847.
10.	**Seringe (N. C.)**, Lyons, &c., 1825–58.
6.	**Seymour (Adm. Sir W.)**, China, 1857–9.
13.	**Seymour (Lord)**, O. of Works, 1850–2.
4.	**Shaw (H.)**, St. Louis, 1856–7.
17.	**Shaw (Norton)**, Royal Geogr. Soc., 1850–62.
2.	**Shephard (W.)**, Quebec, 1829–46.
6.	**Shepherd (H.)**, Bot. Garden, Liverpool, 1826–44.
17.	**Sherbourne**, Prescot, 1842–6.
18.	**Short (C. W.)**, Kentucky, 1832–55.
11.	**Short (Th. Keir)**, Notts, 1835–7.
8.	**Shrewsbury (Earl of)**, Alton Towers, 1847–8.
1.	**Shuter (Jas.)**, Madras, 1824.
48.	**Shuttleworth (R. J.)**, Berne, &c., 1832–46.
6.	**Sieber (F. G.)**, Prague, &c., 1826–52.
1.	**Silliman (B.)**, Yale College, 1828.
25.	**Silvester (E.)**, Chorley, 1839–56.
3.	**Simmonds (P. L.)**, London, 1858.
1.	**Simons (C. T.)**, Assam, 1850.
3.	**Simpson (G.)**, Hudson's Bay House, 1843.
25.	**Sinclair (Andr.)**, New Zealand, &c., 1836–61.
2.	**Skene (D. J.)**, Edinburgh, 1830–1.
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THE publication of the Biographical Notice and Portrait of Sir William Hooker, together with the Title-page, Contents, and Index, completing Vol. XV of the ANNALS OF BOTANY, is unavoidably postponed to the June number.

Tryptophane in Proteolysis.

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THE last number of the 'Annals of Botany' contains a paper (1) in which I adduce evidence to prove that the proteolytic enzyme of *Nepenthes*, as well as those of the Pine-Apple (bromelin) and of the Papaw (papaïn), are essentially 'tryptic' in their mode of action. The evidence consists in the demonstration, by means of the chlorine-water test, of the presence of a substance, known as tryptophane, among the products of digestion. It is, I believe, generally accepted that the formation of this substance is an indication of the disruption of the proteid molecule into non-proteid substances which is held to be characteristic of 'tryptic' digestion. The correctness of this view of the physiological significance of tryptophane has been confirmed by the recent researches of Hopkins and Cole (2), who find that its formula is $C_{11}H_{12}N_2O_2$, and that it abundantly yields skatol and indol on heating.

I propose, in the present paper, to give a more complete account of my observations on bromelin and papaïn, and to describe further experiments which I have made with the enzymes of the Fig (*Ficus Carica*, L.), of the Coco-Nut (*Cocos nucifera*, L), of germinating seeds of the Bean (*Vicia Faba*, L.) and of the Barley (*Hordeum vulgare*, L.), of Yeast (*Saccharomyces Cerevisiae*, Meyen), and of the Bacteria of putrefaction, as also with animal pepsin. I will so far anticipate as to say at once that in all these cases, under appropriate conditions, I have succeeded in finding trypto-

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phane among the products of digestion of fibrin and of Witte-peptone.

It is already known that the action of certain of these vegetable enzymes is 'tryptic,' since it has been ascertained that they cause the formation of leucin and tyrosin in proteolysis. This is the case with bromelin, papaïn, the enzyme of germinating seeds, and with the enzymes of Yeast and Bacteria. The products of digestion by the enzyme of the Fig (*cradeïn*) have not yet been sufficiently investigated from this point of view.

The only attempts at quantitative estimation of the activity of the vegetable enzymes are those of Chittenden (3) regarding bromelin, and of Martin (4) regarding papaïn. The method employed by these observers was that of supplying a known weight of digestible proteid (albumin) and determining the weight of proteid remaining undigested at the close of the experiment. Whilst the results so obtained are of value, the method is open to the criticism that when HCl or Na_2CO_3 is present in a digestive mixture, the solution of the proteid may be due in part to the action of the acid or of the alkali, and to that extent the numerical result would be vitiated. Nor does this method afford any evidence as to whether or not the proteid that has passed into solution is in the same stage of proteolysis in digestions which may have to be compared. In employing the tryptophane-test for this purpose, I have not had any close quantitative estimation in view. My object has been to ascertain, under various conditions and with various enzymes, the time required to form tryptophane; and to compare the intensity of the reactions as indicated by the depth of colour. In this way some rough idea as to the relative activity of proteolysis has been obtained. It would be, I believe, possible to develop a quantitative method on the basis of the tryptophane-reaction, by ascertaining the volume of chlorine-water necessary to produce the same depth of colour in equal quantities of the various digested mixtures; the coloured chlorine-compound in each being extracted by shaking with equal quantities of amyl-alcohol in which it is readily soluble.

However, the difficulty would still remain that it is impossible at present to prepare equivalent standardized solutions of the enzymes to begin with.

Before proceeding to the description of the experiments, a few general remarks as to the methods employed are necessary. The digestions were carried on in an incubator or thermostat, at a constant temperature of 38°–39° C. The fibrin used had been well-washed in water and in alcohol, and preserved in 50 per cent. glycerin ; it was again well-washed in water immediately before use: it was not previously swollen in dilute HCl. That the results obtained on its digestion were not attributable to an enzyme belonging to the fibrin itself, is proved by the fact that digestion of some of it in 0·2 % HCl, for several days, gave rise to no tryptophane; nor was any found when the fibrin was digested with water for a similar period (see expts. with Bacteria, p. 15). Moreover the results obtained with fibrin were checked by those with Witte-peptone, with which they were generally concordant, though they were produced more slowly and were less marked.

A point of experimental importance arose in connexion with the neutralized or alkaline digestions in which crude vegetable juices were used, such as those of the Pine-Apple, of the Fig, and of germinating seeds. It was observed that the neutral or alkaline reaction of these liquids was maintained for some hours; but on prolonging the digestions over night (20–24 hours) the liquids became more or less strongly acid, showing that a secondary development of acid had taken place. The results recorded in such cases are those that were obtained whilst the liquid was still found to be neutral or alkaline. It is noticeable that when a neutralized or alkaline liquid thus becomes acid again, the tryptophane-reaction that it gives is exceptionally strong, indicating that proteolytic action has been more than usually vigorous. I am unable at present to account for these facts. It seems not improbable that some of the recorded observations as to the activity of certain of these enzymes in prolonged digestions of neutralized or alkaline liquids, may be to some extent vitiated by the failure to recognize this re-acidification.

As a rule the tryptophane-test was applied directly to the digestion-liquid, after ascertaining that the reaction of the liquid was acid. When the liquid was too thick, it was previously filtered. In cases in which a comparison had to be instituted, and where the result appeared to be at all doubtful, measured quantities of the liquids were tested, and measured quantities of chlorine-water added.

In the more prolonged experiments it was advisable to use an antiseptic, and for a time I had recourse to thymol. But I found that this substance seemed to interfere with proteolytic action, especially in the case of pepsin; so I replaced it by hydrocyanic acid (HCN), adding a few drops of a strong (Scheele's = about 4 %) solution; and found that it not only acted as an antiseptic, but in certain cases promoted digestion. When using HCN, it was necessary to keep the liquids during digestion in stoppered bottles to prevent loss of the volatile acid.

BROMELIN.

This is the proteolytic enzyme of the Pine-Apple (*Ananas sativus*, Schult.). We owe our knowledge of its properties mainly to the researches of Chittenden (3), who ascertained that it causes the formation of leucin and tyrosin; it is therefore a 'tryptic' ferment, a conclusion confirmed by the fact, to which I have already called attention, that tryptophane is another product of its activity. By means of the weighing method, to which I have alluded, Chittenden found that bromelin is most active in neutral liquids, 'but that the presence of small amounts of acid, especially such as are contained in Pine-Apple juice, and of sodium carbonate (·25 %), interferes with the proteolytic action only slightly.' It is also a very active enzyme, the most active that I have yet met with in plants. Chittenden estimates that, in a neutral liquid, it digested in 2 hours over 20 % per cent. of the albumin supplied, and I have detected the tryptophane-reaction in a bromelin-digestion, whether of fibrin or of Witte-peptone, in 2 hours, in almost all cases.

My results indicate that bromelin is an enzyme adapted for action in an acid medium; nor is this surprising in view of the fact that, according to Chittenden, the natural acidity of Pine-Apple juice is equal, on the average, to about 0·5 % HCl. The divergence between Chittenden's results and my own is probably due to his having used albumin, and I fibrin and Witte-peptone, as the digestible proteids; he himself found the acid juice to digest fibrin more rapidly than did the neutralized. I did not find that the addition of HCl, up to 0·2 %, to the already acid juice had any marked effect upon the tryptophane-reaction as compared with juice of natural acidity. On the other hand, I found neutralized juice to be distinctly less active than the natural acid juice; and further, that alkalinity, though it did not altogether inhibit, very much diminished the activity of the enzyme.

The following example illustrates the general method and results of the experiments.

The expressed juice is strongly acid, and gives a weak tryptophane-reaction. The amount of liquid in each of the bottles was 50 cc.; the duration of the digestion was 4 hours.

A. Natural acidity:
  (1) no proteid added (auto-digestion); faint tryptophane-reaction.
  (2) 1 grm. fibrin added: marked reaction.
  (3) 1 grm. Witte-peptone added: strong reaction.
B. Neutralized juice:
  (4) 1 grm. fibrin added: distinct reaction.
  (5) 1 grm. Witte-peptone added: marked reaction.
C. HCl added to 0·2 %:
  (6) 1 grm. fibrin added: marked reaction.
  (7) 1 grm. Witte-peptone added: strong reaction.
D. Alkaline (0·5 % Na_2CO_3):
  (8) 1 grm. fibrin added: faint reaction.
  (9) 1 grm. Witte-peptone added: weak reaction.

Next morning, after nearly 24 hours' digestion, Nos. 4, 5, 8, and 9 were distinctly acid, and gave more or less strong tryptophane-reaction. I obtained this result also in other experiments, in which HCN was used as an antiseptic.

PAPAÏN.

This is the enzyme of the Papaw (*Carica Papaya*, L.), and is obtained from the latex and more especially from the fruit:

for our knowledge of its properties we are chiefly indebted to the researches of Martin, who experimented, not with the enzyme, but with the dried juice. In his first series of observations (4), Martin established the 'tryptic' character of the enzyme by finding leucin, and traces of tyrosin among the products of digestion, coagulated egg-albumin being the proteid supplied when quantitative estimations were made: in the second series of observations (4 *a*), in which the enzyme digested the proteids of its own juice (globulin, albumose, albumin), leucin was found and the presence of tyrosin more definitely ascertained. He concludes that papaïn is active in neutral liquid; more active in the presence of 0·25 °/₀ of Na_2CO_3, but less active with larger amounts of the alkaline salt up to 1 °/₀; and that it acts slightly in liquid containing 0·05 °/₀ HCl, but not at all with a higher percentage. My own results tend to show that papaïn is more adapted, than Martin found, to an acid medium, and, more especially, that it can act powerfully in a liquid containing ·2 °/₀ of HCl: but Martin's results were obtained with albumin, mine with Witte-peptone and fibrin.

The following are some of the experiments upon which my conclusions are based.

Each of four bottles contained 1 grm. of Witte-peptone, and ·5 grm. of 'pure papaïn' (Christy), which gives a neutral watery solution.

Bottle No. 1 contained, in addition, 50 cc. of distilled water.
,, No. 2 ,, ,, 50 cc. of 0·2 °/₀ HCl solution.
,, No. 3 ,, ,, 50 cc. of 0·5 °/₀ citric acid solution.
,, No. 4 ,, ,, 50 cc. of 0·5 °/₀ Na_2Co_3 solution.

To each were added 5 drops of a 4 °/₀ solution of HCN.

After 3½ hours in the incubator, the only bottle which showed any tryptophane-reaction was No. 3, where it was weak but distinct.

After 22 hours in the incubator, bottles 2 and 3 gave a strong reaction, whilst bottles 1 and 4 gave a weak reaction.

A similar series of experiments was made with fibrin as the digestible proteid.

Four bottles were taken, as before, each containing 2 grms. of fibrin, and ·5 grm. of pure papaïn.

Bottle No. 1 contained, in addition, 50 cc. of distilled water.
" No. 2 " " 50 cc. of 0·2 $^{\circ}/_{0}$ HCl solution.
" No. 3 " " 50 cc. of 0·5 $^{\circ}/_{0}$ citric acid solution.
" No. 4 " " 50 cc. of 0·5 $^{\circ}/_{0}$ Na_2CO_3 solution.

After 23 hours in the incubator, the strongest reaction was given by No. 3 : next in order came Nos. 1, 2, 4, the reaction in No. 4 being very faint.

I had noticed in experiments with other enzymes, that the presence of a considerable proportion of HCN in acid digestions promoted the enzymotic action to a marked degree. I found this to be the case with papaïn. Comparing digestions, as above, of both Witte-peptone and fibrin (Nos. 2) in 0·2 $^{\circ}/_{0}$ HCl alone, with others exactly similar which contained HCN to the extent of 0·2 $^{\circ}/_{0}$ in addition, the tryptophane-reaction was much stronger in the latter than in the former. In fact the reactions in the mixtures containing 0·2 $^{\circ}/_{0}$ HCN were more marked than any of the others. This is not the case when HCN is the only acid present.

CRADEÏN OF THE FIG (*Ficus Carica*, L.).

The presence of a proteolytic enzyme in the latex of this plant was discovered by Bouchut (5) : but its properties were first investigated by Hansen (6), who found that the latex causes the solution of fibrin, in liquid containing 0·2 $^{\circ}/_{0}$ HCl, almost as rapidly as does pepsin ; and also in a liquid containing 2 $^{\circ}/_{0}$ of Na_2CO_3, but much less rapidly. The possibility that the enzyme might have 'tryptic' action was present to Hansen ; for he applied the tryptophane-test to the alkaline digestion, and also sought for tyrosin among the products, but with negative results. It is not clear whether or not he similarly investigated the acid digestion. Subsequently the properties of the latex and of the juice of the fruit were studied by Mussi (7). He obtained from the liquid a precipitate, on treatment with alcohol, which was insoluble in water but soluble in the presence of a trace of acid or alkali, the solution having digestive power. He gave the name *cradina* (cradeïn) to the precipitate which consisted, in part at any rate, of the proteolytic enzyme, and confirmed Hansen's statement that it is active in alkaline and in acid (HCl) liquids, but not in neutral: he does not appear to have investigated the digestive products.

As my experiments have been carried on during the autumn and winter, I have not been able to do much with the latex or with the juice of fresh fruit. I had just time to make one experiment, last October, with a watery extract of the already withering leaves. A mixture, consisting of 50 cc. of the neutral extract, 1 grm. of Witte-peptone, and 0·1 grm. of citric acid, gave a good tryptophane-reaction after 20 hours' digestion. In November, I experimented with the juice of some fresh fruit, and obtained the tryptophane-reaction by the digestion of fibrin: but the material was not satisfactory, and there was the difficulty that the Fig-juice was of a red colour to begin with, so that the tryptophane-reaction could not be readily distinguished. I therefore turned my attention to dried Figs, and obtained satisfactory results with a watery extract. The acid watery extract, digested by itself for 24 hours, gave no tryptophane-reaction; whereas, when either fibrin or Witte-peptone was digested with it, the reaction was marked.

The results that I have obtained with a watery extract of dried Figs do not confirm the conclusions of Hansen and of Mussi that cradeïn is especially active in acid liquids containing HCl, and in alkaline liquids containing Na_2CO_3. On the evidence of the tryptophane-reaction, which I regard as indicating whether or not digestion by the enzyme has taken place, I find that cradeïn is most active in naturally acid liquids; less active in acid liquids containing HCl; and least active in neutral and alkaline liquids. In some cases I observed that the neutralized and alkaline liquids became strongly acid when the digestion was prolonged to 24 hours; and in such cases the tryptophane-reaction was then more or less strongly marked. It is possible that the results ascribed by Hansen and by Mussi to alkaline liquids may have been due to this secondary development of acid.

The following will serve to illustrate the experiments.

Half a pound of dried figs were extracted with 500 cc. of cold distilled water, the mixture allowed to filter all night in a cold room.

The filtered liquid was slightly acid, and gave no tryptophane-reaction: 50 cc. of it were placed in each of 9 bottles, with various additions, as follows:

1. Extract alone.
2. „ + 1 grm. fibrin.
3. „ + 1 grm. Witte-peptone.
4. „ + 0·1 cc. HCl + 1 grm. fibrin.
5. „ + 0·1 cc. HCl + 1 grm. Witte-peptone.
6. Neutralized extract + ·25 grm. Na_2CO_3 + 1 grm. fibrin.
7. „ „ „ + 1 grm. Witte-peptone.
8. „ „ + 1 grm. fibrin.
9. „ „ + 1 grm. Witte-peptone.

To each bottle were added 5 drops of 4 % HCN; the bottles were placed in the incubator at 10 a.m.

After 24 hours' digestion No. 3 gave a marked tryptophane-reaction, Nos. 2 and 5 a weak one; the others gave no reaction; five hours later the result was essentially the same; the experiment was then closed.

THE COCO-NUT (*Cocos nucifera*, L.).

The so-called 'milk' is a watery, slightly turbid liquid, which gives weak xanthoproteic and tryptophane-reactions: it is slightly acid, and on the addition of alkali there is a copious precipitate of phosphates. It may be added that the milk gives a strong peroxidase-reaction with H_2O_2 and tincture of guaiacum, and that this property is destroyed by boiling.

I have found the milk to be feebly proteolytic: the enzyme is more active in acid than in alkaline liquids. Its activity would no doubt be greater were the seed germinated.

The following experiment gives a general idea of the proteolytic activity of the milk. In each case 50 cc. of milk were taken and 5 drops of 4 % HCN added: to each, except No. 5, 0·5 grm. of Witte-peptone was added.

1. Nothing further added.
2. Added 0·1 cc. HCl.
3. Neutralized and added 0·25 grm. Na_2CO_3.
4. Neutralized.
5. Milk only.

After 19 hours' digestion in the incubator, the result was—
Marked tryptophane-reaction in 1 and 2.
Distinct „ „ in 3.
Faint „ „ in 4 and 5:
3 and 4 had not become acid.

GERMINATING SEEDS.

There is a considerable literature upon the subject of the proteolytic enzymes of germinating seeds, but it is not necessary to follow it further back than the publication of Green's researches (8) on *Lupinus hirsutus*, L. He obtained from the cotyledons of seedlings four days old, a glycerine-extract which digested fibrin in the presence of 0·2 °/₀ HCl, and found leucin and tyrosin to be digestive products. He also obtained (8 *a*) these results with germinating seeds of the Castor-Oil plant (*Ricinus communis*, L.). Neumeister (9) subsequently detected a proteolytic enzyme in the seedlings of barley, poppy, wheat, maize, and rape, and ascertained that it is active only in acid liquids; but the acid present must be organic, not mineral: in this respect his results differ from those of Green, a difference which may perhaps be due to the fact that the plants experimented upon were not the same. Still more recently the matter has been investigated by Butkewitsch (10), the seeds used being those of *Lupinus angustifolius*, L., *Lupinus luteus*, L., *Vicia Faba*, L., and *Ricinus major* (?), with results that on the whole confirm those of Green. He found that, on adding water to the crushed seeds, the naturally acid liquid readily digested the proteids of the seeds; and that this auto-digestion was less rapid when the liquid was rendered alkaline to the extent of 0·1 °/₀ NaHO, or acid to the extent of 0·2 °/₀ HCl, but more rapid in the presence of 0·1 °/₀ HCN.

Experiments with Barley (*Hordeum vulgare*, L.).

Whether or not germinated barley contains a proteolytic enzyme is still a debated question: some of the more recent observations upon it are quoted in Butkewitsch's paper (10). On the whole, the balance of evidence seems to be in favour of the existence of such an enzyme, and it is generally alluded to in books relating to the chemistry of brewing under the name of 'peptase,' a name which should now be altered.

My own observations enable me to assert that the enzyme is undoubtedly present, and that it is remarkably vigorous. The experiments were conducted with 'green malt'; that is, barley which had germinated on the malting-floor for 11 days, but had not been dried in the kiln.

An extract was prepared by pounding in a mortar about 200 grms. of the barley with 350 cc. of distilled water to which 2 cc. of chloroform had been added; the thick liquid was set to filter all night in a cold room. On the following morning the filtered liquid was found to have a slight acid reaction, and to give distinct evidence of the presence of tryptophane.

About 100 cc. of the liquid were placed in each of three bottles 1, 2, 3: to (1) nothing was added, except 10 drops of 4 % HCN as an antiseptic; to (2), besides 10 drops of HCN, 0·2 cc. HCl was added; (3) was neutralized, and to it were added 10 drops of HCN, and 0·5 grm. of Na_2CO_3. The three bottles were placed in the incubator at 10 a.m. In two hours (1) and (3) gave a somewhat stronger tryptophane-reaction, (2) a weak one; 2 hours later, the results were much the same. 24 hours later (1) gave a strong reaction, (3) a less strong, and (2) still a weak one; it was observed that (3), which had been alkaline on the previous day, was now strongly acid, and that (1) had become more acid.

No proteid was added in any of these experiments, the reserve proteid of the grain providing the necessary material for digestion (auto-digestion).

From these observations it is clear that the enzyme acts strongly in liquid of natural acidity, and that its action is diminished and perhaps inhibited by the presence of 0·2 % HCl. With regard to the effect of an alkaline liquid, the result is less distinct: but it appears that some digestion occurred during the first day when the reaction was alkaline, whilst the stronger reaction on the second day may be attributable to the fact that the liquid had become acid.

I then proceeded to ascertain if tryptophane is present in kiln-dried pale malt; and, as might be expected, I found it.

The malt had been made from barley which had germinated for 11 days, and had been dried at about 90° C. An infusion of the malt with hot water gave a distinct tryptophane-reaction.

Experiments with *Vicia Faba*, L.

These have not yet been carried far. Some that I instituted on the principle of auto-digestion not having proved satisfactory, further observations were made on liquids to which Witte-peptone had been added. The seeds used had been soaked in water for some days in a warm room, and showed signs of germination. As the following record shows, the enzyme seems to act best in neutral or alkaline solutions, and to be inhibited by HCl.

145 grms. of germinated seeds ground to fine paste and extracted with 400 cc. distilled water; the turbid liquid, strained through muslin, is slightly acid, and gives a trace of tryptophane-reaction: 100 cc. placed in each of 4 bottles, with 1 cc. of 4 $^{\circ}/_{0}$ HCN:—

1. Without any addition.
2. Neutralized.
3. HCl added to 0·2 $^{\circ}/_{0}$
4. Made alkaline to 1 $^{\circ}/_{0}$ Na_2CO_3,

placed in incubator at 4 p.m.: next day at noon—

1. Gives faint tryptophane-reaction.
2. No reaction, is slightly acid.
3. No reaction.
4. No reaction, still alkaline.

As none gave a distinct tryptophane-reaction, I added 1 grm. of Witte-peptone to each; at 3 p.m. the results were—

1. Faint tryptophane-reaction.
2. Marked ,,
3. Faint reaction.
4. Distinct ,,

24 hours later, the results were—

1. Distinct reaction.
2. Strong ,, (slightly acid).
3. Faint reaction.
4. Marked do. (still alkaline).

It will be observed that my results do not exactly agree with any of those to which I have alluded. The diversity of opinion which exists as to the conditions of proteolysis in germinating seeds is, no doubt, due to the great differences in chemical composition presented by the seeds of the various families of plants. Moreover the experimental difficulties are considerable: it is in many cases almost impossible to obtain clear solutions to test; then there is the re-development of acid after neutralization to be taken into account ; and finally, seed-extracts are very liable to putrefy. The whole subject requires systematic re-investigation.

YEAST (*Saccharomyces Cerevisiae*, Meyen).

It is a well-known fact that if Yeast be starved by being kept in a liquid which contains no food-materials, the proteids of the cells undergo digestion, and that this auto-digestion is attributable to a proteolytic enzyme. Thus Salkowski (11) has shown that if Yeast be kept in chloroform-water, the liquid eventually contains leucin and tyrosin which can only have been derived from its own proteids. Moreover the formation of these two substances can only be due to the action of an enzyme, since living Yeast-cells are inhibited from enzymotic action by chloroform. More recently Hahn and Geret (12) have detected the formation of leucin and tyrosin in the expressed juice of Yeast. With regard to the proteolytic action of Yeast upon proteid supplied from without, Hahn (13) has ascertained that Yeast decomposes gelatine in the presence of chloroform.

My earlier experiments were merely tentative. In the first instance, I added 5 grms. fresh Yeast, which had been well washed on a filter, to about 100 cc. of three different liquids each containing 1 grm. of Witte-peptone, with the result that, after 24 hours' digestion, I obtained a marked tryptophane-reaction where the liquid was only distilled water, a weaker reaction where the liquid was 0·2 °/₀ HCl solution, and no reaction where the liquid was 0·2 °/₀ HCN. In a second series of experiments, I ground up fresh Yeast in a mortar with powdered glass and water, and made use of the turbid, faintly acid filtrate, thymol being the antiseptic. In a digestion of 18 hours of a mixture of 20 cc. of the Yeast-extract with 30 cc. distilled water, I obtained a weak tryptophane-reaction when fibrin had been digested, and a strong reaction when 1 grm. Witte-peptone had been digested : in the presence of 0·1 °/₀ citric acid, a fibrin-digestion gave no reaction, and a Witte-peptone-digestion, only a weak one. More recently I have used dried Yeast, prepared by drying fresh brewer's-yeast until it became brittle enough to grind in a mill: 20 grms. of this fine powder were extracted with 400 cc. distilled water for some time, and then thrown on a filter: the whole process of extraction and filtration lasted about 4 hours: the filtered liquid was slightly turbid, distinctly acid, and gave no tryptophane-reaction.

The result of these experiments is to prove the existence in Yeast of a proteolytic enzyme which is active in neutral and in acid liquids, but not in alkaline.

The following mixtures were prepared: each bottle (except No. 1) contained extract of dried yeast diluted with an equal bulk of distilled water, 50 cc. in all; to each 5 drops of 4 $^\circ/_0$ HCN were added.

1. contained 50 cc. undiluted yeast-extract.
2 *a.* added 1 grm. fibrin.
b. „ „ Witte-peptone.
3 *a.* „ „ fibrin + 0·1 cc. HCl (= 0·2 $^\circ/_0$).
b. „ „ Witte-peptone „
4 *a.* „ „ fibrin, neutralized.
b. „ „ Witte-peptone, neutralized.
5 *a.* „ „ fibrin, neutralized, + ·25 grm, Na_2CO_3.
b. „ „ Witte-peptone, neutralized, „

placed in the incubator at 4 p.m.

Next morning at 10 a.m. the results were—

1. weak tryptophane-reaction.

2 *a.* distinct	„	4 *a.* marked reaction.		now slightly acid.
b. marked	„	*b.* strong	„	
3 *a.* faint	„	5 *a.* none	„	both alkaline.
b. marked	„	*b.* faint	„	

In a repetition of the experiment with 4 *a* and 4 *b*, I satisfied myself that the striking reaction is given even when the liquid remains quite neutral throughout.

Bacteria of Putrefaction.

The fact that putrefying proteids undergo a decomposition somewhat analogous to that effected by trypsin, but more far-reaching, has long been known. The formation of tryptophane in putrefaction seems to have been first recorded by Claude Bernard (14), as also the fact that continued putrefaction causes the disappearance of this substance.

It is equally well known that the putrefaction of proteid is due to the action of Bacteria: and although it has not yet been isolated, there is evidence that the immediate agent in the process is a proteolytic enzyme.

My observations on putrefaction were undertaken not so much in the expectation of discovering new facts of a fundamental nature, as with the object of ascertaining whether or not tryptophane is formed under all the various conditions of experiment employed in the other investigations, and of determining the time of its appearance in each case: with the object, that is, of instituting a series of control-observations by which the possibility or probability of Bacterial intervention in the other cases might be checked.

The following series afford an idea of the general plan of these experiments and of their results.

Acid liquids: (1) 0·2 °/₀ HCl.

2 bottles, each containing 100 cc. of 0·2 °/₀ HCl: to the (*a*) one were added 2 grms. of fibrin, to the other (*b*) 1 grm. Witte-peptone.

(*a*) gave no tryptophane-reaction after 10 days in the incubator, nor was there any sign of solution or putrescence:

(*b*) no tryptophane-reaction until the 10th day; on the 5th day Moulds made their appearance (*Penicillium*), and the faint reaction on the 10th day is probably due rather to them than to Bacteria. No offensive odour.

(2) 0·5 °/₀ citric acid.

2 bottles each contained 50 cc. of this solution: to the one (*a*) was added 1 grm. of fibrin, to the other (*b*) 1 grm. of Witte-peptone.

(*a*) no tryptophane-reaction after 7 days in the incubator, nor any sign of putresence.

(*b*) no reaction until the 5th day, when Mould had abundantly developed; the faint reaction then given was doubtless due to this cause.

Alkaline liquid: 0·5 °/₀ Na_2CO_3.

2 bottles each contained 50 cc. of this solution: to the one (*a*) was added 1 grm. of fibrin, to the other (*b*) 1 grm. of Witte-peptone.

(*a*) distinct tryptophane-reaction on the 7th day; putrescent odour on the 3rd day.

(*b*) distinct reaction and putrescent odour on the 2nd day.

Neutral liquid: tap-water.

2 bottles each contained 50 cc. of water: to the one (*a*) was added 1 grm. of fibrin, to the other (*b*) 1 grm. of Witte-peptone.

(*a*) putrescent odour on 3rd day, distinct tryptophane-reaction on the 8th day.

(*b*) putrescent odour and marked tryptophane-reaction on the 2nd day.

Whilst it is probable that the above results may not be of general application, since other proteids and other organisms might behave differently, yet they serve to illustrate the relation of putrefaction to the other experiments that I was carrying on under generally similar conditions. In the first place, the antiseptic influence of acid, even of such a weak acid as the citric, is clearly demonstrated. It is further shown that the putrefactive enzyme works actively, and about equally, in neutral and in alkaline liquids, and that it decomposes Witte-peptone with much greater facility than it does fibrin. From the experiments with fibrin in neutral and alkaline liquids, it would appear that putrescence, as indicated by the odour, and the formation of tryptophane are not necessarily simultaneous, and that the former may precede the latter. It might have been anticipated from the constitution of tryptophane, as determined by Hopkins and Cole (2), that the indol and skatol, to which the putrid odour is due, would be derivatives of tryptophane, and would only become perceptible when the presence of tryptophane could be detected. As this was not the case, it is probable that a portion only of the indol and skatol formed in putrefaction passes through the tryptophane stage.

In one of the neutral putrefactive digestions of Witte-peptone, a chemical fact presented itself that seems to be worth special mention. After 48 hours, when it gave a strong tryptophane-reaction, the liquid had a marked greenish-blue colouration, turning bright yellow on adding a drop of acetic acid. The colouration was no doubt due to the formation of some indol-derivative.

PEPSIN.

In the paper (1) to which I have already alluded, I expressed the conviction that the vegetable enzymes therein referred to, and probably the proteolytic enzymes of all plants, are essentially 'tryptic' in their nature. I arrived at this conviction on the evidence of the tryptophane-reaction, and on the assumption, generally made, that the formation of tryptophane from proteids is characteristic of 'tryptic,' as distinguished from 'peptic,' digestion.

I felt, however, that it was necessary to test the validity of this assumption; to determine experimentally whether or not, as a matter of fact, the formation of tryptophane affords an absolutely reliable distinction between these two modes of proteolysis. I had not been able to find on record any statement to the effect that tryptophane had been found among the products of peptic digestion: but I was aware of the conflict of opinion between the school of Hoppe-Seyler which denied, and the school of Kühne which asserted, that the difference between peptic and tryptic digestion is absolute and fundamental. Lubavin was, I believe, the first to make this suggestion (15), and he did so in consequence of having found leucin and tyrosin among the products of prolonged peptic digestion (9–11 days). More recently Lawrow (16) has stated that he found leucin to be formed in a very prolonged gastric digestion (2 months); and Salaskin (17) and Zunz (18) both assert that crystallizable, nitrogenous, but non-proteid substances are formed under these circumstances [see also Langstein (19)]. There seemed, therefore, to be some probability that tryptophane might be produced in peptic digestion, a probability which has been realized in the investigation that I have made.

It is not necessary, however, that I should give a full account of my experiments; for, when they were complete, I happened to discover that their results had been anticipated; they are, therefore, merely of confirmatory interest. In a paper by Winternitz (20), on the chemistry of the putrefaction of milk, it is stated in a foot-note, that the author had obtained the tryptophane-reaction in a 7-hours' digestion of fibrin with extract of pig's stomach. It is not surprising that under such conditions of publication, this important discovery should have remained comparatively unnoticed. Malfatti (21) has also obtained tryptophane in neutral, acid, and weak alkaline digestions of Witte-peptone with pepsin: he ascribes the formation of tryptophane in the neutral and alkaline digestions to the presence of trypsin. Further, Glaessner (22) finds that in auto-digestion of gastric mucous membrane (3–4 weeks) in a weak alkaline ($Na_2\,Co_3$) liquid, tryptophane is formed. From this he infers that two enzymes are secreted by the stomach; viz. true pepsin, and what he terms 'pseudo-pepsin,' an enzyme which works in alkaline liquids that would destroy pepsin and in acid liquids that would destroy trypsin, and which, unlike true pepsin, forms tryptophane. On this hypothesis he accounts for the many discordant conclusions that have been arrived at as to the nature of the ultimate products of gastric digestion.

Although the position of this question has been thus modified since I began my observations upon pepsin, it is, I think, still worth while to place on record some of the experiments in which I succeeded in detecting tryptophane. The pepsin used was that sold as 'pepsin, pure scales': but I also obtained satisfactory results with glycerin-extract of pig's stomach.

Jan. 24, 50 cc. of solution of 0·2 °/₀ HCl, containing 0·5 grm. of pepsin, were placed in each of two bottles (1) and (2):

(1) to this was added 1 grm. of moist fibrin, } placed in incu-
(2) to this was added 0·5 grm. of Witte-peptone, } bator at 4 p.m.

Jan. 25, 11 a.m., no tryptophane in either: added 0·5 grm. of pepsin to each; also 1 grm. of fibrin to (1), and 1 grm. of Witte-peptone to (2).

4 p.m., faint tryptophane-reaction in both: added more fibrin to (1), and more Witte-peptone to (2).

Jan. 26, 10 a.m., both gave faint tryptophane-reaction: filled up both bottles with 0·2 °/₀ HCl solution.

Jan. 27, 11 a.m., tryptophane-reaction marked in (1), strong in (2).

No antiseptic was used; but in view of the results obtained as to the inhibiting action of 0·2 % HCl on Bacteria (p. 15), the result cannot be attributed to putrefaction.

I may mention that in many experiments I used thymol as an antiseptic, but these were generally unsuccessful. It appeared that thymol arrested the action of the pepsin. I therefore had recourse to hydrocyanic acid (HCN). The following experiment shows that this weak acid promotes peptic digestion, when present in sufficient quantity.

Jan. 22. 50 cc. of 0·2 % HCl, containing 0·5 grm. pepsin and 2·5 cc. of 4 % HCN (= 0·2 %), were placed in each of two bottles (1) and (2):

(1) to this were added 2 grms. moist fibrin, } placed in incu-
(2) to this was added 1 grm. Witte-peptone, } bator at noon.

Jan. 23. distinct tryptophane-reaction in both.

Jan. 24. strong reaction in both.

The tryptophane-reaction was obtained more rapidly in this than in any other of the experiments.

I have not had time to repeat my experiments in the light of Glaessner's (22) hypothesis. But if an enzyme having the properties of his 'pseudo-pepsin' were present in the pepsin that I used, it is clear that this pepsin should produce tryptophane in an alkaline liquid: this, however, I have not found to be the case.

CONCLUSIONS.

The additional instances that I have now given of the production of tryptophane, selected as they are from various classes and from different parts of plants, bear out my previously expressed opinion that the proteolytic enzymes of plants in general are essentially 'tryptic.' This statement will at any rate hold good until definite evidence is adduced to prove the existence of a 'peptic' enzyme. Moreover, these enzymes, with the exception of that of putrefactive Bacteria, are all active in acid media.

In view of the results obtained as to the action of pepsin, the question at issue has become a broader one. At first it related merely to the nature of the vegetable enzymes, the object being to ascertain whether they were 'tryptic' or 'peptic.' But, as I have already pointed out, there is a considerable body of accumulated facts tending to show that pepsin itself is capable of effecting 'tryptic' proteolysis. Hence the question now is whether or not such a thing as a 'peptic' enzyme exists at all; an enzyme, that is, which only hydrolyses the higher proteids to peptones, and does not decompose the proteid molecule. The ascertained facts seem to answer this question in the negative: but in view of Glaessner's (22) contention that the apparently 'tryptic' action of pepsin is due, not to pepsin itself, but to another enzyme, his 'pseudo-pepsin,' this answer cannot at present be definitively accepted. The *onus probandi* remains, however, with those who accept Glaessner's interpretation of the facts, and assume the secretion by the stomach of an enzyme which combines in so singular a manner the properties of pepsin with those of trypsin. In the mean time, the terms 'peptic' and 'tryptic' must be used with the reservation that they may refer, not, as hitherto, to what seemed to be fundamentally different processes of digestion, but to different modes of one and the same process. If it should turn out that they are inapplicable in their old sense, they may still be used to indicate the marked differences which exist between pepsin-digestion and trypsin-digestion. Even if pepsin be finally proved to be 'tryptic' in action, it will still be necessary to employ some terms to express the fact that it acts much more slowly than does trypsin, and, as far as it is possible to institute a quantitative estimate, that it produces tryptophane and other ultimate products in relatively much smaller quantity. Moreover the two enzymes differ materially as to the medium in which they respectively act: the one acts, whilst the other does not, in a HCl solution; and conversely, the one acts in an alkaline liquid whilst the other does not.

In respect of the reaction of the medium, the vegetable enzymes may be taken to show affinity with pepsin on the one hand and trypsin on the other. The results described in the foregoing pages may be conveniently summarized in the form of a provisional arrangement of the enzymes from this point of view, based upon the tryptophane-reaction.

I. *Active in Acid liquid*:
  1. active *only* in acid liquid:
    (*a*) most active with HCl: Pepsin.
    (*b*) active with HCl or natural acid: Nepenthin.
  2. more active in acid than in neutral or alkaline liquid:
    (*a*) equally active with HCl or natural acid: Bromelin: Coco.
    (*b*) more active with natural or organic acid: Papaïn; Cradeïn: 'Peptase' of Barley.
II. *Active in Neutral or Acid liquid*:
  enzyme of Yeast.
III. *Active in Neutral or Alkaline liquid*:
  (*a*) active in either: enzyme of Bean (?): putrefactive Bacteria.
  (*b*) more active in alkaline: Trypsin.

In conclusion, I would add a few words regarding the observation that hydrocyanic acid promotes proteolysis in certain cases. I regard this as a matter of some importance, as it may, if followed up, throw light upon the physiological significance of this acid in plants. Its general occurrence in certain families has long been known; and it was assumed, by a too facile oecology, that its importance lay in the protection which it was assumed to afford, by reason of its poisonous properties, against the depredations of animals. It is only recently that the matter has been seriously investigated. As the result of experiments, extending over several years, made upon *Pangium edule*, Reinw., a tropical tree which contains it in all its parts, Treub (23) has come to the conclusion that hydrocyanic acid is an early product in the nitrogenous anabolism of the plant. The presence of the acid in many germinating seeds, such as the Almond, the Peach, &c., is quite consistent with this view, for it may serve as nitrogenous plastic material for the growing embryo. At the same time the observations that I have made suggest that the acid may also be of importance in facilitating the proteolysis of the reserve-materials of the seed, a suggestion which I propose to test experimentally.

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On the Prothalli of Ophioglossum pendulum and Helminthostachys zeylanica.

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With Plates I, II, and III.

INTRODUCTION.

THE difference of opinion which exists among investigators who have studied the Ophioglossaceae, as to the phylogeny of this small group of Vascular Cryptogams, is well known. Palaeobotany has not afforded decisive indications of connecting links with either the Filicineous or the Lycopodineous phylum and comparative study of the existing forms is alone available in the solution of the problem. Thus the more extended and detailed our knowledge of all the stages of the life-history of the Ophioglossaceae becomes, the better will be the chance of discovering their relationship to other groups. In the present paper only the evidence afforded by the gametophyte is considered. The prothallus is already known in *Ophioglossum pedunculosum*[1] and in *Botrychium Lunaria*[2] and *B. virginianum*[3]. Since the characters of these prothalli are described in the text-books, and will have to be considered in the general discussion below, no summary of

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[1] Mettenius, Filices Horti Botanici Lipsiensis. Leipzig, 1856, p. 119, Pl. XXX.

[2] Hofmeister, Higher Cryptogamia. London, 1862, p. 307, Pl. XLI.

[3] Campbell, Mosses and Ferns. London, 1895, p. 225. Jeffrey, The Gametophyte of *Botrychium virginianum*. Trans. Canadian Institute, 1896-7, p. 265.

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the literature need be given here. The prothalli of *Ophioglossum pendulum* and *Helminthostachys zeylanica*[1] will first be described, so that comparison can be made on the basis of a knowledge of this stage in all three existing genera. The material on which the investigation of these prothalli has been made was obtained from the Barrawa Reserve Forest at Hanwella in the Western Province of Ceylon. The prothallus of *O. pendulum* was collected on a visit to this locality in October, 1900: this was made in the company of Mr. F. Lewis, to whom I am indebted for great assistance in the search, and for the facts, regarding the peculiar conditions, which obtain in this low-lying forest. Those of *Helminthostachys* were collected in the beginning of the succeeding March, and the material which I obtained was supplemented by more than fifty prothalli obtained from the same locality by Mr. A. K. Coomara Swamy a few weeks later and kindly forwarded to me. I wish to express my thanks to Mr. Coomara Swamy for generously placing this large stock of material at my disposal for the purpose of this investigation: without it certain facts would have been missed and others could not have been investigated so fully. The large number of prothalli under observation has also removed doubts as to the characters noted being normal. I have further to thank my friend Mr. Willis, the Director of the Peradeniya Botanic Gardens, for much assistance in selecting localities in which to search for these prothalli.

OPHIOGLOSSUM PENDULUM.

The sporophyte of this plant was frequently seen hanging from masses of epiphytic Ferns, its roots being embedded in the humus accumulated by the Ferns. It sometimes grows upon plants of *Cycas* or *Phoenix*, hanging from the stem below the crown of large leaves. A number of specimens, which grew on *Asplenium nidus* and *Polypodium quercifolium*, were carefully examined. In the humus collected by a mass of the latter Fern numerous prothalli were found. They were

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[1] A preliminary statement on these prothalli has been published in the Proc. Roy. Soc., vol. lxviii, 1901, p. 405.

distributed throughout the humus but were most numerous close to the rhizome of the *Polypodium*, often being situated between its ramenta. The following account is based on the examination of this material.

The first stages in the germination of the spore of this plant have been described by Campbell[1]. After a year and a half the largest prothalli consisted of but three cells and were still partially enclosed in the exospore. Chlorophyll had not been developed in them.

The smallest prothalli found in nature, one of which is represented in Pl. I, Fig. 1, are, as the side view shows, narrow below and widen out rapidly above. The gently convex upper surface is smooth, while the sides are covered with short unicellular hairs. The basal region is light brown, the upper part white. Regarding the colour of the prothalli it may be said generally that the younger regions are white, the older parts being more or less discoloured. Viewed from above or below, the outline of the prothallus of this age is circular, and a comparison of the different aspects shows that it is radially symmetrical. This radial symmetry is retained in all the branches of the older prothalli.

Sometimes the young prothallus continues its growth without branching, but as a rule branching occurs in prothalli which have reached the size of that just described. Usually two or three branches of equal size are developed (Figs. 2–4). These are connected by a region, which corresponds to the lower portion of the unbranched prothallus. The specimen in Fig. 2, in which the origin of two branches is visible, was attached to a fragment of tissue in the humus. That shown in Fig. 3 had evidently given rise to two branches, one of which has again branched. In Fig. 4 a prothallus with three branches is seen, and this is also the case in the older prothallus represented under a lower power in Fig. 5. The first branches, as these figures show, have a slight upward direction. In larger prothalli the primary branches have in turn branched, sometimes in a horizontal, at other times in a vertical plane,

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[1] Mosses and Ferns, p. 224.

and the old prothalli (Fig. 6) thus come to consist of short, stout branches radiating in all directions into the humus.

All the branches are similar in external form. The end of one is represented as seen from the side in Fig. 7. As this figure shows, the apical region is conical and its surface smooth. A short distance from the growing-point, however, the branch has attained its full thickness, and its surface has become covered with short wide hairs. Rhizoids appear to be entirely wanting. Both kinds of sexual organs occur on the same branch, but only the antheridia are conspicuous on external examination.

The general structure of a young prothallus is shown in longitudinal section in Fig. 8. The details of apical growth and of branching have not been followed in the few specimens of this age, but this omission is the less important, since there is no reason to expect any essential differences in this respect between the young prothallus and the branches of older ones. The tissue of the young prothallus is throughout parenchymatous: the cells of the lower half contain an endophytic Fungus, while those of the upper portion are free from it. At the extreme base, where presumably the spore membrane was attached, the surface is smooth and a few superficial cells contain the endophyte. A little above this the superficial layers become free from the Fungus, and throughout the further growth of the prothallus the endophyte is confined to internal tissue, the outer cells being only traversed by infecting hyphae. Many of the cells of the outermost layer give rise to short wide hairs, but these are absent at the extreme base and over the meristematic region. The breadth of the apical region in this specimen probably indicates that it was destined to give rise almost at once to several branches. Other specimens, while agreeing in general structure, have this region less flattened, and were probably about to continue their growth without for the time branching (Fig. 9).

A more detailed account must be given of the structure of a branch of the prothallus such as that described above (Fig. 7). The apical growth of such a branch can be referred to a single initial cell. In longitudinal section this is seen to be triangular in form (Fig. 10); in transverse section it is four-sided (Fig. 11). The apical cell is thus a four-sided pyramid with a convex base, and segments are cut off in regular succession by walls parallel to the four sides. Each segment becomes subdivided by periclinal and anticlinal walls, the general direction of which will be evident from the figures. These first periclinal divisions do not appear to mark off definite structural regions, but a short distance behind the apex a superficial zone, in which the divisions are mostly parallel to the surface, can be distinguished from the central tissue of the branch. It is in this outer zone that the sexual organs originate, periclinal divisions in the cells between them keeping pace with their growth. Slightly further from the apex the tissues have become fully developed, but are still free from the endophytic Fungus. In this region the sexual organs become mature and open. On passing to the still older part of the branch, the Fungus is found occupying the internal tissue. These regions are shown in the longitudinal section through a branch (Fig. 12), which also shows the slight histological differentiation in the prothallus, due to the central cells being somewhat elongated. In transverse section (Fig. 13) these central cells are rounded, while towards the periphery of the section the cells are flattened parallel to the surface. The section represented in this figure passes through the region in which the endophyte is just making its appearance.

The short wide hairs (Fig. 14), the appearance of which in surface view has been seen, originate from single superficial cells of the branch a short distance behind the apex of the latter. Each cell giving rise to a hair projects as a conical papilla; the projecting part is then cut off by a periclinal wall. The hair remains unicellular[1]. Its nucleus, which is often suspended in the centre of the cell, may be round or be more or less elongated in the direction of the length of the

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[1] The abundance of these hairs in this epiphytic prothallus suggests a comparison with the multicellular paraphyses known in the prothalli of several species of *Lycopodium* and especially well developed in some epiphytic forms.

hair. Numerous colourless plastids are present in the cytoplasm around the nucleus. The outer cell-walls, whether of the hairs or of other superficial cells, possess a moderately thick cuticle.

To complete the description of the vegetative portion of the prothallus, the distribution and structure of the endophytic Fungus must be referred to. It has been seen that the Fungus in the young prothallus occupies the superficial cells at the base and extends into the central tissue of the lower half of the prothallus. This distribution is also recognizable in the old branched prothallus when the section passes through the central region, which corresponds to the base of the young prothallus. In the further growth of the prothallus, however, one or two superficial layers of cells always remain free from the endophyte, save for hyphae making their way into the deeper tissue. The diagram (Fig. 15) will make this clear. In the older region of a branch the Fungus occupies all the cells save the superficial zone of one or two layers. On passing towards the apex of the branch the Fungus may disappear from the central cells also, persisting however for a longer or shorter distance in an intermediate zone of tissue. In other cases the endophyte stops at the same level in both the axial and the more external cells.

Since the first stages of germination of the spore have not been followed information as to the first infection of the prothallus with the symbiotic Fungus is wanting. There is however a process of repeated infection, to which the extension of the Fungus towards the apex of the branch must in great part be ascribed. It will be convenient to trace the entrance of the Fungus at one of these points of infection and to consider the several structures in the order of their appearance.

When a branch is examined from the surface, coarse brown hyphae can be seen more or less closely applied to its surface. The filaments which penetrate the prothallus are in connexion with these, and as a rule enter by one of the hairs. That they are branches of the external mycelium entering at these points, and not branches of the endophytic mycelium making their way out to ramify in the soil, is clear from the relations of the hyphae at the points in question. Thus the entering filament is almost always given off at right angles from a hypha crossing the outside of a hair, and, when the first branching of the hypha within the prothallus is visible, it always suggests the subdivision of an entering hypha (Fig. 16). The penetrating hyphae, like those on the outside of the prothallus, are of considerable thickness. They are at first straight and run at right angles to the surface. Sometimes the hypha branches while in the hair, but more often this does not take place until it has penetrated to the hypodermal layer. In this there is often a considerable horizontal extension of branches from which vertical hyphae in turn originate. In the cells below the hypodermal layer other structures begin to make their appearance, these are small thin-walled vesicles (Fig. 17), the connexion of which in bunches borne on fine hyphae can now and then be traced. A number of these vesicles occur in each cell, often close to the nucleus. They are filled with protoplasm, in which a number of small nuclei are distributed. Other cells contain thick coiled hyphae, while in the older regions thick-walled, irregularly-shaped bodies of a brown colour are occasionally found. The mode of development and the function of these latter bodies is uncertain.

The general characters of the mycorhiza of the prothallus of *Ophioglossum pendulum* agree closely with those of the Fungus found by Janse[1] in the roots of the plant. The starch-containing vesicles, mentioned by him, have however not been seen. Numerous plastids occur in the cells of the prothallus, and these, both towards the apex of the branch and in cells occupied by the Fungus, contain abundant starch.

The antheridium originates from a single superficial cell, the first division in which is parallel to the surface. The outer of the two cells thus separated gives rise to the one-layered wall: the inner undergoes numerous divisions and

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[1] Ann. Jard. Bot. Buitenzorg, xiv, Pl. IX, Figs. 11–13.

produces the group of spermatocytes (Figs. 18–20). The first divisions in the inner cell are as a rule anticlinal, followed by a periclinal division in each of the resulting segments.

The mature antheridia do not project from the surface of the prothallus and are only conspicuous on external examination by reason of the mass of spermatocytes, showing through the thin outer wall (Fig. 7). In vertical section (Fig. 21) the large oval mass of spermatocytes, the greatest diameter of which is parallel to the long axis of the branch, is seen to be surrounded by a limiting layer of flattened cells. This layer and the one outside it are never invaded by the hyphae of the Fungus (Fig. 23). The true wall of the antheridium is of small extent, flat or very slightly convex. It is a single layer of cells thick[1] and in surface view shows a triangular opercular cell (Fig. 22), which breaks down to give exit to the spermatozoids. The latter were unfortunately not examined when the material was collected, and it has not been found possible to ascertain their exact form or the number of cilia they possess from the study of those still in the antheridium.

The archegonium also arises from a single cell, which divides into three by two periclinal walls (Pl. II. Fig. 24). The outermost of these gives rise to the neck, the middle to the central series, while the lowest of the three is the basal cell. The basal cell usually undergoes a few divisions, but its outline remains clearly recognizable in mature archegonia. The cell which gives rise to the neck divides by anticlinal walls into four; each of these gives origin to one of the four rows of cells (Fig. 27) of which the neck consists. There are as a rule four cells in each row, but sometimes only three. The neck hardly projects above the general surface (Fig. 25). The central cell early divides into two, the upper of which insinuating itself between the neck-cells is the neck-canal-cell (Fig. 25). This becomes binucleate (Fig. 26), but no cell-division has been observed to follow, nor has the division of the middle

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[1] Exceptionally the cells of the wall undergo a periclinal division in old antheridia.

cell into ovum and ventral canal-cell been observed, though analogy suggests that it will be found to take place.

The segmentation of the ovum has also not been traced, but embryos were present on a few of the prothalli. They were all of about the same age and presented the appearance represented in Fig. 28, the embryo being conspicuous as a globular projection from the side of a branch of the prothallus. Up to this stage the embryo is completely enclosed by the tissues of the gametophyte and surmounted by the brown archegonial neck. These embryos were rather old to do more than indicate the order of segmentation, and too young to make the delimitation of the primary members of the young plant certain. A median vertical section (Fig. 29) shows the main structural features most clearly. The whole of the lower portion is evidently to be regarded as foot; the smaller upper portion consisted of cells with more abundant contents, but the position of the primary organs could not be determined in it. The first wall separating these epibasal and hypobasal halves can be clearly traced and, as a series of transverse sections through another embryo showed, the quadrant and octant walls followed in each of these halves. The resemblance of these embryos to one stage of the embryo of *Botrychium virginianum*, which will be evident on comparing Fig. 29 with Fig. 46 of Jeffrey's paper on the latter plant, makes it probable that the earlier and later stages will also be found similar in the two genera.

HELMINTHOSTACHYS ZEYLANICA.

The prothallus of *Helminthostachys* was looked for in a number of localities in Ceylon and the Malay Peninsula. The sporophyte is found growing under very various conditions in its different habitats. In native compounds under Coco-nut palms it grows in rather dry soil, owing its success and its spread, so far as could be seen, to its power of continued growth and to vegetative multiplication. The same conditions appear to obtain in the Botanic Gardens at

Heneratgoda, and here also the fronds appear among the grasses covering the soil. In other localities isolated plants were found close to streams growing in the mud. At Hanwella the plant grows commonly in the dry compounds, but is also abundant in a small Teak plantation and in Barrawa Reserve Forest. In both these situations the soil is covered with dead leaves and the undergrowth is scanty. The reserved forest of Barrawa is situated on the Puselli Oya, a branch of the Kelani river, and is about eighteen miles from Colombo. It stands about forty feet above sea-level and is very frequently flooded. These floods depend on the abundance of the rainfall round the head waters of the Kelani river which drains one of the wettest districts in Ceylon, and not directly on the rainfall of Barrawa. The flood covers the land with water to a depth of fifteen to twenty feet, and, as the outflow is not swift, lasts for several days at a time. In October, 1900, when this locality was first visited, the forest was in flood and no *Helminthostachys* was found. On revisiting the forest in the following March the floor of the jungle was dry and was found to be composed of fallen leaves mixed with fine-grained mud. In the low-lying parts there were very few undergrowth plants, *Helminthostachys* being the most abundant. In the spots where the mature plants grew, young plants could be recognized by the small ternate lamina which appears above the surface. These were still attached to the prothallus and, by searching in the leaf-mould around, a few free prothalli were obtained. The following description is based on the material thus collected, supplemented by the prothalli obtained by Mr. Coomara Swamy, on a subsequent visit to the same locality, which he generously put at my disposal.

The Prothallus.

The prothalli are subterranean and occur at a depth of about two inches. In colour they are brown, the apex and younger parts being white. Their position in the soil is variable, but most commonly the long axis is vertical, the apex being directed upwards. Prothalli of different sizes were found, but the earlier stages of development were not seen. The smallest prothallus obtained is represented in Fig. 30. Fig. 31 represents a rather larger prothallus, which was however capable of further growth, while that in Fig. 30 has almost attained its full size. Both of them show a more or less swollen lower region, which bears rhizoids and is of a brown colour. From this a cylindrical growth has arisen, at the apex of which the growing-point is to be found, the antheridia arising in acropetal succession behind the latter. The distinction into a lower portion bearing rhizoids and an upper on which the sexual organs are situated is most clearly seen in Fig. 31. It can be traced in all the prothalli, and since the endophytic Fungus is contained in the lower portion this will be spoken of as the vegetative region, and the longer or shorter cylindrical upper part as the sexual region.

The relative development of the vegetative and sexual regions, and consequently the general form of the prothallus, differs according to whether the prothallus bears antheridia or archegonia. There is in fact an imperfect sexual differentiation analogous to that known in the gametophyte of some other homosporous Vascular Cryptogams. Certain prothalli produce antheridia only; others, after a few antheridia have been produced, bear archegonia. The fact that the female prothalli nearly always bear a few antheridia first, makes it probable that, up to a stage like that represented in Fig. 31, there would be little or no difference between the two forms.

Three male prothalli are represented in Figs. 32–34. In them the vegetative region is relatively small. It is slightly lobed in the prothallus represented in Fig. 32, more strongly in the other two. This lobing of the basal region is not a true branching, but results from unequal growth of the originally unlobed basal region. A true branching, referable to the growing-point, has in no instance been observed, and may safely be regarded as exceptional. The sexual region is cylindrical, of fairly uniform thickness, and attains a considerable length. Its lower portion bears spent antheridia, while towards the apex mature and young antheridia are found.

The prothallus represented in Fig. 35 is of interest, since it presents characters intermediate between those of the typical male and female prothalli. Its vegetative region is larger and more strongly lobed than in the male prothalli, while the sexual region, though shorter and thicker than in the latter, is of considerable length. A number of antheridia are present on its lower part, while above these archegonia have formed. The more ordinary type of female prothallus is illustrated by Figs. 36 and 37. In these the lobed vegetative region forms the greater part of the prothallus, the sexual region being very short and wide: both these prothalli bore embryos.

The general structure of the prothalli will be evident from the diagrams (Figs. 38–40), which represent in longitudinal section one of the youngest prothalli, a full-grown male and a female prothallus respectively. In all the diagrams the region occupied by the endophytic Fungus is shaded, and the position of the sexual organs is indicated; these characterize the vegetative and sexual regions, which have already been distinguished in considering the external morphology. In the young prothallus (Fig. 38) the sexual region is still relatively small, only a few antheridia (*an.*) having been produced behind the apex (*a.*). The beginning of the formation of lobes of the vegetative region is seen at *l.l.* The further growth of the older male prothallus (Fig. 39) is seen to have been mainly due to the increase in length of the sexual region, the vegetative region having in this case become only slightly lobed. In the female prothallus (Fig. 40), on the other hand, the region containing the endophyte is large and strongly lobed, while that bearing the archegonia (*ar.*) is short; owing to the presence of a fairly large embryo on this prothallus the apex could not be distinguished. A few antheridia are present behind the archegonia; they are indeed in such cases often situated on the region containing the Fungus. All the diagrams indicate the freedom of the superficial layers of the vegetative region from the Fungus.

Owing to the growth in length and formation of new sexual organs having ceased in almost all the available prothalli, the apex was somewhat difficult to investigate. It was however determined that growth was referable to a single apical cell; in longitudinal section this appears triangular (Fig. 41), in cross section or in apical view it is four-sided. Thus, as was the case in *Ophioglossum pendulum*, the apical cell is here a four-sided pyramid. The segments, which are cut off by walls successively parallel to the four sides, soon divide by periclinal walls; the inner cells contribute to the axial tissue, while the layer in which the sexual organs are formed can be traced to the superficial segments.

The structure of the sexual region is most clearly shown in the male prothalli. Fig. 42 represents a median longitudinal section through this region, and Fig. 43 a transverse section. The uniform distribution of the antheridia round the circumference of the latter section makes the radial symmetry of the prothallus evident. The tissue between the antheridia shows indications of having arisen by periclinal divisions of superficial cells keeping pace with the increase in size of the antheridia. The central tissue consists of elongated cells, which are polygonal in cross section. They have thin transverse septa. The appearance of this tissue suggests that it is useful in the conduction of plastic material from the vegetative region to the growing-point. The structure of the short wide sexual region in the female prothallus is essentially similar, but the elongation of the central cells is less marked.

The outer two or three layers of cells of the vegetative region (Fig. 44) are somewhat flattened. Here and there cells have grown out into rhizoids, the bases of which alone remain in the specimen figured. An uninjured rhizoid is shown in Fig. 46; it is unicellular, and is separated from the underlying cell by a wall parallel to the surface of the prothallus. A cuticle, staining yellow with Schultze's solution, is present on the rhizoids and extends continuously over the surface of the prothallus; all the other walls stain blue with this reagent. The tissue containing the endophyte comes within these superficial layers. It is composed of parenchymatous cells, no marked elongation being recognizable even in the axial region. The cells containing the Fungus are mixed in about equal numbers with others similar in size and shape, which contain numerous starch-grains (Fig. 45). Starch is also to be found in cells containing the Fungus.

It has already been mentioned that the appearance of the lobes of the vegetative region does not suggest their origin as branches referable to the apical growth. Fig. 45, which is a section through a young lobe of the prothallus shown in Fig. 38, indicates that the lobe arises by divisions taking place in a considerable number of cells of the outer layers. The tissue resulting from this generalized meristematic activity is at first free from the Fungus; subsequently the latter extends to the central tissue of the lobe, which then presents the same appearance in section as the unlobed vegetative region (Fig. 44).

The distribution of the endophytic Fungus has been indicated above. It remains to consider its structure and the changes it undergoes during the growth of the prothallus. In nearly every rhizoid, hyphae were seen, which presumably enter from the soil. In the older prothalli the rhizoids often break down, exposing the hyphae (Figs. 46, 47). The hyphae run down within the rhizoid and enter the underlying cell, across the cavity of which they usually pursue a straight course. In the outer two or three layers the filaments may branch and sometimes run for a short distance parallel to the surface, but they do not give rise to other organs as in the deeper tissues. In the cells of the latter, when sections through a young prothallus are examined, large oval or spherical vesicles with thin walls are found (Fig. 48). These may occur singly or several together, and vary in size. Occasionally their connexion with the fine hyphae entering the cells can be observed. The vesicles have a protoplasmic body, which, in some cases, completely fills them; in most it forms a thicker or thinner lining to the wall. Small nuclei are present in the protoplasm either distributed or aggregated together. The cells, in which these structures lie, are healthy; starch is as a rule, though not always, absent from them. It is abundantly present in the adjoining cells, from which the Fungus is absent (Fig. 48), and in smaller grains in those of the superficial layers.

In prothalli, only slightly larger than the one on which the above description is based, a remarkable change has come over the whole of the endophytic Fungus. Instead of healthy hyphae and vesicles there is found in each of the fungus-containing cells a number of small shrivelled bodies, which can sometimes be seen to be attached together by fine hyphae (Fig. 49). It is thus clear that the existence of the endophyte is arrested long before the growth of the prothallus is completed. The materials for this are present in the form of starch, the distribution of which has been noted above. The starch can be traced up to the apex, but is absent from the peripheral tissue between the mature and old antheridia. By comparing older male prothalli the gradual withdrawal and utilization of this reserve starch can be followed, the last traces of it being detected in the cells close to the apex. With this last condition the arrest of growth of the sexual region is correlated, and in such prothalli mature or emptied antheridia are present close to the apex, instead of the young ones which occupy this position in prothalli capable of further growth.

It would thus appear that the relation between the prothallus and the mycorhizal Fungus is somewhat peculiar in *Helminthostachys*, in the sharp distinction between a stage, in which organic substance is manufactured, and one in which it is utilized. During the former stage the Fungus is healthy, but the growth of the sexual region has barely commenced before the Fungus dies; the further growth of the sexual region takes place at the expense of, and up to the limit permitted by, the amount of the reserve material. There is thus a definite limit to the full size of each male prothallus; but since the amount of reserve material is different in different individuals, a corresponding variation in size is found. That size is no safe guide to the age of the prothallus a comparison of Figs. 30 and 34, which represent prothalli on the eve of arrest of growth owing to the exhaustion of their reserve food, clearly shows.

In the above account the nutrition of this prothallus has been regarded chiefly as shown in the male individuals. An equally full series of the female prothalli was not available, and in all examined the Fungus was in the shrivelled, dead condition described above. In prothalli such as those in Figs. 36 and 37, in which the young plant is just becoming visible, nearly all the cells of the large, lobed, vegetative region are packed with starch-grains. The cessation of growth does not here depend on the exhaustion of the food material, but on the fertilization of an archegonium and the subsequent changes. Judging from a large number of female prothalli attached to young plants, fertilization usually occurs when only a short sexual region bearing archegonia has formed. The large amount of reserve material remaining is here available for the nourishment of the embryo and young plant; its exhaustion is not complete, though nearly so, when the first leaf of the latter is expanded and exposed to the light.

The position of the sexual organs has been indicated above. It remains to describe their structure and development. The antheridium is referable to a single superficial cell, the first division in which is periclinal, and separates the wall from the cell which forms the spermatozoids. Figs. 50–52 (Pl. III) are from median sections of developing antheridia, and Fig. 52 should be compared with Fig. 53 *a*, *b*, which represent two horizontal sections through an antheridium of corresponding age. A certain regularity exists in the earlier divisions in both the outer and inner cells. The former is first divided into four by anticlinal walls; the latter becomes divided by successive walls into octants and, by further divisions, is converted into the mass of small spermatocytes.

The mature antheridium presents some peculiarities. Like those of the other Ophioglossaceae, it projects very slightly from the general surface. The large oval mass of spermatocytes is surrounded by a layer of flattened cells, derived from the cells around that which gave origin to the antheridium. The true wall of the antheridium, derived from the outer segment of the mother-cell, is, however, different in some respects from that of any other known antheridium. It is shown in section in Figs. 54 and 56, and in surface view in Fig. 55. For the greater part of its extent it is two-layered, a periclinal division having taken place in most of the cells, into which it had divided by anticlinal walls. A few cells, however, remain undivided, so that at these spots the wall is one-layered. These single cells are large and prominent both in section and surface view, and also stand out in contrast to the others by reason of their more deeply staining contents. It is by the breaking down of one of these cells that the dehiscence of the antheridium takes place. Rarely a single dehiscence-cell is found in a nearly central position; usually two, three, or four exist, situated close to the periphery of the antheridial wall. When old antheridia are looked at from the surface, all these cells appear darker brown, but only one is found to have broken down to give exit to the spermatozoids. The latter were unfortunately not examined alive, and, as in the case of *Ophioglossum pendulum*, the examination of those in the antheridium has only shown a general agreement in form with those of other Ophioglossaceae: it was not found possible to determine the number of cilia.

All the female prothalli which were found had young plants or, in the case of two or three, large embryos. A satisfactory study of the archegonium was thus impossible, and the following description is based on the unfertilized archegonia borne on the prothalli with the youngest embryos. As fertilization appears in all cases to arrest the growth of the prothallus, the development of the archegonium could not be followed. Fig. 57 represents an archegonium in median section. The neck projects considerably from the surface of the prothallus: the projecting portion consists of four rows

(Fig. 58) of cells, each row consisting of about six cells, somewhat flattened parallel to the surface. The cells of the neck turn dark brown in old archegonia. The central series could only be imperfectly made out: there is a large ovum, but the number of canal-cells could not be determined. From the arrangement of the cells at the base of the ovum, it seems probable that a basal cell will be distinguishable in the developing archegonium. The possibility of some slight distortion due to the growth of surrounding cells must of course be borne in mind in considering the structure of such old archegonia, but was probably inconsiderable in the example figured.

A number of archegonia had apparently been simultaneously fertilized on a few of the prothalli which were attached to young plants. The preservation of the arrested embryos, which were present in addition to the plant, was not good enough to make a study of the segmentation possible. It was however clear that, as in *Botrychium*, the young embryo soon becomes deeply seated. The larger embryos present on the prothalli represented in Figs. 35–37 were all about the same age. One of them is represented in approximately median section in Fig. 59. The large hemispherical foot is deeply inserted in the tissue of the prothallus. The upper portion of the embryo had burst through the covering layers of the latter; in it can be distinguished the primary root (*r*), the median plane of which fell in another section of the series; the first leaf (*l*), the tip of which is injured, and, (covered over by the sheath of the first leaf), the depressed apex of the stem (*st.*). The position of the organs of the embryo is thus essentially similar to what is found in *Botrychium virginianum*. The apical region of the stem of the embryo of *Helminthostachys* is shown in Fig. 60. At the base of the depression filled with hairs the initial cell is visible, and segments can be seen to have been cut off parallel to the sides and the truncated base.

Morphology and Anatomy of the young Sporophyte[1].

Two young plants still attached to prothalli are represented in Figs. 61 and 62. In the former the first leaf has fully expanded, and is seen to have a ternate lamina borne on a long, slender leaf-stalk. Close to the insertion of the primary root the foot is enclosed in the prothallus. An internode of some length occurs below the separation of the first leaf, and just above this the second root (*r*) has emerged. The second leaf is about to break through the sheath of the primary leaf.

The plant shown in Fig. 62 is older, the second leaf having expanded, while the third root, which corresponds to the leaf still enclosed in the bud, has commenced to elongate. The oldest plant found attached to a prothallus bore three expanded leaves. All the young plants were dorsiventral even in the first internodes, which are usually vertical: the leaves are given off from one side of the axis and the roots from the other. Farmer and Freeman have recently shown that no definite relation exists between leaf and root in the older plants. In the young plant there is a correspondence in number between these organs, the primary root corresponding to the primary leaf, and a root arising from the stem just below each succeeding leaf-trace. The root attains a considerable length before the leaf, below which it arises, commences to grow. Even in the young plant, however, it arises from the stem-stele, and not from the leaf-trace. The constant relation, which for a time exists between the leaf and root, while doubtless important physiologically, does not appear to possess any great morphological importance.

The structure of the mature plant of *Helminthostachys* has recently been fully investigated by Farmer and Freeman[2], so that the observations made on the plants attached to prothalli need only be briefly described. This will supplement

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[1] I am indebted to Mr. Gwynne-Vaughan for assistance and advice in the study of the young plants.

[2] Annals of Botany, vol. xiii, p. 421.

the account of the mature plant, and show in what particulars differences exist between them.

The general plan of construction of the roots of the young plant is similar to that of those springing from old rhizomes. As in these, root-hairs are absent, the outer walls of the superficial cells being at most bulged outwards to form short papillae. There is a broad parenchymatous cortex, in a middle zone of which an endophytic Fungus is present in the first two or three roots (Fig. 63). This appears to constitute a mycorhiza, as is the case with all the roots in some other Ophioglossaceae. The stele is surrounded by an endodermis with corky radial walls ; within this comes a single layer of pericycle. The stele of the first root (Fig. 64) is constantly triarch. The three groups of xylem, with which the small phloëm-groups alternate, usually surround a small pith, though they are sometimes joined together. The second root is similar, but the stele is tetrarch (Fig. 63). The same holds for succeeding roots which show a gradual increase in thickness ; the fourth root had its cortex free from Fungus and densely filled with starch, like the roots of the mature plant.

The internode below the first leaf varies in length and thickness in different individuals. The single stele also presents slight differences, though the general plan of construction is constant. It is limited on the outside (Figs. 65, 66) by a well-characterized endodermis, within which come one or two layers of fairly large clear cells, constituting the pericycle. The phloëm, which consists of narrow elements, surrounds the xylem. The xylem is in some cases a solid central strand, but more usually a few parenchymatous cells are present in it. These are often conspicuous in the centre, constituting a more or less distinct pith (Figs. 64, 65). Just below the origin of the first leaf-trace the pith, if present, increases in size, and is continuous with the parenchyma intervening between the xylem of the departing leaf-trace and that of the stele. If the stele is solid in the lower part of the internode parenchyma appears in the centre of the xylem in preparation for the departure of the trace. As a rule the stele after a leaf-trace has been given off is at first solid (Fig. 67), though centrally situated parenchyma usually reappears at a slightly higher level.

It depends on the individual plant how soon the stele begins to have a larger pith and approximate to the structure described and figured by Farmer and Freeman. The simple type just described may persist for a number of internodes. The material did not afford stages old enough to allow of the transition to the condition of things in the old rhizome being followed. The most advanced stage found was closely similar to the simplest stele described by Farmer and Freeman [1]. At this stage the stele as a whole was larger than that in Fig. 65; the pith consisted of a considerable number of cells as seen in cross section, though tracheides were distributed through it. No internal endodermis was present and the departing leaf-trace did not even at this stage leave a leaf-gap, the ring of xylem closing up immediately.

In the solid steles and in those with a small pith the protoxylem is at, or nearest to, the centre and the development of the xylem is centrifugal. The elements of the protoxylem are spiral while the later formed tracheides are pitted. This endarch position of the protoxylem persists for several internodes in most cases (Fig. 70). Whether in the cases, in which tracheides were distributed through the pith, the protoxylem was mesarch or endarch could not be determined.

The origin of the first leaf-trace, with which succeeding traces originating from the more or less solid stele agree, is represented in Figs. 67 and 68. At the level at which the sections figured are taken the endodermis is still complete, and encloses the stele together with the leaf-trace. At a slightly higher level it ceases to be continuous and immediately closes around the stele; it remains visible for some distance on the outside of the trace, and near the base of the latter forms a separate and complete sheath. The common type of leaf-trace is that shown in Fig. 67, which is throughout endarch. In one or two cases even the first trace was at its origin and

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[1] Farmer and Freeman, loc. cit., Fig. 23.

for the greater part of its course through the cortex somewhat different (Fig. 68). The difference consisted in the presence on the adaxial face of the bundle, separated from the protoxylem by some parenchymatous cells, of a few larger tracheides; the trace was thus mesarch. This agrees with what is found in the mature plant and suggests that the stele was in these cases probably mesarch also. The trace passes obliquely through the cortex, and may either enter the leaf-stalk as a single bundle or before doing so have divided into two bundles which face inwards and slightly towards one another (Fig. 69). No further divisions occur in the petiole[1].

In most cases, even in relation to the first leaf, the slit-like organ, described for the older rhizome by Mr. Gwynne-Vaughan in the present number of this Journal, could be traced down to the stele in front of the leaf. In the examples it was possible to study fully a similar disturbance of the endodermis to that described for the older plant was found in relation to this organ where it approaches the stele.

It is unfortunate that a complete series of stages between the solid monostele of the young plant and the stele of the mature plant with an internal endodermis was not available. The facts mentioned in the above description with regard to the variations in the size of the pith in the seedlings suggest that the transition is a gradual one, taking place by the increase in size of the pith, its limitation from the xylem by an indefinite endodermis and the appearance of definite leaf-gaps. The study of the young plant thus supports the view, expressed by Farmer and Freeman, that the occurrence of the internal endodermis in this plant is secondary and is connected with the appearance of leaf-gaps.

SUMMARY.

Ophioglossum pendulum.

1. The prothallus is a colourless saprophyte; it is usually branched, the short branches radiating in all directions into

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[1] Sometimes an intercellular space arises by the breaking down of cells on the adaxial face of the bundles in the leaf-stalk, but this is not a constant feature.

the surrounding humus. The growth of the young prothallus and of the branches is apical, a four-sided initial being present. Rhizoids are absent, but the surface is covered with short unicellular hairs.

2. A symbiotic Fungus is present in the internal cells of the prothallus. Repeated infection takes place through the unicellular hairs.

3. The prothallus is monoecious, the sexual organs arising in acropetal succession.

4. The antheridium originates from a single superficial cell. The mature antheridium is sunken; its outer wall is one layer of cells thick; the oval mass of spermatozoids is surrounded by a layer of flattened cells free from the endophyte.

5. The archegonium is developed from a single superficial cell. Its neck, which consists of four rows of cells, hardly projects from the surface. The ovum and a binucleate canal cell can be distinguished in the central series. A basal cell is present.

6. The embryogeny could not be completely studied; the stage found showed a general agreement with other Ophioglossaceous embryos. Young plants were not seen.

Helminthostachys.

1. The prothalli are subterranean and wholly saprophytic; they consist of a lobed basal portion (vegetative region), from which a cylindrical process (the sexual region) arises: the growth is apical, by means of a single initial cell. Rhizoids are present on the vegetative region.

2. A symbiotic Fungus is present in the cells of the vegetative region; it dies about the time that the sexual region begins to elongate, and growth is completed at the expense of the accumulated starch.

3. There is an imperfect sexual differentiation; the vegetative region is larger and more strongly lobed, and the sexual region shorter and thicker in the female prothalli, than in those which bear antheridia.

4. The antheridia, which originate from single superficial cells, are sunken. Their wall is in part two-layered, but the

dehiscence-cells, of which several are present, do not undergo the periclinal division ; only one of these cells breaks down on the opening of the antheridium.

5. The structure of the archegonia, which have long necks, like those of *Botrychium*, was not satisfactorily determined.

6. The old embryo resembles that of *Botrychium* ; it has a large foot ; the primary root, first leaf, and the stem-apex seem referable to the epibasal half.

7. The young plant remains attached to the prothallus until several leaves are formed. The first leaf has a ternate lamina and reaches the light. For a time a single root is developed below each leaf.

8. The first root is triarch, succeeding ones tetrarch. A mycorhizal Fungus is present in a medio-cortical zone of the first few roots.

9. The stele of the stem is at first endarch and may be solid or have a small pith ; it is surrounded by a well-marked endodermis. The first leaf-traces are endarch or mesarch and do not leave definite leaf-gaps.

10. Gwynne-Vaughan's organ is present even in relation to the first leaf.

COMPARATIVE REMARKS.

Although for the sake of completeness the anatomy of the young plant of *Helminthostachys* has been included in the preceding description, the following discussion will have reference only to the evidence as to the affinity of the Ophioglossaceae afforded by the gametophyte. The relative independence of the two generations in the *Pteridophyta* appears to justify such a separate consideration. The embryogeny may, however, be conveniently considered along with the prothallus, since the structure and mode of life of the latter are important factors in the environment of the embryo.

The prothalli of the three living genera of Ophioglossaceae, while differing in details, present essential points of agreement with one another. They are all wholly saprophytic and live beneath the surface of the soil or humus. They are normally devoid of chlorophyll, but this was developed when the prothallus of *O. pedunculosum* reached the surface and was exposed to light. In all the cases, in which its presence has been looked for, a symbiotic Fungus has been found in the tissues. Besides this physiological agreement, which might of course be due to independent adaptation, there are common characters in the general symmetry, the structure of the sexual organs and the embryogeny, to which a higher degree of morphological weight attaches. In all, the growth is localized in an apical meristem, behind which the new organs arise in acropetal succession. In *Ophioglossum* and *Helminthostachys* the general form is that of a rather stout cylinder, which may be more or less branched ; in the distribution of its organs this exhibits strict radial symmetry. In both *Botrychium Lunaria* and *B. virginianum*, however, a tendency towards a thick-flattened form can be recognized ; this is less marked in the forms in which the sexual organs occur on all sides of the prothallus. In *B. virginianum* they are definitely localized on the upper surface, the antheridia occupying a median ridge, while the archegonia are found on the flanks. Whether the flattened form of prothallus in *Botrychium* was derived directly from the unknown autophytic ancestry of the Ophioglossaceae, or has arisen by modification of the cylindrical type, an adaptive significance may be recognized in it. For the position of the sexual organs on the upper side of a flattened subterranean prothallus would be of advantage in arresting the water percolating downwards through the soil and allowing it time to bathe the sexual organs and permit of fertilization. Support is lent to the idea of some such view by the flattening of some of the subterranean types of *Lycopodium* prothalli, which, on this view, would be regarded as presenting an analogous but independent adaptation.

The sexual organs are also constructed on the same type throughout the Ophioglossaceae. The antheridia are large and sunken ; the outer wall may be one-layered and dehiscence take place by the breaking down of a triangular opercular cell

(*O. pendulum*), but in all the genera a tendency to the doubling of the outer wall by periclinal division exists. This occurs exceptionally in *O. pendulum*, normally and in all the cells in *O. pedunculosum* and *Botrychium*, while in *Helminthostachys* several cells, through one of which dehiscence occurs, remain undivided. It may be assumed with probability that the one-layered wall represents the primitive condition, from which the other modifications have been derived. So far as is known (*O. pedunculosum*, *Botrychium*) the spermatozoids are multiciliate. The archegonia have a rather deeply sunken venter and a neck of four rows of cells which may hardly project from the surface (*Ophioglossum*), or be longer and project considerably (*Botrychium*, *Helminthostachys*). A basal cell has been found in all in which its presence has been looked for. The most extensive central series seen consisted of the ovum, a ventral canal-cell, and a bi-nucleate neck-canal-cell (*B. virginianum*).

The embryogeny is not completely known in all three genera, but the advanced stages of *Ophioglossum* and *Helminthostachys* show essential agreement with *Botrychium*, in which the segmentation is known in detail. No suspensor is formed. The whole of the hypobasal half forms the large hemispherical foot, while the first root, first leaf and stem-apex become distinguishable rather late in the epibasal half. The apex of the stem comes to occupy a depression in front of the first leaf.

Having thus reviewed the common characters of external form, reproductive organs and embryogeny in the Ophioglossaceae, the question arises whether a similar assemblage of characters is to be found in any of the three existing phyla of Vascular Cryptogams. There is little to suggest a close relationship between the Ophioglossaceae and the Equisetales, and the former group has usually been compared with the Lycopodiales or the Filicales[1]. In such comparisons it is

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[1] Without summarizing the views expressed by these authors the discussions of the evidences of affinity afforded by the Ophioglossaceous prothallus by Bower (Studies II, *Ophioglossaceae*, London, 1896, p. 62), Jeffrey (loc. cit.) and Goebel (Organographie, p. 410) may be referred to.

important to determine as far as possible the relatively primitive and the highly modified forms of prothallus in each group, and to confine the comparison mainly to the former. The heterosporous forms will therefore be left out of account here and only mentioned when they seem to weaken the evidence afforded by the homosporous forms.

The Lycopodiales may be taken first, since in this group prothalli, which are practically autophytic, and subterranean holosaprophytic forms occur: this makes it possible to ascertain the characters which remain constant in spite of this profound physiological change. In a previous paper [1] reasons have been given for regarding the *Lycopodium cernuum* type of prothallus as the relatively primitive one in this group. The recently discovered prothallus of *Phylloglossum* [2] gives further support to this view. In these prothalli an outstanding feature of the general plan of construction is the intercalary position of the meristem: from this additions are made to the vegetative region below, while the sexual organs originate above the meristematic zone, the youngest being found nearest to it. This special type of radial symmetry is retained in many of the subterranean forms, so that it is not necessarily obscured or lost in relation to such a change in the economy. Now the radial symmetry of the Ophioglossaceous prothalli, and the apical position of the meristem in them, stand in marked contrast to this and afford no suggestion of a common origin. Comparison is however at first sight more justifiable between the Ophioglossaceous prothalli and those of *Lycopodium Phlegmaria.* The fine cylindrical branches of the latter have apical growth, though, when sexual organs are formed, they originate on the upper side above the meristem. In the paper cited above reasons have been given for regarding this type of *Lycopodium* prothallus as derived from the type with an intercalary meristematic zone by limitation of growth

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[1] Lang, Prothallus of *Lycopodium clavatum.* Annals of Botany, vol. xiii, 1899, p. 279.

[2] Thomas, Preliminary Account of the Prothallium of *Phylloglossum.* Proc. Roy. Soc., 1902.

to special points in the latter; the various forms of *L. Selago* prothallus indicate how this may have come about. If this interpretation, on which the *L. Phlegmaria* type would be regarded as a highly specialized one, is correct, little weight can be attached to the resemblance between it and the prothallus of *Ophioglossum*; the resemblance is further not a very close one.

Important points of difference are also found when the sexual organs of the Ophioglossaceae and the Lycopodiaceae are compared. The general construction of the antheridia is indeed not dissimilar, but, since the plan of these organs is alike in all the eusporangiate Vascular Cryptogams, no weight can be attached to this. A point of difference is found in the spermatozoids, which are multiciliate in the Ophioglossaceae, biciliate in the Lycopodiales[1]. The archegonia in both groups exhibit a series from short-necked to long-necked forms. Their development affords a constant difference in the presence of a basal cell in the Ophioglossaceae and its absence in the Lycopodiales. The presence of a suspensor in the embryo of the latter group, and the origin of the primary leaf and root and the apex of the stem from the end furthest from the suspensor, are important points of difference.

To sum up the comparison between the Ophioglossaceae and the Lycopodiales, it does not appear too much to say that, while some general resemblances standing in relation to similar modes of life can be traced, there are no characters, the morphological value of which is attested by constancy throughout obviously allied groups, indicating affinity between the two. On the other hand, important points of difference exist in type of symmetry, in the sexual organs, and in the embryogeny.

The Ophioglossaceae are usually included in the Filicales, and a similar comparison must now be made with this phylum

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[1] The isolated heterosporous genus *Isoetes* has multiciliate spermatozoids, and also differs from the other Lycopodiales in the absence of a suspensor. Without attempting to estimate the weight to be attached to these exceptions, it may be pointed out that their existence does not seriously affect the above comparison of the prothalli of the homosporous Lycopodiales and the Ophioglossaceae.

to ascertain whether the evidence from the gametophyte renders this view probable or not. The eusporangiate Marattiaceae must be specially considered, but the general similarity in all the homosporous Filicales justifies the use of evidence from the leptosporangiate forms also. In considering the general symmetry the difficulty presents itself that no holosaprophytic fern-prothalli are known. In the flat green prothalli the meristem is apical and the succession of the sexual organs acropetal. The latter are developed on the under surface of the dorsiventral prothallus, but this distribution is well known to be due to an irritability to light. When, under cultivation or in nature, this and possibly other stimuli act more uniformly on all sides of the prothallus, the flattened form is lost and the prothallus may continue its growth as a cylindrical process with an apical meristem[1]. This growth-form presents points of resemblance with the prothalli of *Ophioglossum* and *Helminthostachys* in its symmetry, its apical growth, and the uniform distribution of the sexual organs on its surface. Something similar is seen in *Gymnogramme leptophylla*[2], in which the process which bears the archegonia buries itself in the soil; this was early compared by Goebel to the Ophioglossaceous prothallus, though his suggestion that a preliminary green stage might occur in them also has not been borne out. These modifications of the common flat prothallus in the Filicales suggest that, were it possible to cultivate them below the surface of the ground, the form of a cylindrical structure with apical growth would probably be maintained throughout life. As regards form and symmetry the type of prothallus which might be expected to result is realized in the Ophioglossaceae, and it will be remembered that when the cylindrical process of *O. pedunculosum* reached the light it became flattened and lobed.

The structure of the sexual organs affords support to such an origin of the Ophioglossaceous gametophyte from

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[1] Cf. Lang, On Apogamy, &c. Phil. Trans., 1898, Ser. B, p. 187, Pl. VII, Figs. 1–5.

[2] Outlines of Classification and Special Morphology, p. 245.

eusporangiate Ferns. The antheridia might well be derived from a type like those of the existing Marattiaceae, the multiciliate spermatozoids constituting an additional point of resemblance. The archegonia are closely similar in development and structure in the two groups, in both of which a basal cell is constantly present. The embryogeny does not agree exactly, but the similarities are greater than between the Ophioglossaceae and the Lycopodiales. In the Marattiaceae no suspensor is present, and the apex of the stem and the primary leaf are derived from the epibasal half, but the primary root arises with the foot from the hypobasal half. This difference may find its explanation in the need for a large foot in a embryo attached to a deeply buried prothallus. At any rate an analogous disturbance of the primary members is evident when the species of *Lycopodium* with deeply buried prothalli are compared with those, the prothalli of which grow on or just beneath the surface.

To sum up the comparison with the Filicales, the form of the prothallus, structure of the sexual organs, and, though less clearly, the embryogeny of the Ophioglossaceae are such as might be expected in saprophytic forms derived from prothalli of the general type found in the Filicales. On the other hand, there appear to be no fundamental points of difference.

It was mentioned above that there is little to suggest the idea of any close relationship between the Ophioglossaceae and the Equisetales. The gametophyte of the latter has a general resemblance to that of the Filicales. It will be sufficient to say here that, while it seems quite possible that the Ophioglossaceous prothallus could have been derived from the Equisetaceous type, there is nothing to suggest such an origin as even equally probable to an origin from the Filicales.

From the above comparisons it would appear that the available evidence points to the origin of the type of prothallus found in the Ophioglossaceae from forms not unlike the gametophyte of the existing Marattiaceae, though possibly belonging to a more primitive group. It would further appear that little or nothing indicates an origin from the type of prothallus found in the homosporous Lycopodiales. This conclusion is essentially that at which Jeffrey[1] arrived as a result of a similar comparison. When however it is borne in mind how little is known of the variation of the characters of the gametophyte under altered conditions, it is clear that this can only be regarded as a provisional view. The results of experimental cultures if critically interpreted might afford valuable additional evidence.

In the above discussion the characters of the sporophyte have been left out of account. If indications of sufficient weight—to render the origin of the Ophioglossaceae from a Filicineous stock improbable, and to connect them closely with the Lycopodiales—were afforded by the sporophyte, the value of characters of the gametophyte as indicating relationship between large groups would have to be reconsidered. Such evidence in the present case would require to be sufficiently clear to override the indications of a Filicineous affinity afforded by the prothallus. In the author's opinion such preponderating evidence has not been advanced, and it may indeed be questioned whether, in the case of this particular group, the characters retained by the gametophyte do not deserve to be given special weight.

[1] Loc. cit., p. 289.

EXPLANATION OF FIGURES IN PLATES I, II, AND III.

Illustrating Dr. Lang's paper on the prothalli of *Ophioglossum* and *Helminthostachys.*

PLATE I.

Ophioglossum pendulum.

Fig. 1. Young prothallus viewed from the side (*a*), from above (*b*), and from below (*c*). (× 25.)

Fig. 2. Slightly older prothallus seated on a fragment of tissue in the humus. (× 25.)

Figs. 3, 4. Prothalli, showing the origin of the first branches. (× 25.)

Figs. 5, 6. Mature prothalli seen from above; that shown in Fig. 6 is the largest found. (× 7.)

Fig. 7. Portion of a branch of one of the larger prothalli more highly magnified, showing the smooth apical cone, the unicellular hairs, and the antheridia. (× 80.)

Figs. 8, 9. Young prothalli in longitudinal section. (× 70.)

Fig. 10. Median longitudinal section of the apex of a branch, showing the segmentation of the initial cell. (× 200.)

Fig. 11. Transverse section of a similar apex. (× 200.)

Fig. 12. Longitudinal section of a branch of the prothallus. (× 25.)

Fig. 13. Transverse section of a branch, passing through the region in which infection by the Fungus is taking place. (× 70.)

Fig. 14. One of the unicellular hairs in vertical section. (× 200.)

Fig. 15. Diagrammatic section of an old prothallus, passing through the organic centre and traversing two branches longitudinally; the regions inhabited by the endophyte are shaded. *an.* antheridia, *ar.* archegonia.

Fig. 16. Part of a transverse section of a branch, showing the entrance through a hair of an infecting hypha of the Fungus. (× 200.)

Fig. 17. Two cells of the prothallus containing the vesicular swellings of the Fungus. *n.* nucleus, *h.* hyphae, *v.* vesicles. (× 750.)

Figs. 18, 19, 20. Three stages of development of the antheridium represented in vertical section. (× 375.)

Fig. 21. Vertical section of an almost mature antheridium from a transverse section of a branch. (× 375.)

Fig. 22. Tangential section through the outer wall of a mature antheridium, showing the triangular opercular cell. (× 375.)

Fig. 23. Vertical section of an opened antheridium from a longitudinal section of a branch. The shading indicates the tissue inhabited by the endophyte. (× 200.)

PLATE II.

Figs. 24–29. *Ophioglossum pendulum.*

Fig. 24. Vertical section of a young archegonium. (× 375.)

Figs. 25, 26. Vertical sections of two nearly mature but unopened archegonia. (× 375.)

Fig. 27. Transverse section of the neck of an opened archegonium. (× 375.)

Fig. 28. Prothallus bearing an embryo (*em.*). (× 7.)

Fig. 29. Median longitudinal section of the embryo shown in the preceding figure. (× 100.)

Figs. 30–49. *Helminthostachys.*

Figs. 30, 31. Two of the smallest prothalli of *Helminthostachys* found. (× 7.)

Figs. 32, 33, 34. Three male prothalli. (× 7.)

Fig. 35. Prothallus bearing antheridia, and, nearer the apex, archegonia and an embryo. (× 7.)

Figs. 36, 37. Two female prothalli bearing embryos. (× 7.)

Figs. 38, 39, 40. Diagrammatic median longitudinal sections of one of the smallest prothalli, of a male prothallus, and of a female prothallus respectively, showing the relative proportions borne to each other by the vegetative and sexual regions. *a.* apex, *l.l.* lobes of the vegetative region, *an.* antheridia, *ar.* archegonia, *e.* embryo. (Fig. 38, × 25, the others × 7.)

Fig. 41. Median longitudinal section of the apex, showing the segmentation of the initial cell. (× 200.)

Fig. 42. Longitudinal section through the sexual region of a male prothallus. (× 25.)

Fig. 43. Transverse section through the sexual region of a male prothallus. (× 50.)

Fig. 44. Similar transverse section through the unlobed vegetative region of the same prothallus. (× 50.)

Fig. 45. Part of a longitudinal section of the vegetative region of a young prothallus, showing a young lobe. The shaded cells of the internal tissue contain the endophyte. (× 100.)

Fig. 46. A single rhizoid containing a fungal hypha. (× 200.)

Fig. 47. Two rhizoids containing hyphae; the tips of the rhizoids have broken down. (× 200.)

Fig. 48. The internal tissue of a young prothallus, showing the Fungus bearing numerous vesicles; the intervening cells contain starch. (× 375.)

Fig. 49. Corresponding tissue from a slightly older prothallus; the Fungus is shrivelled and dead, while the cells of the prothallus are packed with starch. (× 375.)

PLATE III.

Helminthostachys.

Figs. 50, 51, 52. Vertical sections of young antheridia. (× 200.)

Fig. 53. Transverse sections through a young antheridium about the same age as that in Fig. 52; *a.* through the wall; *b.* through the mass of spermatocytes. (× 200.)

Fig. 54. Vertical section through an almost mature antheridium, showing one dehiscence-cell in the wall. (× 200.)

Fig. 55. Surface-view of the outer wall of an opened antheridium, showing two dehiscence-cells, one of which has broken down. (× 200.)

Fig. 56. Vertical section of two antheridia, the wall of one of which shows two dehiscence-cells. (× 110.)

Fig. 57. Vertical section of an unopened archegonium. (× 200.)

Fig. 58. Cross section of an archegonium neck. (× 200.)

Fig. 59. Median section of the embryo borne on the prothallus shown in Fig. 35. *f.* foot, *r.* primary root, *l.* first leaf, *st.* apex of stem. (× 50.)

Fig. 60. Apical region of the stem of the embryo in the preceding figure, showing the form and segmentation of the initial cell. *h.* hairs in the apical depression, *l.t.* first leaf-trace. (× 250.)

Fig. 61. Young plant attached to the prothallus. (Nat. size.)

Fig. 62. An older plant attached to the prothallus. (Nat. size.)

Fig. 63. Transverse section of the second root of a young plant, showing the position of the mycorhizal fungus. (× 50.)

Fig. 64. Transverse section of the stele of the primary root. (× 110.)

Fig. 65. Transverse section of the stele of the stem below the origin of the first leaf. (× 110.)

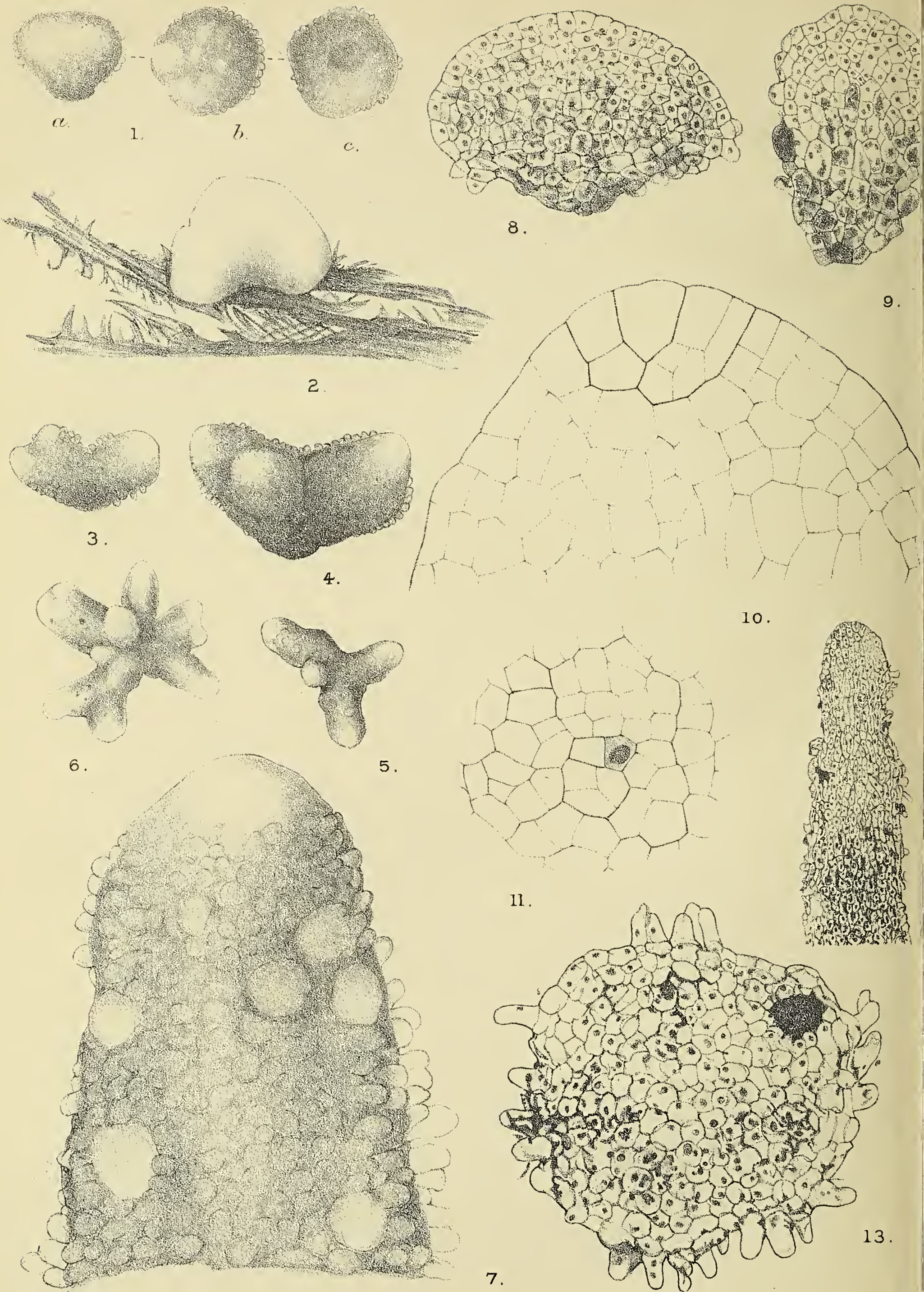
Fig. 66. One half of a transverse section of this stele more highly magnified. *en.* endodermis, *pc.* pericycle, *phl.* phloem, *x.* xylem, *p.* pith. (× 330.)

Fig. 67. Transverse section of the stele represented in Fig. 65, showing the origin of the first leaf-trace. (× 110.)

Fig. 68. Similar section of another stele, showing the origin of a leaf-trace with centripetal tracheides. (× 110.)

Fig. 69. Transverse section of the two vascular bundles at the base of a leaf. *i.sp.* adaxial intercellular space. (× 110.)

Fig. 70. Transverse section of the stele of a young plant near to the apex, showing the first developed tracheides around the pith. (× 110.)



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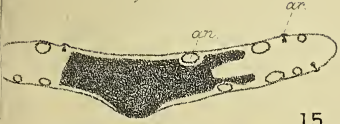

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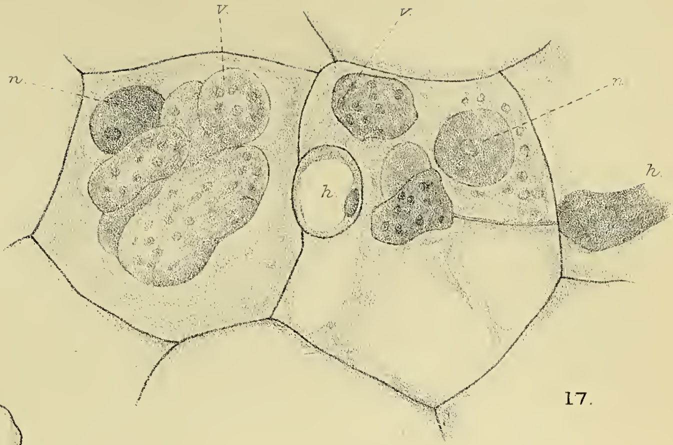

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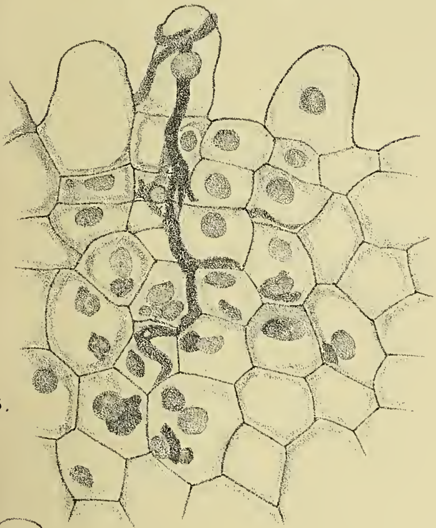

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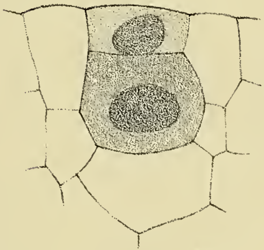

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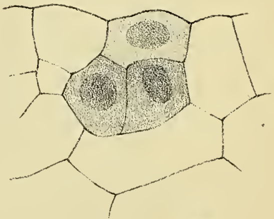

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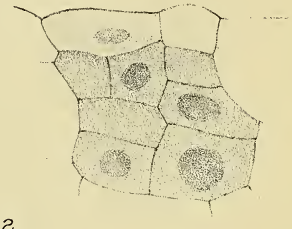

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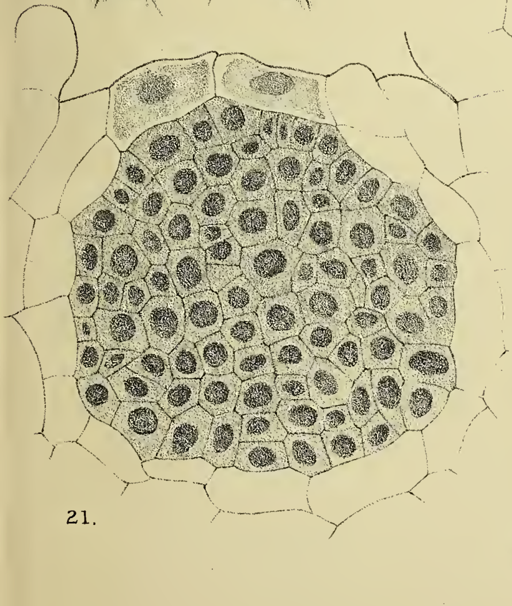

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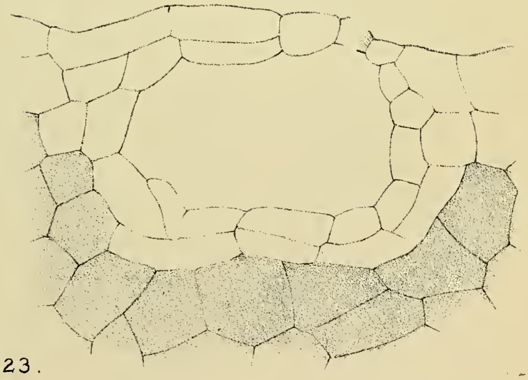

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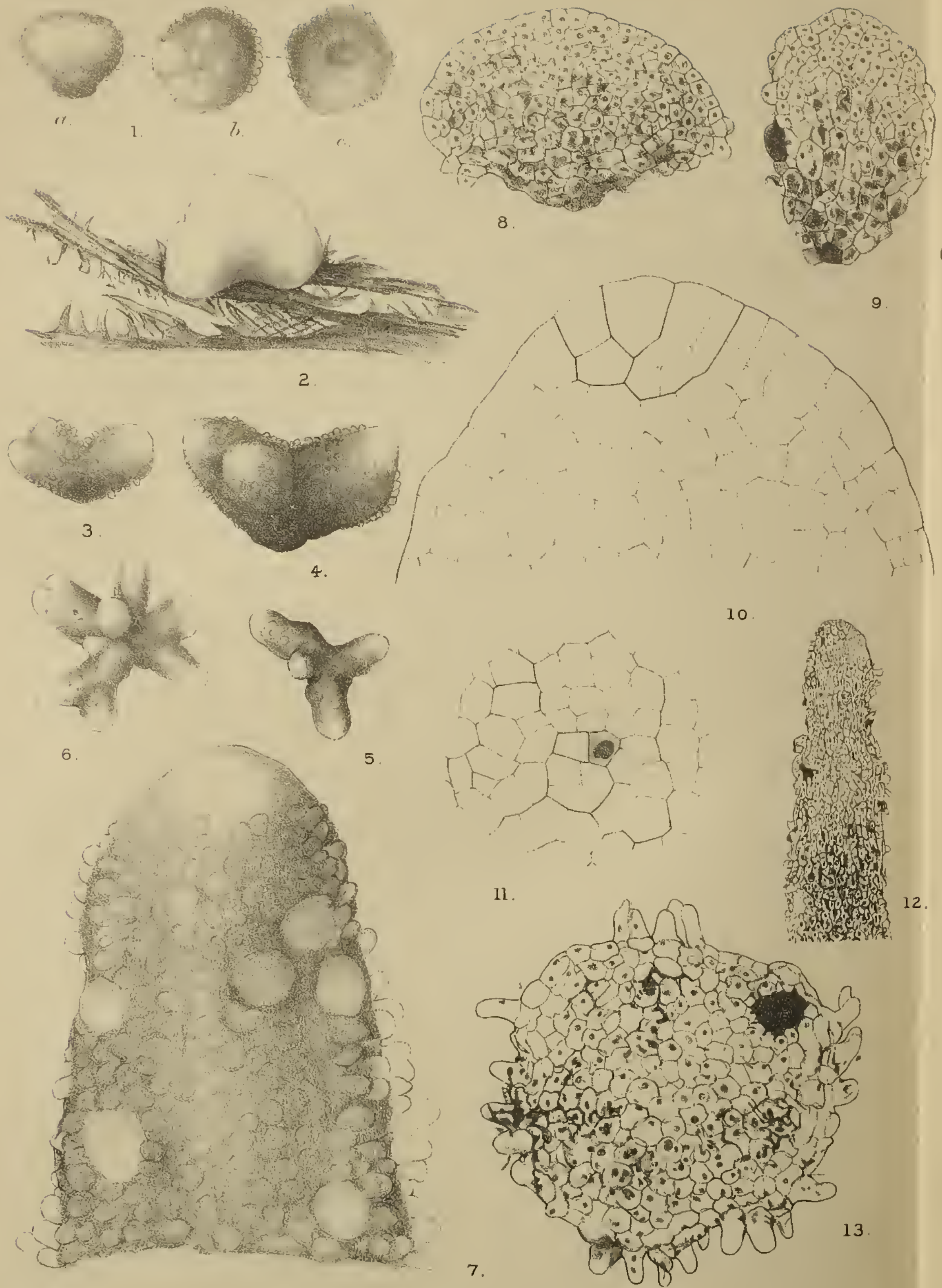

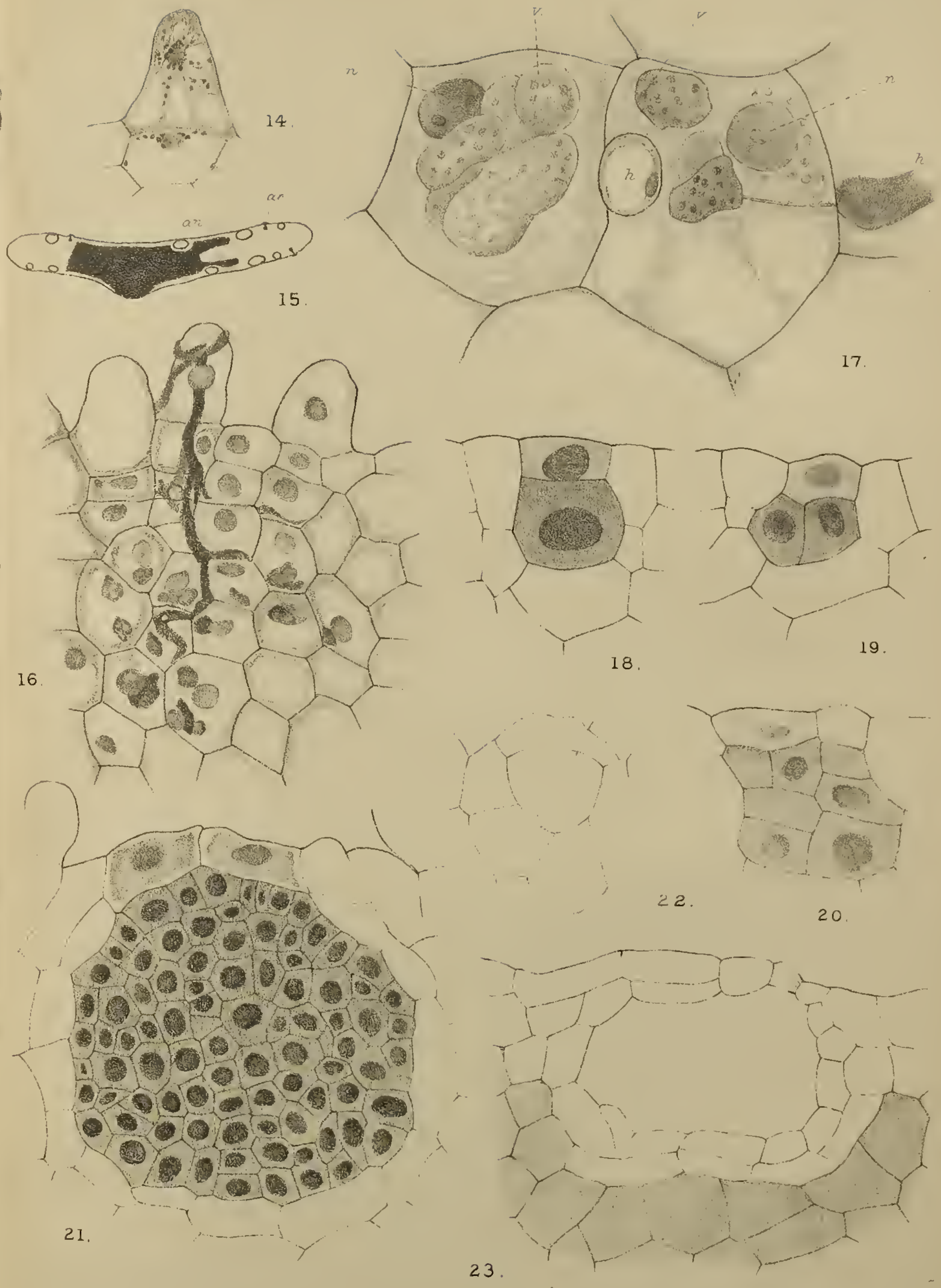

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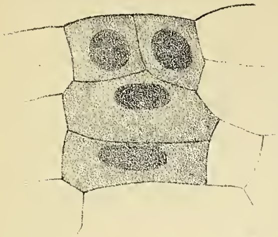

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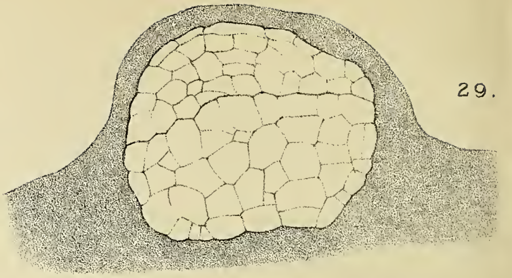

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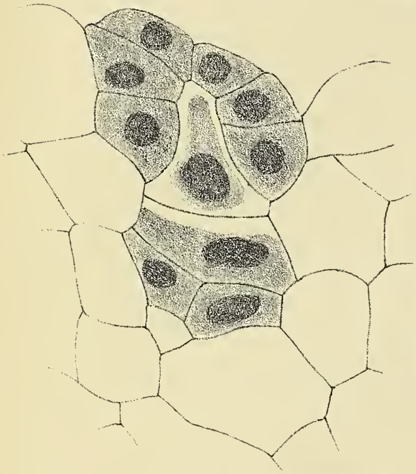

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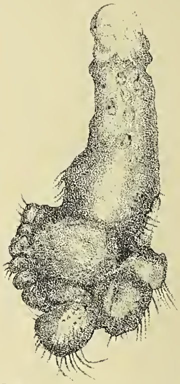

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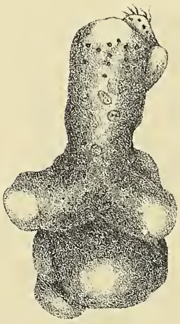

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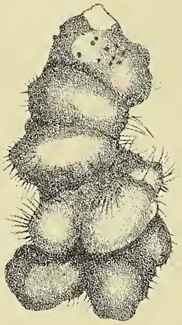

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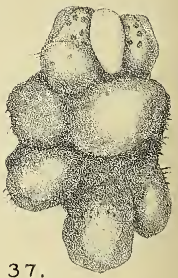

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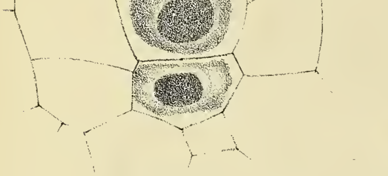

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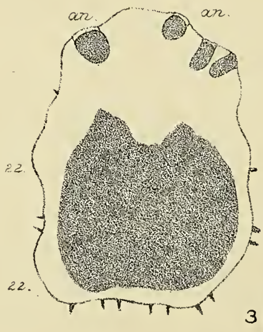

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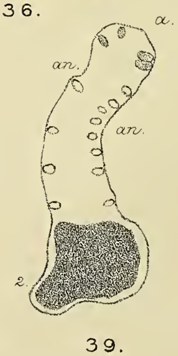

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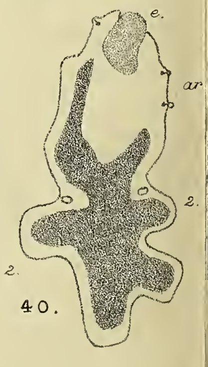

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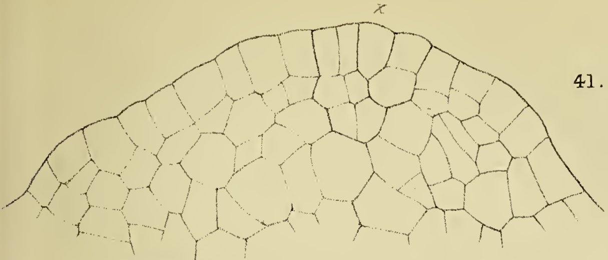
LANG.— OPHIOGLOSSUM PENDULUM Figs. 24-29.

HELMINTHOSTACHYS Figs. 30-49.



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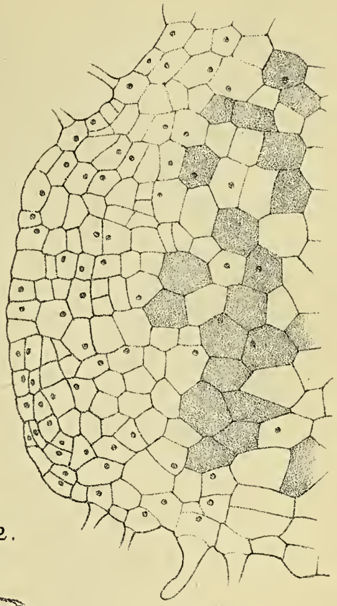

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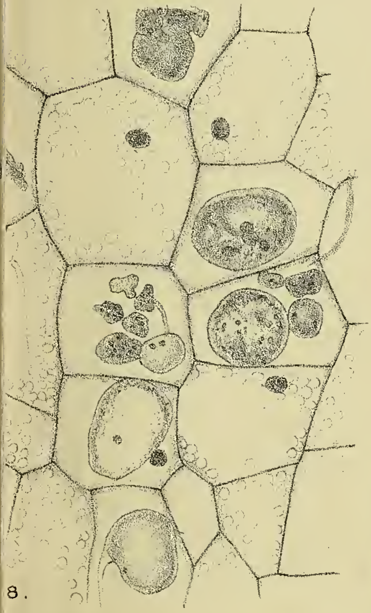

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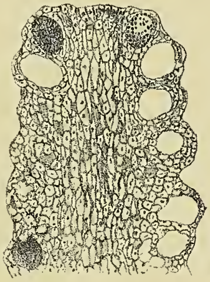

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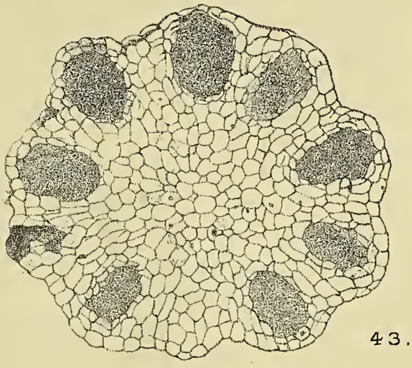

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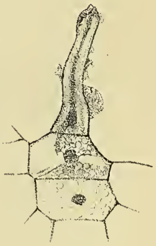

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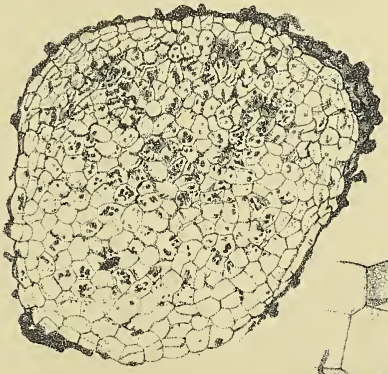

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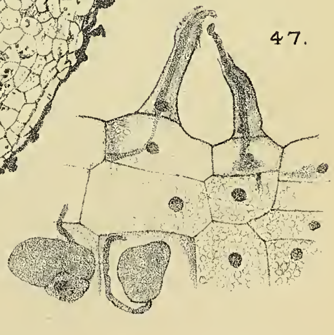

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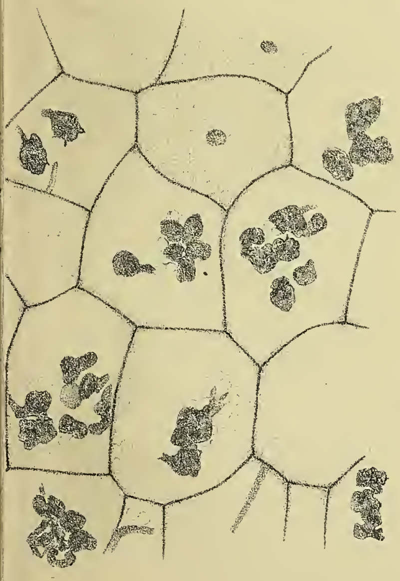

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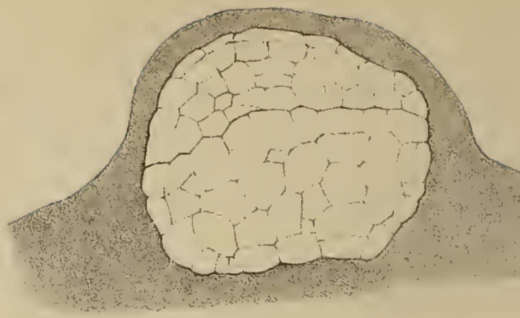

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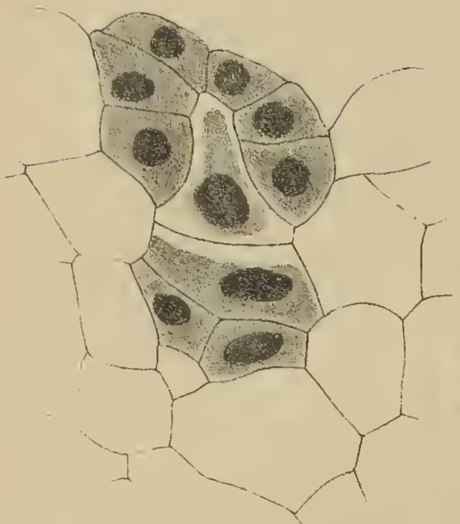

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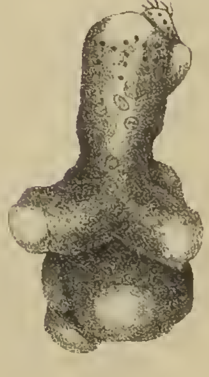

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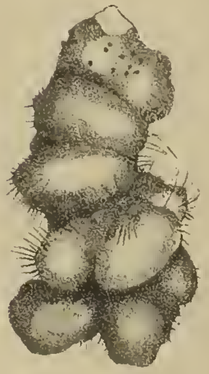

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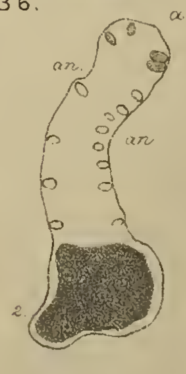

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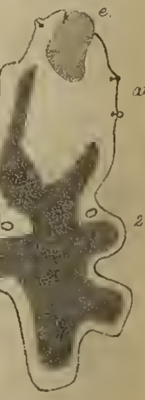

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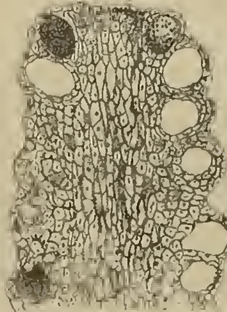

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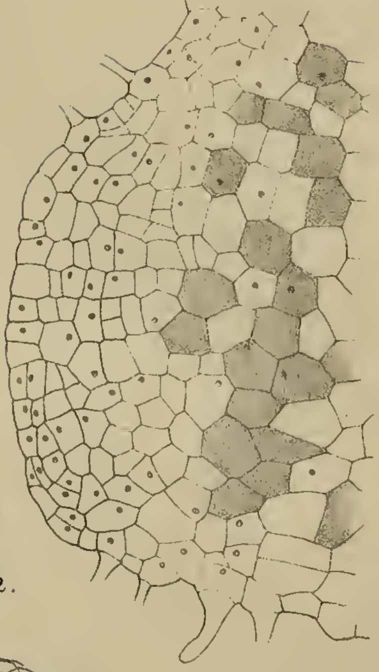

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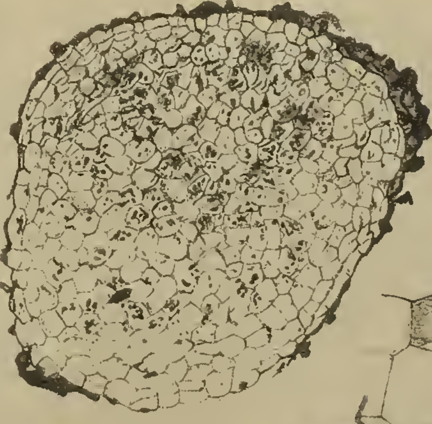

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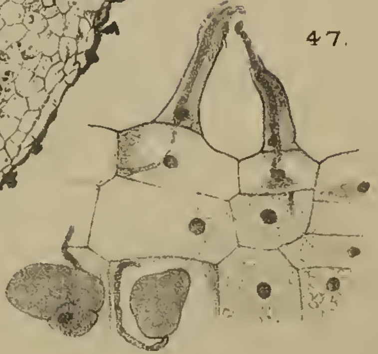

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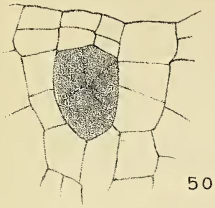

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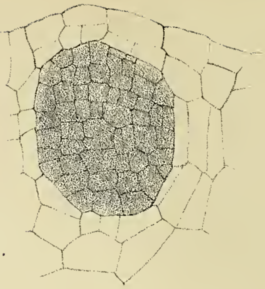

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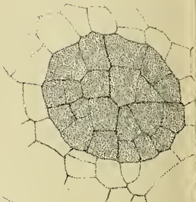

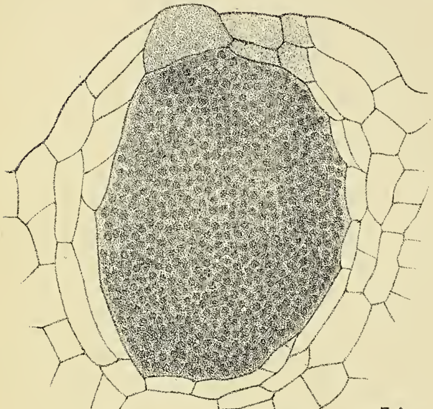

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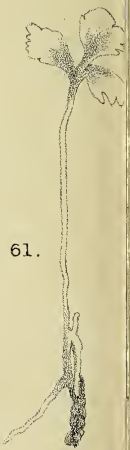

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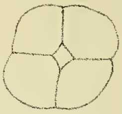

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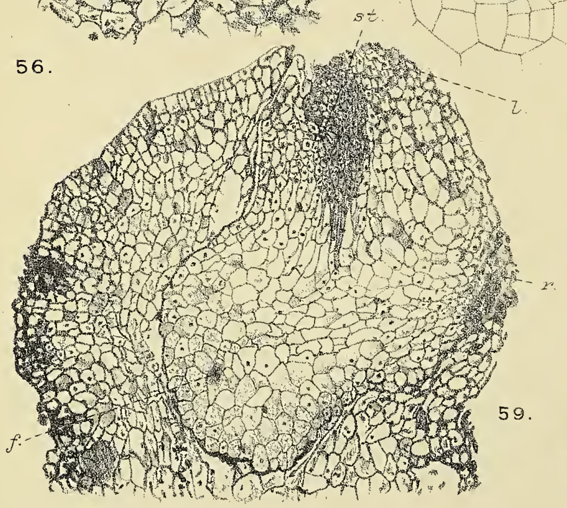

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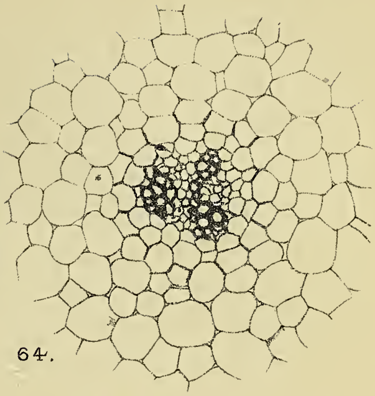

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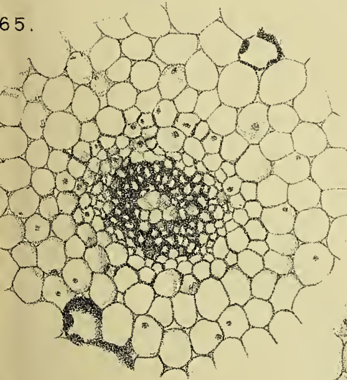

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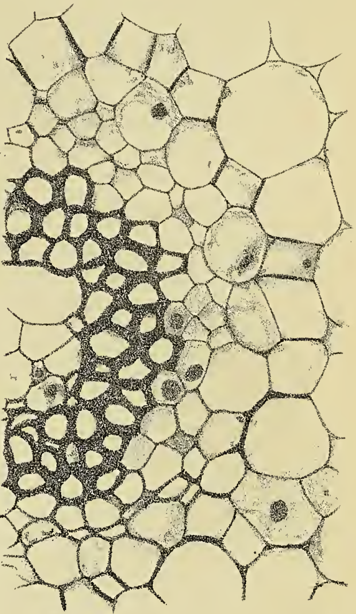

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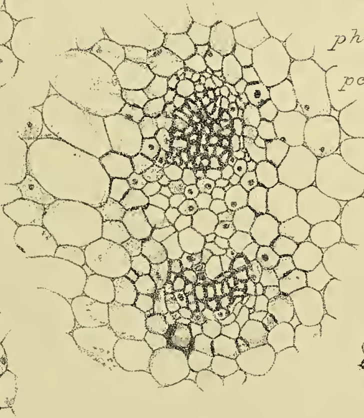

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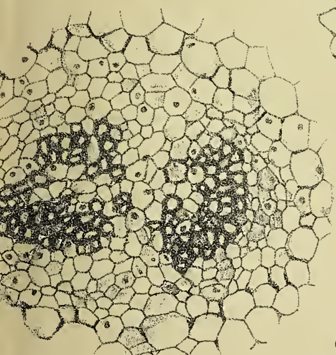

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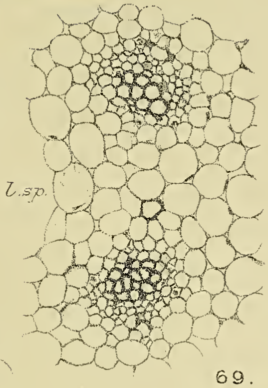

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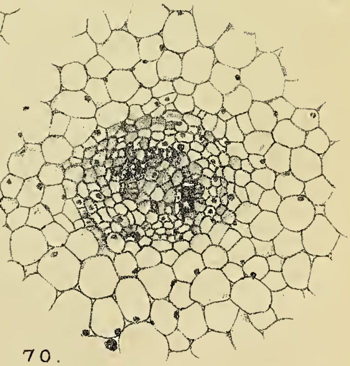

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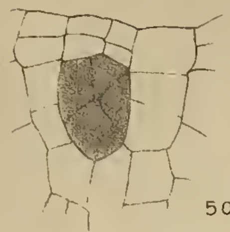

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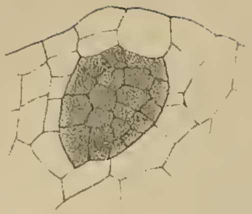

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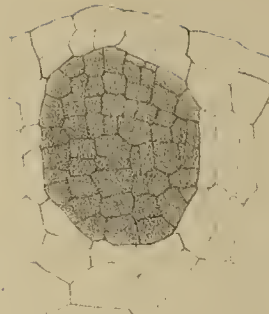

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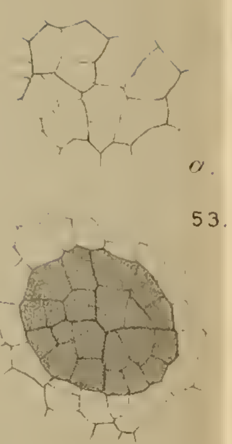

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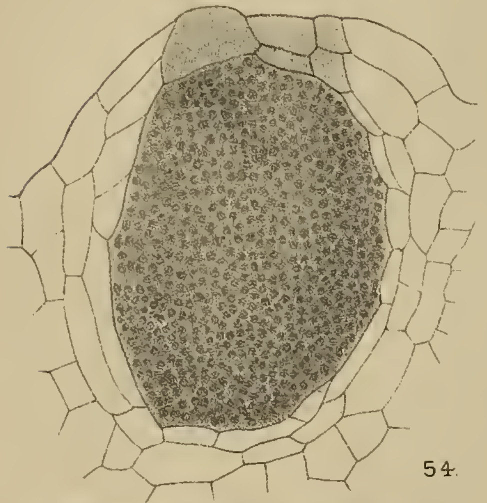

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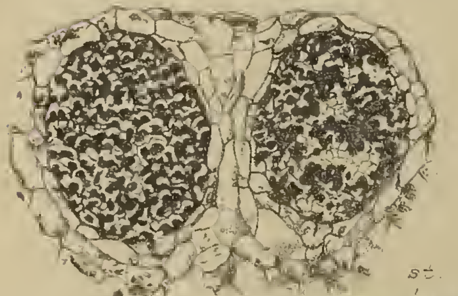

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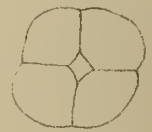

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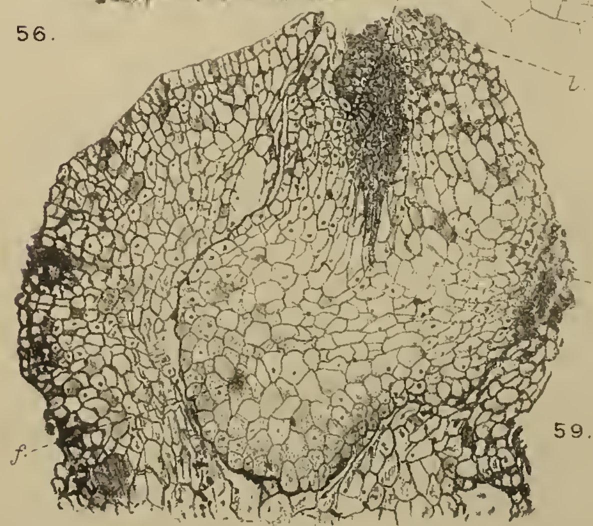

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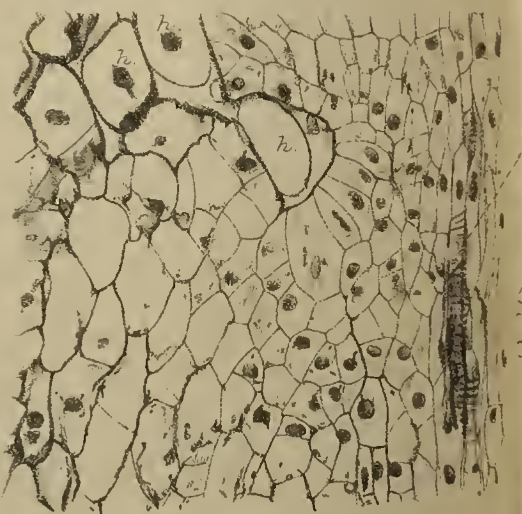

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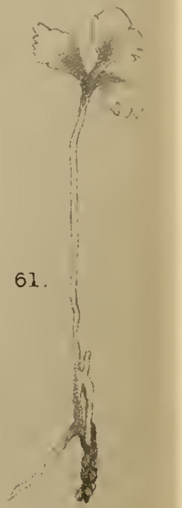

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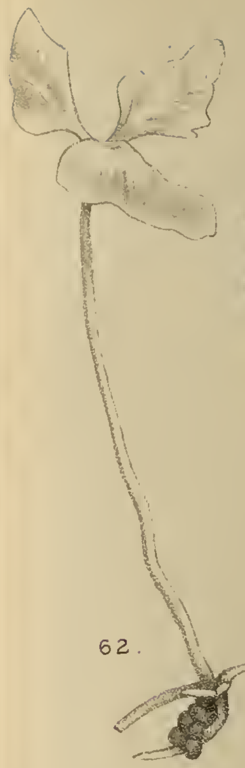

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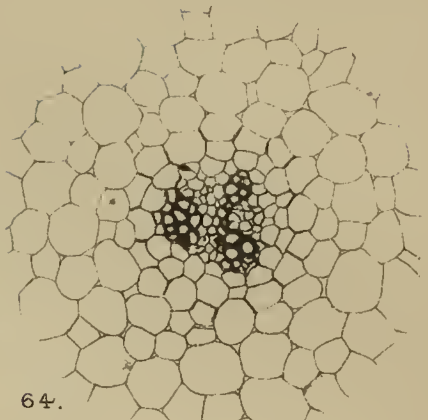

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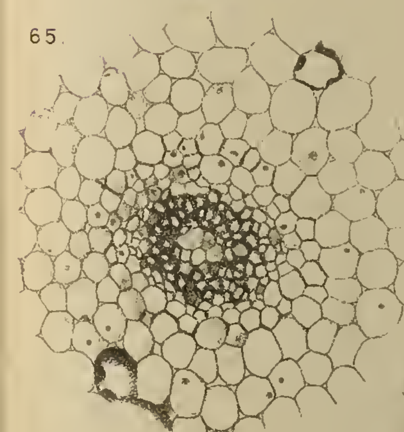

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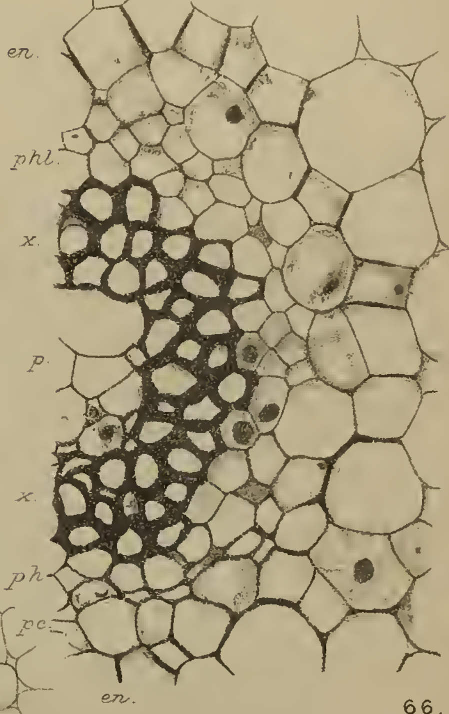

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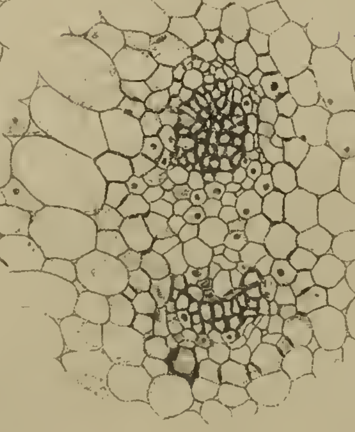

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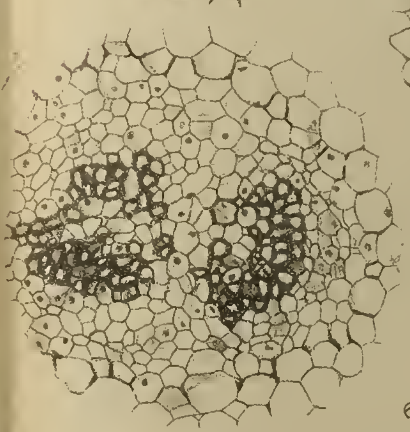

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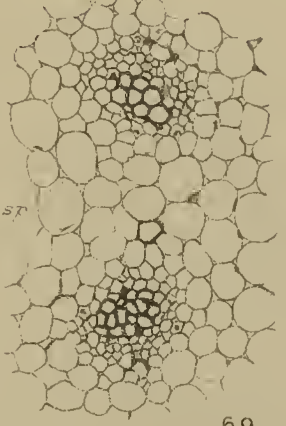

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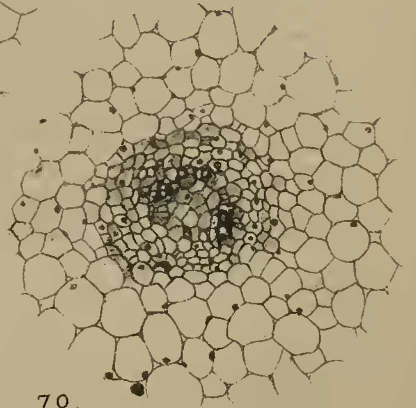

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Researches on Coprophilous Fungi. II[1].

BY

GEORGE MASSEE, F.L.S.,

Herbarium, Royal Botanic Gardens, Kew,

AND

ERNEST S. SALMON, F.L.S.

With Plates IV and V.

IN our previous paper (1) allusion was made to the generally accepted opinion that the spores of many coprophilous Fungi are capable of germination only after having passed through the alimentary canal of an animal. So far as we are aware, no direct evidence on this point has been recorded, save that given by Janczewski (2).

This author, having failed to germinate spores of *Ascobolus furfuraceus* in nutrient solutions, fed a rabbit with bread containing spores of this species, and observed that they had commenced germination when the dung was deposited. In order to investigate this point further, we have carried out the following experiments. A portion of the intestine of a recently killed rabbit containing dung was tied up at the two ends before being removed from the body. The tied-up portion of the intestine was then removed and placed in a sterilized vessel covered by a bell-jar, the dung being exposed by cutting the skin of the intestine. At the expiration of six days, during which period the bell-jar had not

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[1] Read before the Linnean Society, June 20, 1901.

[Annals of Botany, Vol. XVI. No. LXI. March, 1902.]

been removed, the dung was covered with a profuse growth of *Pilaira anomala*, Schroet., *Pilobolus crystallinus*, Tode, *Mucor mucedo*, L., *Chaetocladium Jonesii*, Fres., parasitic on the *Mucor*, and *Coprinus niveus*, Pers. A second portion of rabbit-dung, obtained under conditions similar to those described above, yielded at the expiration of a fortnight all the species enumerated above under the first experiment, and in addition *Gymnoascus Reessii*, Baran., *Humaria granulata*, Sacc., *Sporormia intermedia*, Wint., and *Sordaria decipiens*, Wint. A third experiment conducted with sheep-dung, obtained directly from the intestine as before, and only removed from it when placed under a bell-jar, yielded *Pilaira anomala*, Schroet., *Pilobolus crystallinus*, Tode, *Chaetocladium Jonesii*, Fres., *Ascobolus immersus*, Pers., and a Hyphomycete belonging to the genus *Geotrichum*, Pers.

The above experiments, conducted with all possible care to prevent contamination with spores from outside sources, prove conclusively that the various species of Fungi occurring on dung originate from spores swallowed by the animal along with its food. This statement applies more especially to those Ascomycetes having the spores accompanied by mucilage (e. g. *Thelebolus stercoreus*, Zukal, *Ascobolus glaber*, Pers., *A. perplexans*, Mass. and Salm., species of *Sordaria*, &c.), and to the species of Phycomycetes. We may observe here that we have found in May the agglutinated masses of the spores of some species of *Ascobolus* on dead grass growing round the place where dung had been deposited in the previous winter. With the Hyphomycetes, where the conidia are dry and powdery, inoculation may frequently be caused by wind-borne conidia; besides which, very few, if any, of the Hyphomycetes are confined to dung, but occur indiscriminately on various kinds of decaying or dead vegetable substances. Rabbit-dung was selected for the experiments described above for two reasons—the facility with which the animal could be procured, and the frequency of Fungi on such dung. Saccardo (3) enumerates seventy-two different species of Fungi recorded as occurring on rabbit-dung.

Many very interesting species belonging to the Hyphomycetes and to the Sphaeropsideae—groups frequently placed under the heading *Fungi imperfecti*—are common on the dung of various animals. Some recent authors have entirely omitted the above groups from their schemes of natural arrangement of the Fungi, for the reason that certain forms belonging to these groups have been shown to be phases only in the life-cycle of other Fungi belonging to the Ascomycetes or the Basidiomycetes. Such relationship has in some few instances been proved beyond doubt, but it must be admitted that in the majority of cases this genetic relationship between Hyphomycetes and Ascomycetes is based on contiguity alone, or in the persistent sequence in development of two given forms on a particular substratum, a condition of things which, while admittedly suggesting genetic relationship, cannot be held to prove such, lacking as it does the definite proof formulated by De Bary (4) as follows:—'Das erste Postulat einer morphologisch-entwickelungsgeschichtlichen Untersuchung [ist] der Nachweis der zu irgend einer Zeit nothwendig vorhandenen *organischen Continuität* successiver Entwickelungszustände, bei welcher also das später auftretende Glied als ein Theil des nächstfrühern beginnt.' Under the circumstances we have deemed it advisable to consider as entities, for the time being, all those Hyphomycetes, &c., that have not been proved to be phases in the life-cycle of other Fungi.

It is very important that the species of Hyphomycetes should not be placed in water for examination, as in this medium the conidia immediately fall away from their support; so that their mode of origin, arrangement, &c., cannot be determined, and serious mistakes, such as that recorded at p. 82 of this paper, are likely to occur.

Material for microscopic examination should be placed in glacial acetic acid, when the conidia remain *in situ*, and not at all contracted as is the case when placed in alcohol. Such material can be afterwards stained with methylene blue, and preserved in glycerine.

Summarizing our results from a systematic standpoint, the occurrence of two new genera is to be noted : *Arachnomyces* (Perisporiaceae), with two new species *A. nitidus* and *A. sulphureus*; and *Gymnodochium*, related to Berkeley's genus *Endodesmia*, in the Tubercularieae. New species, belonging to the following genera, have been found :—Ascomycetes: *Ascodesmis Volutelloides*, *Arachniotus citrinus*, *Myxotrichum Johnstoni*, *M. spinosum*, *Chaetomium arachnoides*, *C. simile*, *Nectria ornata*; Hyphomycetes: *Cephalosporium succineum*, *Acremonium fimicolum*, *Sepedonium niveum*, *Oedocephalum ochraceum*, *Trichothecium inaequale*, *Trichosporium insigne*, *Chaetostroma fimicolum*, *Graphium Comatrichoides*. The following species, new to the British Flora, have occurred :—Hymenomyceteae: *Coprinus velox*, Godey. Ascomycetes: *Arachniotus candidus*, Schroet., *Gymnoascus setosus*, Eidam, *Myxotrichum aeruginosum* (Mont.), *Anixiopsis stercoraria*, Hans., *Magnusia nitida*, Sacc., *Chaetomium bostrychoides*, Zopf, *Sordaria bombardioides*, Auersw., *Poronia punctata*, Ell. and Everh. Sphaeropsideae : *Sphaeronaemella fimicola*, March. Mucoraceae: *Mucor racemosus*, Fres., *Syncephalis intermedia*, van Tiegh., *Circinella umbellata*, van Tiegh. and Le Monnier, *Helicostylum piriforme*, Bainier. Hyphomycetes: *Botrytis pilulifera*, Sacc., *Botryosporium foecundissimum* (Sacc. and March.), *Aspergillus clavatus*, Desmaz., *Arthrobotrys superba*, Corda, *Trichocladium asperum*, Harz., *Sporodesmium piriforme*, Corda, *Stysanus fimetarius* (Karst.), *S. stercorarium*, March.

In the following enumeration of the species of Fungi observed, it will be noticed that several have occurred on the dung of exotic animals. We obtained this dung, through the kindness of Mr. C. Bartlett, Superintendent, fresh from the Zoological Gardens, Regent's Park, and kept it subsequently under bell-jars at Kew.

HYMENOMYCETEAE.

Coprinus Gibbsii, Mass. and Crossl.

Hab.—On Horse-dung, Sheffield, Yorksh. (T. Gibbs, Nov. 1901).

C. velox, Godey.

C. velox, Godey, in Gillet's Champ. France, Hymen., p. 614, with fig.; Sacc. Syll. Fung. v, 1107 (1887).

Pileus cylindrical then obovate, finally expanded, at first entirely covered with white floccose down, becoming naked and grey, striate, disc and grooves minutely scurfy, 3–4 mm. across, membranaceous; gills narrow, attenuato-free, not deliquescing; spores elliptic-oblong, brown with a purple tinge, 7 × 5 μ, cystidia absent; stem 1·5–3 cm. long, filiform, slightly thickened at the base, translucent, colourless, at first floccosely downy, becoming glabrous except at the base.

Hab.—On Horse-dung, Kew, Jan. 1902. (Distrib.—France, on Cow-dung.)

ASCOMYCETEAE.

Gymnoascaceae. Ascodesmis Volutelloides, sp. nov. (Figs. 13–17).

Ascomatibus punctiformibus circ. 150 μ diam., primo niveis demum dilute stramineis globulosis pilis longis 120–500 μ filiformi-setaceis basi plus minus inflatis rectis vel flexuosis hyalinis septatis e membrana basilari parenchymatica orientibus cinctis, ascis piriformibus vel oblongis breviter stipitatis citissime diffluentibus 28–35 × 14–16 μ, octosporis, sporis globosis 10 μ diam. hyalinis vel dilute stramineis minute asperis; paraphysibus paucis filiformibus septatis apice curvatis circ. 40 μ longis mox evanescentibus.

Hab.—In fimo *Macropodis gigantei* (Kangaroo), Kew, Mar. 1901.

The present Fungus appeared on some Kangaroo-dung, after it had been kept some months, where it formed minute scattered specks, which were at first snow-white, subsequently turning to pale yellowish. It is at once distinguished from the two species of *Ascodesmis* hitherto recorded—*A. nigricans*, van Tiegh., and *A. aurea*, van Tiegh.—by the presence of the long seta-like hairs surrounding the ascophore, which give to the present Fungus a superficial resemblance to species of the Hyphomycetous genus *Volutella*. The setae spring from a delicate cellular structure at the base of the ascophore.

A. nigricans, van Tiegh.

Hab.—In great profusion on Ostrich-dung, Kew, June, 1901.

Arachniotus citrinus, sp. nov. (Figs. 86–88).

Glomerulis gregariis subglobosis pulvinatis albidis dein laete citrinis ·5–1 mm. diam., hyphis irregulariter ramosis septatis laevibus 3 μ crassis flavidis laxe intricatis; ascis subglobosis congestis 8–10 μ diam., octosporis, mox diffluentibus; sporis ovatis vel subglobosis leniter compressis 4–5 × 2·5–3·5 μ flavidis laevibus.

In fimo *Macropodis gigantei* (Kangaroo), Kew, Mar. 1901.

Tufts at first white, soon changing to a clear deep lemon-yellow. The hyphae are very slender, and remain permanently thin-walled. The species appears to be most closely allied to *A. aureus*, Schroet., from which it differs more especially in the smooth—not warted—spores and the absence of spirally wound hyphae. The colour also of the present species is lemon-yellow, not golden-yellow as in *A. aureus.*

A. candidus, Schroet. (Figs. 11, 12).

Gymnoascus candidus, Eidam, 1886 (fide Schroeter).

Arachniotus candidus, Schroet., in Cohn's Krypt.-Fl. Schles. Bd. iii, Hälfte 2, 210 (1893); Sacc. Syll. Fung. xi, 438 (1895).

Tufts roundish, gregarious, up to 1 mill. in diam., sometimes becoming confluent, forming persistently snow-white downy patches; hyphae irregularly branched, scanty, thin-walled, smooth, delicate; asci minute, densely crowded into a snow-white mass, globose, 5–6 μ diam., 8-spored, evanescent; spores broadly ellipsoidal, conglobate, smooth, colourless, 3–3·5 × 2·5 μ.

Hab.—On an old nest of a Wild-bee (*Bombus* sp.), Kew, Feb. 1901; and on the dung of Common Roe (*Capreolus capraea*), Kew, Mar. 1901. (Distrib.—Germany, on dung and rotting animal and vegetable substances.)

Distinguished among the species of the genus by remaining persistently snow-white. The minute spores remain for a long time conglobate in little balls of eight.

A. ruber (van Tiegh.), Schroet.

Hab.—On Cats' dung, Aburi, Gold Coast, Africa (W. H. Johnston, 1901).

An interesting occurrence, as the species has not hitherto been known out of Europe. The patches formed by this species are at first pale yellow, but soon turn to orange, and finally become dark reddish-orange.

Gymnoascus setosus, Eidam (Figs. 18–22).

G. setosus, Eidam, in Bot. Centralbl. x, 107 (1882); Sacc. Syll. Fung. viii, 824 (1889); Schroet. in Cohn's Krypt.-Fl. Schles., Bd. iii, Hälfte 2, 212 (1893).

Effused and forming more or less continuous patches of a cinereous colour; vegetative hyphae much branched, dark brown, bearing long straight spine-like branches, which bear 2–3 opposite or whorled short spinous branchlets; asci very numerous, forming a snow-white mass towards the interior, minute, broadly oval or subglobose, 7–8 μ diam.; spores hyaline, subfusoid, subinaequilateral, 5–7 × 2 μ.

Hab.—On an old nest of a Wild-bee (*Bombus* sp.), Kew, Feb. 1901. (Distrib.—Germany; on an old Wasp's nest.)

A very beautiful species, distinguished from all other members of the genus by the central mass of asci remaining permanently snow-white. The cinereous colour of the whole Fungus is due to this white mass of the balls of asci being seen through the exterior network of the brown vegetative hyphae.

Gymnoascus Reessii, Baran.

Syn.—*Myxotrichum ochraceum*, Berk. and Br., **coprogenum*, Sacc., in Mich. ii, 372 (1881).

M. coprogenum, Sacc. Syll. Fung. iv, 319 (1886).

M. coprogenum, Sacc., var. *malaccense*, Sacc. and Paol., in Sacc. Syll. Fung. x, 593 (1892).

Saccardo has described in Mich. ii, 372 (1881) a Fungus under the name of '*Myxotrichum ochraceum*, B. and Br., Grev. 1874, p. 184, **coprogenum*. In stercore humano putri Newfield, *Ellis*, sed ad maturitatem culturâ provectum Padova, Febr. 1881,' as follows: 'Caespituli e roseo ochracei, pulvinati, laxe gossipini, ½ mill. d.; hyphae assurgentes repetite dichotome ramosae, parce septatae, 4 micr. cr. ramuli ultimi saepius curvuli flavo-ochracei, granulosi; sporae ad apicem ramulorum tenuiorum initio *intra vesiculam sphaericam*, 8½–10 micr. d, conglobatae, saepius octonae, globoso-depressae, 3–3½ micr. d. e fronte, 2 micr. e latere, flavo-ochraceae, denique, vesicula dilabente, varie inspersae.' In the Syll. Fung., vol. iv, Saccardo described the species as '*M. coprogenum*, Sacc., nec *M. ochraceum*, B. and Br.,' and added the record 'in fimo murino, Bruxelles Belgii (Marchal).' In Syll. Fung. vol. x, Saccardo described a new variety of *M. coprogenum* as 'var. *malaccense*, Sacc. et Paol., Myc. Malac. n. 120,' with the description, 'A typo differt sporidiis paullo majoribus, nempe 5 μ diam., 4 μ e latere crassis; ascis 10 μ diam. Hab. in fimo gallinaceo, Malacca (Scortechini).' Prof. Saccardo has kindly sent us the type specimens of *M. coprogenum* and its var. *malaccense*, and we have identified them as being certainly *Gymnoascus Reessii*, Baran. In the example sent labelled '*M. coprogenum*, typicum,' the spores measure 3–4 × 2–2·5 μ; the ultimate branches of the hyphae have exactly the form characteristic of *G. Reessii* (see Fig. 35). In the specimen sent labelled '*f. malaccense*' the hyphae are similarly branched, but the spores are a little larger, though slightly variable in size. In front view they average 4 μ, and vary from 3·5–4·5 μ; seen from the side they measure 2–2·5 μ (not 4 μ as stated by Saccardo). The habit in both specimens is that of *G. Reessii*, and the size of the spores also agrees with that found in this species.

M. Johnstoni, sp. nov. (Figs. 113–118).

Glomerulis gregariis, subrotundis, 90–120 μ diam., primo luteis deinde laete flavo-viridibus, hyphis dense intricatis irregulariter ramosis septatis 5–6 μ crassis ramulis apice bifurcato-uncinatis, appendicibus radiantibus teneris sparsis flexuosis ad apicem sensim attenuatis peripherice instructis; ascis subglobosis 8–9 μ diam., octosporis, sporis hyalinis e fronte orbicularibus 3·5–4·5 diam., e latere ellipticis 2 μ diam.

Hab.—In fimo murino, Aburi, Gold Coast, Africa (W. H. Johnston, 1901).

A very interesting species, occupying a somewhat intermediate position between the genera *Gymnoascus* and *Myxotrichum*, agreeing with the former in the dense protective network of hyphae being provided with numerous simple, or forked, uncinate free ends; and with the latter genus in the habit of the nearly globose glomerules, and in the radiating appendages. These latter, however, are primitive in type, and scarcely differ from ordinary hyphae, being not yet differentiated into the rigid appendages—spine-like or with a curved or circinate apex—which are found in the typical species of *Myxotrichum*.

The Fungus was sent in fine condition on Rats' dung from Aburi, Gold Coast, Africa, by Mr. W. H. Johnston, F.L.S.

M. spinosum, sp. nov. (Figs. 63–66).

Gymnoascus Caltrop, Renny MSS. in Herb. Berk. Glomerulis gregariis globosis ochraceo-brunneis circ. 1 mm. diam., reticulo myceliali ex hyphis asperulatis arcuato-protuberantibus composito peripherice in ramos setiformes subulatos rectos rigidos atro-brunneos opacos glabros undique radiantes exeunte, ascis numerosissimis globosis octosporis 6 μ diam., sporis ellipsoideis hyalinis laevibus 3 × 2 μ.

Hab.—In ramis emortuis corticatis *Fraxini.*

A very beautiful and distinct species. The peripheral network consists of brown, minutely asperate hyphae, and the outermost portions of the mesh are strongly arched and bear long smooth spine-like branches, which radiate in all directions from the central ball. The affinity of the species is with *M. aeruginosum*, Mont., from which it differs in the smaller spores, strongly arched ribs of the peripheral network, and, so far as we have observed, in the spine-like appendages never becoming hooked at the apex. The present species was collected by Renny, and is now in Berkeley's herbarium at Kew. No locality is given, but the species is in all probability British.

M. aeruginosum, Mont. (Figs. 76–79).

M. aeruginosum, Mont., in Ann. Sci. Nat. sér. II, vi, 34 (1836); Mont. Syll. Crypt. 307 (1856); Sacc. Syll. Fung. iv, 319 (1886).

M. ochraceum, Berk. and Broome, in Ann. Mag. Nat. Hist. ser. iv, vol. xv, p. 37, nr. 1475, pl. 1, f. 4 (1875), seems, at least in part, to belong here. In Berkeley's herbarium at Kew, the type specimen, which is labelled '*Myxotrichum ochraceum*, Berk. and Br., nr. 402, Mar. 21, 1874,' only contains examples of *M. deflexum*, Berk. (see Figs. 80–82), mixed with immature plants of a species of *Chaetomium*. On this specimen there was already written, in an unknown handwriting, '*M. deflexum*'; and we were not able to find in it anything resembling Berkeley's figures (l. c.). The only other specimen in Berkeley's herbarium is one labelled '*Myxotrichum ochraceum*, Berks. and Br., C. E. B., Jan. 28, 1874.' This proves to be *M. aeruginosum*, Mont.; and the same is the case with the specimens sent out as '*M. ochraceum*, Berk. and Br. mss.,' in Rab. Fung. Eur. nr. 1863, collected by Broome at Batheaston, in March, 1874.

M. aeruginosum, Mont., has hitherto been recorded only from France.

M. chartarum, Kunze.

Hab.—On Grouse-dung, Balmoral Forest, Scotland. Sept. 1901.

M. uncinatum (Eidam) Schroet.

Hab.—On Rats' dung, Kew, Aug. 1901.

A small form of the species, with the appendages sometimes bifid at the apex, and each branch uncinate at the tip.

Ascobolaceae. **Thelebolus stercoreus**, Zukal.

Hab. On Rabbit-dung, Sheffield, Yorksh. (T. Gibbs, Nov. 1901).

Ascobolus perplexans, Mass. and Salm.

Hab.—On dung of Bactrian Camel and Llama, Kew, June, 1901.

A. immersus, Pers.

Hab.—On dung of Bactrian Camel, Kew, June, 1901.

Saccobolus Kerverni (Cr.), Boud.

Hab.—On dung of Bactrian Camel, Kew, June, 1901.

S. neglectus, Boud.

Hab.—On dung of Bactrian Camel, Kew, June, 1901.

Ascophanus ochraceus (Cr.), Boud.

Hab.—On dung of Bactrian Camel, Kew, June, 1901.

Pezizaceae. **Humaria salmonicolor** (Berk. and Broome), Sacc.

Peziza (*Humaria*) *salmonicolor*, Berk. and Broome, in Ann. Nat. Hist. xviii, 124, Pl. iv, f. 19 (1866); Cooke, Mycogr. f. 48, and in Grevillea, iii, f. 202.

Humaria salmonicolor (Berk. and Br.), Sacc. Syll. Fung. viii, 123 (1889); Mass. Brit. Fung. Fl. iv, 420 (1895).

Hab.—On Hares' dung, Kew, April, 1901.

This very interesting species of *Humaria*, which does not appear to have been hitherto met with since its original discovery in England, 'on the side of a ditch, Woodnewton,' in 1858, occurred in some plenty on Hares' dung after this had been kept for a few weeks under a bell-jar. The apothecia are remarkably translucent in appearance, and are salmon-coloured or of a reddish-orange colour. When young, the apothecia are surrounded by delicate white hyphae, proceeding from the basal cortical cells, forming a kind of subiculum just as in *H. domestica* (Sow.), Mass. The apothecia in our specimens measured $\frac{3}{4}$–1 mm. across. The asci are about 280 μ long, and 30–34 μ wide; the spores, which are irregularly biseriate towards the apex of the ascus, measure 20–22 × 11–12 μ, and, when mature, have a very minutely rough epispore.

H. salmonicolor appears to be essentially distinct from *H. domestica* in the broadly clavate or oblong (not cylindrical) ascus and the irregularly biseriate spores. Cooke's figure of the ascus in Mycogr. is not correct, and the colour there given of the apothecium is far too red; the figure of the ascus given in Grevillea represents the shape better.

Perisporiaceae. Anixiopsis stercoraria, Hans. (Figs. 27, 28).

Eurotium stercorarium, Hans., in Vidensk. Meddel. 1876, 310 (1876–77); Sacc. Syll. Fung. i, 27 (1882).

Anixiopsis stercoraria, Hans., in Bot. Zeit. lv, 131, Taf. 11, Fig. 8 (1897); Sacc. Syll. Fung. xiv, 464 (1900).

Perithecia minute, globose, about 240 μ in diam., scattered, at first brownish, then dull yellowish; mycelium inconspicuous; wall of perithecium delicate, membranaceous, distinctly cellular, cells about 4 μ wide; asci very numerous, subglobose to oblong, about 10 μ in diam., wall very evanescent. 6–8-spored; spores very minute, irregularly globose to subelliptic, conglobate at first, 4 μ in diam., rough with minute scattered points.

Hab.—On Owl-castings, Kew, July, 1901. (Distrib.—Denmark, on old dung of Fox, containing remains of mammals; cultivated on Rabbit-dung, beer-wort, cooked rice, &c.)

Resembling a minute species of *Eurotium*, and best recognized by the minute rough spores, at first conglobate in the ascus. Only a few perithecia were observed on the Owl-castings.

Hansen succeeded in germinating spores of the present Fungus in various media (beer-wort, cooked rice, decoction of Rabbit-dung, &c.) after the spores had been kept for twenty-one years. The spores produced on germination a mycelium composed of colourless septate branched hyphae. The mycelium produced aerial branches which bore conidia. These conidia were intercalary or terminal, and were very irregular in shape and size; often, however, they were pyriform or clavate in shape, and measured 7–19 μ long. The conidia are usually produced singly, but sometimes form *oïdium*-like chains. After about eighteen days from the time of germination perithecia began to be formed. Hansen believes the above to be the normal life-cycle of the species, and considers that the occurrence of the above-described conidia in the place of an *Aspergillus*-conidial form is sufficient to exclude the present Fungus from *Eurotium*.

It may, perhaps, be well to point out that in *Eurotium insigne*, Wint., we find the rough spores conglobate at first in the ascus in the same manner as in the present species.

Eurotium microsporum, Mass. and Salm.

Hab.—On dung of Argali Sheep, Kew, August, 1901.

E. insigne, Wint.

Hab.—On dung of Llama, Kew, June, 1901.

Arachnomyces, gen. nov.

Perithecia globosa simplicia astoma membranacea parenchymatica appendicibus fuscis eumorphis instructa, ascis minutis numerosis globosis, sporis primum conglobatis continuis fuscis.

A *Pleuroasco*, Mass, et Salm., differt subiculi defectione et appendicibus fuscis, a *Magnusia*, Sacc., ascis globosis et sporis conglobatis.

A. nitidus, sp. nov. (Figs. 127–131).

Peritheciis globosis $\frac{1}{10}$–$\frac{1}{3}$ mill. diam. nigris nudis nitidis tenui-membranaceis fragilibus contextu parenchymatico e cellulis polygonis irregularibus 5–10 μ latis composito, appendicibus e parte perithecii inferiore orientibus paucis flexuoso-contortis atro-fuscis 5–6 μ latis nitentibus semiopacis septatis perithecii diametro 5–7-plo longioribus apice rectis vel simpliciter circinatis, ascis numerosissimis subglobosis circ. 10 μ diam. mox evanescentibus, sporis primum octono-conglobatis sphaeroideo-compressis, 3–4 × 2·5 μ, fuscis.

Hab.—In plantis putridis, Kew, Sept. 1901; Cadeby, Yorkshire (Chas. Crossland, Sept. 1901); in fimo murino, Thornton Hough, Cheshire, Sept. 1901.

The above Fungus would seem to be not uncommon on fragments of rotting plants (especially stems of grasses) when heaped together, although on account of the small size of the perithecium it may easily be passed over. Under a lens the shining wall of the perithecium attracts attention; when the Fungus is perfectly ripe the wall becomes extremely brittle, and cracks at the slightest pressure. The perithecia are usually found connected together in groups of five or six by means of their interlaced appendages. We have met with the Fungus in two localities at Kew on fragments of rotting plants, and it has been found on the same substratum at Cadeby, Yorkshire. Curiously enough, it also occurred on some Rats' dung from Thornton Hough, Cheshire.

It may be noted that in the present genus the spores, which remain in little balls of eight for some time, strongly resemble in their great number, size, arrangement, &c., those of *Pleuroascus Nicholsoni*, Mass. and Salm.

A. sulphureus, sp. nov. (Figs. 55–60).

Peritheciis globosis $\frac{1}{2}$–$\frac{2}{3}$ mill. diam. superficialibus indumento sulphureo arcte adhaerente obtectis tenui-membranaceis fragilibus contextu parenchymatico e cellulis polygonis irregularibus 5–10 μ latis composito basin versus appendicibus paucis flexuosis 5–6 μ latis perithecii diametro 3–4-plo longioribus divergentibus atrofuscis nitentibus semiopacis septatis apice circinatis vel circinato-contortis cinctis, ascis numerosissimis minutis globosis 7–8 μ diam. mox evanescentibus, sporis sphaeroideo-compressis 3–4 × 2·5 μ octono-conglobatis fuscis.

Hab.—In nido vetusto *Bombi* sp., Kew, April, 1901.

The Fungus described above appeared among the débris of an old nest of a Wild-bee (*Bombus* sp.) dug up in the Royal Gardens, Kew, after the nest had been kept for about a month in a tin box. The perithecia occurred superficially on the bits of straw, &c., composing the nest, and were often held together in groups of three or four by their interlaced appendages. The wall of the perithecium is pale yellowish-brown, and the sulphurous colour of the perithecium is due to the presence of the indumentum closely adhering in strands to the wall, and completely surrounding each perithecium. The appendages originate from the basal cells of the wall of the perithecium; the cells of the wall at the place of origin are sharply marked off from the rest by being very thick walled and brownish in colour. The appendages are very flexuous, somewhat rigid and shining, with delicate transverse septa; the apex is variously contorted in a more or less circinate manner. Each spore seen from the front is orbicular in outline; from the side, broadly elliptical.

The present species appears to differ specifically from *A. nitidus* in the slightly larger size of the perithecium, and especially in the indumentum surrounding each perithecium; the appendages also in *A. nitidus* are longer, and apparently never spirally contorted at the apex as in the present species. The size and arrangement of the spores are the same in both species.

Magnusia nitida, Sacc. (Figs. 1–5).

M. nitida, Sacc., in Michel. i, 123 (1878); Sacc. Syll. Fung. i, 38 (1882); Zopf and Syd. Myc. March. nr. 100 (figs.); Wint. in Rabenh. Krypt.-Fl. Deutschl. Bd. i, Abth. ii, 55 (1887); Schroet. in Cohn's Krypt.-Fl. Schles. Bd. iii, Hälfte 2, 221 (1893).

Perithecia scattered or subgregarious, superficial, subglobose, membranaceo-carbonaceous, black, about ½ mill. diam., wall dense, parenchymatous, fragile, composed of small distinct polygonal cells about 5 μ diam., appendages springing from the apex of the perithecium 15–30, or rarely as many as 50, erect or horizontally spreading, 1½–2½ times the diameter of the perithecium, somewhat rigid, dark brown, opaque, about 9 μ wide towards the base, all regularly circinate at the apex; asci oblong or oblong-pyriform, 20–30 × 12–15 μ, octosporous, very evanescent; spores broadly elliptical, acute at both ends, about 10 × 7 μ, smooth, at first hyaline, becoming steel-grey.

Hab.—On dung of Sinaitic Ibex (*Capra sinaitica*), Kew, Feb. 1891; on Rabbit-dung, Reigate, Feb. 1891. (Distrib.—Germany; on rotten pine-wood, and on Camel-, Rabbit-, and Horse-dung).

It is with some hesitation that we refer our Fungus to the species *Magnusia nitida*, Sacc., although there seems no doubt that the plant belongs to that genus. In Saccardo's original description of the genus the appendages are described as springing from the base of the perithecium. In the full description of *Magnusia nitida*, however, given by Zopf and Sydow (l. c.), the appendages are described as springing from the poles or blunt angles of the perithecium, and the statement is made that Saccardo's description is erroneous. As regards the shape of the perithecium, this is evidently very variable. Saccardo, in Michelia (l. c.), describes the perithecia as 'e globoso horizontaliter oblonga,' and as 'applanato-oblonga'; although in the key to the genera of the *Perisporiaceae* (Syll. i, p. 25) they are described simply as 'globosa.' Zopf and Sydow speak of the perithecia as 'e globoso vel ovato horizontaliter producta, plus minus elongato-ellipsoidea vel obtuse triangularia'; and add 'Die Exemplare auf Mist treten meist nur in der kurzellipsoïd oder dreieckigen Form auf.' Schroeter (l. c.) describes the perithecia as 'kuglig, länglichrund oder stumpfeckig.' Our Fungus has nearly globose perithecia, with the appendages all springing from the apex. In other characters it agrees with the descriptions given of *M. nitida*. The ripe asci, in our plant, measure 20–30 × 12–15, and the ripe spores 10 × 7 μ. Zopf and Sydow describe the asci as measuring 13–14 × 9–10 μ, and the spores 5–6 × 3–4 μ. It is, however, only after the perithecia have been kept growing for a long time that asci and spores are found fully mature and of the larger size given above; in the immature—and commoner—stages, our Fungus showed asci and spores, the latter faintly coloured and escaping in water from the asci through the deliquescence of the ascus-wall, of the size given by the above authors for *S. nitida*.

Under the circumstances it seems better to consider our plant as a form of *M. nitida* than to describe it as a new species. It is distinct from *M. Bartlettii*, Mass. and Salm., in the stouter appendages circinate at the apex.

Sphaeriaceae. Chaetomium arachnoides, sp. nov. (Figs. 97–103).

Peritheciis parvulis globosis subumbonatis sparsis vel gregariis nigris contextu parenchymatico e cellulis polygonis circ. 8 μ latis composito in parte superiore pilis fuscis longissimis flexuosis valde divergentibus simplicibus gracilibus 4–5 μ crassis laevibus septatis apice plus minus uncinatis undique vestitis, ascis clavatis circ. 36 × 12 μ citissime diffluentibus, sporis e fronte late ellipsoideis vel subglobosis utrinque acutatis leniter compressis 7–9 × 5–6 μ fulvidis.

Hab.—In fimo ovino et in charta, Kew, Nov. 1901.

The above species appeared on some Sheep-dung sent from the Gold Coast, Africa, by Mr. W. H. Johnston, after the dung had been kept for a month or so at Kew. The *Chaetomium* soon appeared also on the paper surrounding the dung. *C. arachnoides* is very different in appearance from the commoner species of the genus, such as *C. murorum*, Corda, *C. elatum*, Kze, &c., on account of the extremely long flexuous hairs, which exceed ten times or more the diameter of the perithecium, and which diverge widely on all sides. These hairs are often fasciculate at the base, and more or less uncinate at the apex, below which they are sometimes angularly bent. In the early condition the perithecium is almost naked, a few short hairs being present only round the apex. These hairs afterwards grow out into the long flexuose divergent appendages, while the lower portion of the perithecial wall disappears. When perfectly ripe the Fungus is found to consist of an interwoven mass of hairs, containing fragments of the perithecial wall amongst a dense mass of loose clear yellowish-brown spores. At maturity each perithecium, owing to the disappearance of its lower part, becomes perfectly loose and free on the substratum.

C. simile, sp. nov. (Figs. 8, 9).

Peritheciis gregariis, 0·50–0·75 mm. altis, subglobosis, undique olivaceo-pilosis, pilis superioribus dense confertis, intricatis, crispis, fuscis, pluries irregulariter spiraliter contortis, apice uncinatis, plerumque aseptatis, laevibus; ascis cylindricis breviter stipitatis circ. 80 × 9–10 μ octosporis; sporis monostichis late ellipticis vel subglobosis polo uno minute apiculatis, altero plus minus rotundatis, 8–10 × 7·5, leniter compressis, olivaceo-fuscis.

Hab.—In fimo canino vetusto, Kew, England, Feb. 1901.

Species *C. crispato*, Fckl. simillima, sed setis terminalibus angustioribus laxius convolutis apice evidentius uncinatis nec non sporis minoribus polo uno rotundatis distincta videtur.

The above species, which appeared on Dogs' dung after it had been kept for some time, much resembles in many characters *C. crispatum*, Fckl. A close examination, however, shows the existence of several slight, but apparently constant, differences, so that it seems impossible to consider the present plant as belonging to that species. In the first place, the terminal hairs on the perithecium of *C. crispatum* are slightly thicker, and more closely coiled at shorter intervals almost up to their apex (see Fig. 10); in the present species the narrower hairs are less closely wound, and terminate in a more evident uncinate or circinate apex (see Fig. 9). In *C. crispatum*, also, the spores are apiculate at both ends, and measure, in the example in Fckl. Fung. Rhen. nr. 2022, where they are greenish and immature, 12 × 10 μ. In *C. simile* the spores are decidedly smaller, 8–10 × 7·5 μ, and are apiculate at one end only, the other being rounded.

C. bostrychoides, Zopf (Figs. 6, 7).

C. bostrychoides, Zopf, in Sitzungsber. Bot. Ver. Brandenb. xix, 173 (1877); Zopf, Entw. d. Chaet. 81, t. 7, f. 14–28 (1881); Sacc. Syll. Fung. i, 224 (1882); Zopf and Syd., Myc. March. nr. 43 (fig.); Wint. in Rabenh. Krypt.-Fl. Deutschl. Bd. i, Abth. ii, 155 (1887); Schroet. in Cohn's Krypt.-Fl. Schles. Bd. iii, Hälfte 2, 283 (1894).

Perithecia scattered or subgregarious, oval or elliptical, $\frac{1}{2}$–1 mill. high, with numerous crowded mostly spirally wound terminal hairs, which are fuscous and many septate, and often become very rough, lateral hairs spreading, simple, straight; asci clavate, shortly pedicellate, 8-spored, 40–50 × 12–15 μ, very evanescent; spores biseriate in the ascus, subglobose, minutely apiculate at each end, 6–7·5 × 5 μ, olivaceous, becoming fuliginous.

Hab.—On the dung of Giraffe (*Camelopardalis giraffa*) and Burrhel Wild Sheep (*Ovis burrhel*), Kew, Mar. 1901; on Mouse-dung, Kew, April, 1901. (Distrib.—Germany; on dung (Goats', &c.), and on rotting animal and vegetable substances.)

A fine species, easily known by the appendages wound in a corkscrew-like manner, and the small spores. It occurred very sparingly on the dung of Giraffe and Burrhel Wild Sheep, associated in the latter case with an abundant growth of *C. murorum*, Corda.

C. murorum, Corda.

Hab.—On dung of Llama and Common Camel, Kew, June, 1901.

Sordaria bombardioides, Auersw.

S. bombardioides, Auersw., in Niessl. Beitr. zur Kenntniss der Pilze, p. 37, Tab. vi, f. 4 (1872); Sacc. Syll. Fung. i, 233 (1882); Griffiths in Mem. Torr. Bot. Club, xi, 43, Pl. 4, ff. 4–7 (1901).

Perithecia gregarious, superficial, often confluent at the base in small groups, elliptical or oblong, base narrower, slightly rugulose, at apex umbilicate and minutely papillate, bay then blackish, 1–1·5 mm. high; asci cylindrical, narrowed below into a short stalk, 160–220 × 20–25 μ; spores 8, obliquely 1-seriate, elliptical, greenish then purple, finally opaque brown, with a thin external mucilaginous layer, 24–29 × 12–14 μ; paraphyses slender, agglutinated.

Hab.—On dung of Llama (*Lama guanaco*), Kew, Sept. 1901. (Distrib.—Germany, on Hares' dung; United States, on dung of Horse and Cow.)

The wall of the perithecium is readily separable into two layers: an outer tough and elastic one, with the component hyphae more or less obliterated and fused into a homogeneous mass; and an inner obovate, very thin, hyaline cellular membrane enclosing the asci.

S. neglecta, Hans. (Figs. 44–48).

S. neglecta, Hans., in Vidensk. Meddel. 1876, 335, Tab. ix, ff. 12–18 (1876–77); Sacc. Syll. Fung. i, 232 (1882).

We have already (I. p. 339) noticed the occurrence of this species of *Sordaria* in Britain. In its usual form the perithecia are glabrous and subimmersed in the dung. An interesting form has occurred on Giraffes' dung, after it had been kept for some time in a tin box. In this form the perithecia are superficial, and are enveloped right up to the neck in white floccose mycelium, the hyphae of which originate from the wall of the perithecium. When the perithecia are densely gregarious, this mycelial weft often becomes more or less confluent, as shown at Fig. 45. The long cylindrical asci (about 470 × 30–45 μ) contain eight monostichous spores, which measure 45–50 × 25–28 μ, and possess a stout, subpersistent, often curved appendage at each end (Fig. 46). The perithecia are large, about 1 mill. high and 1 mill. broad, with a black papilliform neck. These features are all characteristic of *S. neglecta*, and there seems no doubt that the form under consideration belongs to that species. We may, perhaps, consider the mycelial outgrowth as due to the superficial position (doubtless caused by the dense composition and hard surface of Giraffes' dung) of the perithecia, causing the wall of the perithecium, usually immersed in the dung, to be exposed, when it requires some protection.

Another striking form of *S. neglecta*—or perhaps a distinct species—occurred on Horse-dung, Kew, Nov. 1900. In this the asci are only about 190 μ long, about 26 μ thick, and the spores measure 30–34 × 18–20 μ. The appendages of the spores are smaller, but otherwise identical with those of typical *S. neglecta*. In the smaller size of the spores this form seems identical with that recorded by Hansen (l. c. *résumé*, p. 58), who remarks, speaking of *S. neglecta*: 'J'ai rencontré sur du vieux crottin de cheval, à Holte, en Sélande, une variété plus petite, dont les sporocarpes n'ont que ½–1 millim. de haut, et les spores 33–40 μ de long sur 18–21 d'épaisseur. Les paraphyses étaient en outre un peu plus épaisses que chez la forme principale, et les articles, un peu renflés. Les spores avaient souvent une forme anormale.' In our specimens the perithecia have a rather long, cylindrical, sometimes curved neck (Fig. 47); Hansen, as is seen from the above quotation, does not describe the form of the perithecium in his 'small form.' Investigation is required to ascertain if the small spores and asci are always found associated with a long-necked perithecium, as if this is the case, these correlated characters are sufficient to elevate the present form to the rank of a species.

S. fimicola (Rob.), Ces. and De Not.

Hab.—On dung of Llama, Kew, June, 1901.

S. setosa, Wint.

Hab.—On dung of Llama and Argali Sheep, Kew, June, 1901.

S. decipiens, Wint.

Hab.—On dung of Argali Sheep, Kew, June, 1901.

Sporormia minima, Auersw.

Hab.—On dung of Llama, Kew, June, 1901.

S. intermedia, Auersw.

Hab.—On dung of Llama, Kew, June, 1901.

Microascus variabilis, Mass. and Salm.

Hab.—On Rats' dung, Thornton Hough, Cheshire, Aug. 1901.

Poronia leporina, Ell. and Everh. (Figs. 121–123).

P. leporina, Ell. and Everh., in Proc. Acad. Nat. Sci. Phil. 1890,

p. 229; Sacc. Syll. Fung. ix, 542 (1891); Ell. and Everh. N. Amer. Pyren. 660, pl. 39, ff. 13–16 (1892).

Stroma stipitate, discoid, upper surface reddish-grey, rather coarsely and sparsely mammillate from the projecting perithecia, 2–4 mm. diam.; stem slender, of equal thickness throughout, 3–4 mm. long, more or less immersed in the substratum; perithecia ovate, ostiola prominent, black; asci cylindrical, narrowed below into a short stalk, about 125 × 12 μ; spores 8, obliquely 1-seriate, elliptical, subinaequilateral, 15–18 × 7–8 μ, at first translucent green, becoming blackish purple and opaque at maturity, surrounded by a narrow hyaline mucilaginous border.

Hab.—On Rabbit-dung, Cadeby, Yorkshire (C. Crossland, Oct. 1901). (Distrib.—On Rabbit-dung, Missouri, United States.)

Differs from *P. punctata* (L.), Fr., in the sparsely scattered prominent perithecia, which give to the surface of the stroma a coarsely mammillate or warted appearance. *P. oedipus*, Mont., differs in the swollen base of the stem and other features.

HYPOCREACEAE.

Hyalodidymae. Nectria ornata, sp. nov. (Figs. 29–32).

Peritheciis sparsis minutis subglobosis dein vertice subdepressis $\frac{1}{3}$–$\frac{1}{2}$ mill. diam. ostiolo minuto obscuro aurantiacis basin versus squamulis argenteo-nitentibus patulis undique instructis; ascis cylindricis vel cylindraceo—clavatis 65–75 × 9–11 μ octosporis; sporis primo monostichis deinde irregulariter distichis ellipsoideis utrinque obtusatis 12–14 × 4–5 μ, hyalinis, uniseptatis, ad septum haud constrictis.

Hab. In fimo equino, Kew, England, April, 1901.

A very fine species, having the perithecium bristling with silvery scales, each of which is composed of a fascicle of hyphae. Allied to *N. Ralfsii*, Berk. and Broome, from which it differs in the smaller spores.

SPHAEROPSIDEAE.

Nectrioideae. Sphaeronaemella fimicola, March. (Figs. 38–43).

S. fimicola, March., in Bull. Soc. Roy. Bot. Belg. xxx, pt. 2, 143 (1891); Sacc. Syll. Fung. x, 407 (1892).

Perithecia gregarious or scattered at short intervals, superficial, reddish-yellow, about 1 mill. high and 150–200 μ in diam., membranaceous, soft, glabrous, basal part globose, wall parenchymatous, composed of delicate polygonal cells about 10 μ wide, abruptly narrowed into the long (700–800 μ) narrow subulate beak, which is subhyaline and penicillate at the apex; spores narrowly elliptical, 6–7·5 × 2–2·5, hyaline, straight or slightly curved, involved in mucus, at maturity expelled at the mouth of the beak in a white ovoid mucilaginous drop.

Hab. On Rabbit-dung, Leith Hill, Surrey, England, Feb. 1901; on Hares' dung, Kew, Mar. 1901; on dung of Deer, Epping Forest, Oct. 1901; on Rabbit-dung, Sheffield, Yorks. (T. Gibbs, Nov. 1901).

This interesting Fungus was first collected on Rabbit-dung, at Leith Hill, Surrey, in Feb. 1901. Subsequently it appeared in hundreds on Rabbit-dung, brought from the same locality, and kept for a few days in a moist atmosphere under a bell-jar. When mature, the Fungus, by reason of its superficial position and bright colour, is somewhat conspicuous, the long reddish-yellow beak surmounted by a pallid mucilaginous drop attracting attention.

Marchal (l. c.) describes a variety—*minor*—growing on Rabbit-dung, differing in the shorter (500–580 μ) regularly cylindrico-conical beak; our plants, however (on Rabbit-dung), possess a very long subulate beak, and so evidently belong to the type. The hyphae at the apex of the beak are more or less hyaline, and run out into long processes, forming a penicillate mouth; between these processes the spores are held in mucilage (see Fig. 40). In our specimens, amongst the normal examples, individuals not uncommonly occurred in which the perithecium possessed two beaks;—one of these perithecia is shown at Fig. 39.

Marchal (l. c.) considers that *Sphaeronaemella fimicola* probably represents the spermogonial stage of some *Melanospora.*

PHYCOMYCETEAE.

Mucoraceae. Mucor racemosus, Fres. (Figs. 93–96).

M. racemosus, Fres., Beitr. Myk. 12, t. 1, ff. 24–31 (1850); Sacc. Syll. Fung. vii, 192 (1888); Fischer in Rabenh. Krypt.-Fl. Deutschl. Bd. 1, Abth. iv, 192 (1892).

Chlamydomucor racemosus, Brefeld, Untersuch. viii, 223, Taf. vii, ff. 1–11 (1890).

Sterile hyphae creeping, branched, septate; sporangiophores erect, septate, irregularly branched near the apex, each branch bearing a terminal globose amber-coloured sporangium, 25–35 μ diam., sometimes larger, sprinkled with particles of lime; columella elliptical; spores broadly elliptical, 7–8 × 4–5 μ, hyaline; zygospore globose, epispore yellowish brown, bluntly warted, or striate, 70–80 μ diam.

Hab. On Pigeons' dung, Kew, March, 1901. (Distrib.—Germany, Italy, France, Belgium, U.S.A.; on decaying substances both animal and vegetable, also on dung.)

Readily distinguished by the branched sporangiophore, each branch of which bears a small globose amber-coloured sporangium. Interstitial tun-shaped chlamydospores or 'gemmae' are met with abundantly on the prostrate mycelium.

Pilobolus exiguus, Bain.; Fischer in Rabenh. Krypt.-Fl. Deutschl. Bd. i, Abth. 4, 267 (1892); Sacc. Syll. Fung. vii, 187 (1888).

Hab.—On Goose-dung, Kew, Dec. 1900.

Syncephalis intermedia, van Tiegh. (Figs. 23–26).

S. intermedia, van Tiegh., in Ann. Sci. Nat. sér. vi. I, 127, pl. 3, f. E (1875); Sacc. Syll. Fung. vii, 231 (1888); Fischer in Rabenh. Krypt.-Fl. Deutschl. Bd. i, Abth. 4, 304 (1892).

Conidiophores single, unbranched, smooth, erect, aseptate, about ½ mill. high, 20–45 μ wide at the base, gradually tapering upwards to 13–22 μ wide, apex swollen into a broadly obovate vesicle, 40–70 μ wide, bright yellow to yellowish brown; basidial cells numerous, springing from evident warts scattered over the upper half of the vesicle, variable in shape on the same head, either simple or bluntly triangular, or regularly heart-shaped, or asymmetrical with one long and one very short protuberance, according to their shape with one or two chains of conidia; conidia in upright chains, surrounded by mucilage, 10–15 in a chain, cylindrical or slightly barrel-shaped, pale yellowish-brown, 6–10 × 4–5 μ.

Hab.—On Rabbit-dung, Leith Hill, Surrey, Mar. 1901. (Distrib.—France and Germany, on Horse-dung, and also parasitic on *Mucorineae.*)

S. intermedia is characterized by the great variability in the shape of the basidial cells. These latter, intermixed on the same head, are found to be partly regularly cordate, resembling those found in *S. cordata*, van Tiegh. and Le Monn., and partly asymmetrical, like those of *S. asymmetrica*, van Tiegh. and Le Monn. (see Figs. 25, 26). The present plant is, therefore, clearly intermediate between these two species. To the naked eye *S. intermedia* appears as minute yellow stalks bearing yellowish-brown shining globular heads.

Piptocephalis Freseniana, De Bary and Woron. ex Bain.; Sacc. Syll. Fung. vii, 226 (1888).

Hab.—On Hares' dung, Kew, Feb. 1901.

Circinella umbellata, van Tiegh. and Le Monnier (Figs. 109–112).

C. umbellata, van Tiegh. and Le Monnier, in Ann. Sci. Nat. sér. v, xvii, 300, pl. 21, ff. 18–23 (1873); Sacc. Syll. Fung. vii, 216 (1888); Fischer in Rabenh. Krypt.-Fl. Deutschl. Bd. i, Abth. 4, 216, Fig. 34 (1892).

At first colourless, then slightly brownish; sporangiophore erect, 1–6 cent. or more high, simple or branched, flexuous, aseptate, flaccid, terminating in a sterile apex, bearing in a sympodial manner two rows of alternating branches, which bear 2–20 short unbranched usually septate more or less crowded branchlets curved at the apex; sporangia drooping, borne singly on each branchlet, subglobose, 60–120 μ in diam., wall covered with minute particles of lime, columella large, oblong or pyriform, spores globose or subglobose, smooth, 7–10 μ diam.

Hab.—On Ostrich-dung, Kew, June 1901; on dung of Cat, Kew, Oct. 1901. (Distrib.—France, Holland, Germany; on dung of Man, Dog, Gazelle, Rat, and on rotten vegetable substances; cultivated on damp bread, orange, and plum-decoction.)

A somewhat variable species, but easily recognized by the sympodially-borne 'umbels.' In its robuster form, which occurred on Ostrich-dung, each 'umbel' was composed of 12–20 more or less crowded branchlets; in the smaller form, on Cats' dung, the number of the branchlets was reduced to two or three.

Helicostylum piriforme, Bainier (Figs. 105–108).

H. piriforme, Bain., in Bull. Soc. Bot. France, xxvii, 227, pl. 5, ff. 5–11 (1880); Bain. in Ann. Sci. Nat. sér. vi, xv, 85, Taf. 4, ff. 5–11 (1883); Sacc. Syll. Fung. vii, 210 (1888); Fischer in Rabenh. Krypt.-Fl. Deutschl. Bd. i, Abth. 4, 252 (1892).

Sporangiophore upright, smooth, colourless, aseptate, with or without a large erect terminal sporangium, irregularly branched with two kinds of branches: branches of the first kind long, solitary, spreading, sterile or terminating in a large sporangium; branches of the second kind lateral, very short, thick, horizontally spreading, whorled, bearing at their apex numerous crowded, whorled, short, forked and lobed branchlets which bear a great number (100 or more) of long-stalked sporangiola; terminal sporangium globose, blackish, about 168 μ in diam., with an ovate, colourless, smooth columella; sporangiola pyriform, drooping, about 25 μ in diam., white, columella not evident, spores broadly ellipsoid, 6–8 μ long, 4–5 μ broad, smooth.

Hab.—On Mouse-dung, Kew, Oct. 1901. (Distrib.—France; on dung; also cultivated on bread and Horse-dung.)

A very beautiful and apparently uncommon species. In the Kew examples, no terminal sporangia were observed. The species is at once recognized by the mass of densely crowded pyriform sporangiola on rather long delicate stalks; the sporangiola arise laterally from the main axis in the manner shown at Fig. 108. The Mouse-dung on which the Fungus appeared was originally sent from the Gold Coast by Mr. W. H. Johnston; the dung was kept damp at Kew for a week or so, at the end of which time the *Helicostylum* appeared in some plenty.

HYPHOMYCETEAE.

Mucedineae Amerosporae. Cephalosporium succineum, sp. nov. (Fig. 34).

Caespitulis minutis sparsis succineis, hyphis fertilibus erectis simplicibus parce septatis apice nodulosis 60–80 × 5–6 μ; conidiis in capitulum subglobosum vel subclavatum congestis globosis succineis asperulis 9–11 μ diam.

In fimo ovino, Reigate, England, Jan. 1901.

Forming very minute scattered patches on Sheep's dung. Distinguished among the species of the genus by the amber colour of all its parts.

Acremonium fimicolum, sp. nov. (Fig. 92).

Caespitulis albis minutis; hyphis repentibus filiformibus sparse septatis furcatis hyalinis 4 μ crassis, ramulis fertilibus subulatis 5–8 μ longis hic inde in caespitulis irregulariter positis; conidiis globosis hyalinis 6–8 μ diam.

Hab.—In fimo cuniculorum, Kew, Nov. 1900.

Forming minute snow-white tufts which sometimes become confluent. The short fertile branchlets or conidiophores are arranged in clusters at intervals along the prostrate hyphae. Apparently allied to *A. Brassicae*, Sacc. and Schulz, but distinguished by the distinct clusters of conidiophores.

Sepedonium niveum, sp. nov. (Fig. 70).

Caespitulis effusis denique pulverulentis niveis; hyphis intertextis hyalinis septatis 5–6 μ diam. vage furcatis hic inde ramulos fertiles breves patulos ferentibus; conidiis in pedicello subulato 9–10 × 2 μ ad ramorum apicem acrogenis, globosis initio laevibus dein papillatis hyalinis 18–20 μ diam.

Hab.—In fimo *Cervi elaphi* (Red Deer), Kew, Nov. 1900.

Forming very delicate effused snow-white patches, which eventually become powdery owing to the accumulation of conidia on the surface. Apparently most nearly allied to *S. sphaerosporum* (Berk.), Sacc., a Brazilian species occurring on the gills of an agaric.

Several members of the form-genus *Sepedonium* are known to be the conidial condition of species of the ascigerous genus *Hypomyces*, Tul.; many others, however, to which must be added the species described above, have not as yet been connected with any higher form, and must for the present be considered as entities.

Oedocephalum ochraceum, sp. nov. (Figs. 83–85).

Effusum, pallide ochraceum; hyphis sterilibus repentibus ramosis hyalinis, fertilibus erectis fasciculatis cylindraceis sparse septatis vel aseptatis, circ. 200 × 7–8 μ ochraceis apice in vesiculam globosam verruculosam 30 μ diam. desinentibus, conidiis ex verruculis oriundis oblongo-ellipsoideis pallide ochraceis 4–5 × 2 μ.

Hab.—Supra fimum cuniculorum, Kew, Dec. 1900.

Forming pale ochraceous downy patches on Rabbit-dung. Most closely allied to *Oe. fimetarium* (Riess.), Sacc., which differs in the conidiophore being distinctly narrowed upwards, and in the larger spores. The last-named species is considered by Brefeld to be the conidial condition of *Peziza vesiculosa*.

Oe. glomerulosum (Bull.), Sacc. (Fig. 119).

Haplotrichum glomerulosum (Bull.), Harz. Hyph. 33, T. 1, f. 1.

Oedocephalum glomerulosum (Bull.), Sacc. Syll. Fung. iv, 47 (1886); A. L. Smith in Trans. Brit. Myc. Soc., 1899–1900, p. 151.

Gregarious, at first pure white, then tinged with rose colour or more frequently pale salmon-colour with a tinge of yellow; stem subcylindrical or slightly attenuated upwards, about 200 × 10 μ, transverse septa variable in number, sometimes absent, inflated head globose, verruculose, 30–40 μ diam., conidia elliptic-oblong, smooth, 22–28 × 13–18 μ.

Hab.—On Horse-dung, Mulgrave Woods, Whitby, Yorkshire, Sept.

1900; on manure, Kew, Dec. 1900. (Distrib.—France, Germany, Italy, Belgium; on *Tubercularia* and *Sclerotia*, and on branches of trees.)

Densely gregarious, forming a delicate film, white at first, then tinged rose- or salmon-colour. Distinguished from its allies by the large size of its conidia. Saccardo states that the present species grows on *Tubercularia* and on *Sclerotia*, and on branches of trees, but in this country it has been met with only on dung. (Smith's record (Trans. Brit. Myc. Soc. 1899–1900, p. 151) of the species occurring in Yorkshire 'on *Tubercularia* and *Sclerotia* on branches of trees' is an error, the substratum being Horse-dung.)

Sterigmatocystis dubia (Berk. and Br.), Sacc.

Hab.—On Mouse-dung, Kew, Aug. 1901.

Botrytis pilulifera, Sacc. (Fig. 120).

Botrytis pilulifera, Sacc., in Mich. ii, 122 (1880); Sacc. Fung. Ital. t. 695 (1881); Sacc. Syll. Fung. iv, 118 (1886).

Forming dense snow-white floccose tufts; sterile hyphae prostrate, branched, interwoven; fertile hyphae assurgent with simple or forked branchlets towards the apex, conidia globose hyaline, 18–24 μ, minutely verruculose at maturity.

Hab.—On Fowls' dung, Kew, Jan. 1901. (Distrib.—France, on Cats' dung.)

A very fine species, persistently snow-white, and scarcely agreeing in habit with the typical condition of *Botrytis*, differing in the very compact, interwoven sterile mycelium.

Botryosporium foecundissimum (Sacc. and March.) (Figs. 71–75).

Cladorhinum foecundissimum, Sacc. and March., in Bull. Soc. Roy. Bot. Belg. xxiv, pt. 1, 64, pl. 1, ff. 1, 2 (1885); Sacc. Syll. Fung. iv, 330 (1886).

Tufts at first white, then greyish, rather dense, sub-velvety; fertile hyphae creeping, repeatedly and intricately branched at right angles, 4–5 μ thick, closely septate; conidiophores short lateral patent, swollen at the apex into one or two minutely spinulose globose heads; conidia minute, crowded into a globose head, at once dispersing in water, globose, hyaline, 1·5–2 μ diam., springing from the minute spines on the swollen head of the conidiophore.

Hab.—On the dung of Giraffe (*Camelopardalis giraffa*), Kew, Feb. 1901. (Distrib.—Belgium, on the dung of Wild Boar.)

In the work cited above, Saccardo and Marchal founded the new genus *Cladorhinum* on the present species, which proves on careful examination to belong to the previously described genus *Botryosporium.* The mistake probably arose through examination of the material in water, in which medium the true conidia immediately fall away from the asperulate swollen apex of the conidiophore on which they are produced, and these one or two swollen portions of the conidiophores were, as is shown by the figures given by the authors, mistaken for the conidia of the Fungus.

Acrostalagmus cinnabarinus, Corda, Icon. Fung. ii, 15, f. 66 (1838); Sacc. Syll. Fung. iv, 163 (1886); Mass. Brit. Fung. Flor. iii, 331 (1893).

Hab.—On Pigeons' dung, Kew, Nov. 1900.

This beautiful Fungus, which forms effused patches of a deep reddish-orange or vermilion colour, is not uncommon on decaying vegetable matter, but has not been hitherto recorded as occurring on dung in this country.

Verticillium lateritium, Berk., in Cooke's Handb. 635 (1871); Sacc. Syll. Fung. iv, 156 (1886); Mass. Brit. Fung. Fl. iii, 330 (1893).

Hab.—On Hare- and Rabbit-dung, Kew, Dec. 1900 and Feb. 1901.

A common species forming dull orange or brick-red patches on various decaying vegetable substances, but not previously recorded as growing on dung.

Closely resembling *Acrostalagmus cinnabarinus*, Corda, in colour and in the verticillate arrangement of the branches, but readily distinguished by the minute conidia being solitary at the tips of the branchlets.

Rhopalomyces elegans, Corda; Sacc. Syll. Fung. iv, 50 (1889); Mass. Brit. Fung. Fl. iii, 291 (1893).

Hab.—On Hares' dung, Kew, April, 1901; on Cats' dung, and on earth intermixed, Kew, Aug. 1901.

This species appeared in profusion on the dung, after this had been kept for some weeks under a bell-jar. It has not been previously recorded on dung.

Aspergillus clavatus, Desmaz. (Fig. 104).

A. clavatus, Desmaz., in Ann. Sci. Nat. sér. ii, II, 71, pl. 2, f. 4 (1834); Sacc. Fung. Ital. t. 701 (1881); Sacc. Syll. Fung. iv, 67 (1886).

Sterile hyphae creeping, effused, dirty white; fertile hyphae aseptate, erect, 3–4 mill. high, firm, 34–40 μ wide, often attenuated towards the base, swollen at the apex into a clavate vesicle 250–350 μ long, 80–100 μ wide; head at first white, then becoming more or less glaucous, densely covered with conidia; conidia concatenate, minute, hyaline, elliptic with obtuse ends, 4–5 × 2–2·5 μ, borne on short simple distinct basidia.

Hab.—On cardboard among dung, Kew, Oct. 1901. (Distrib.—France, Italy, Belgium, N. America, on Fowl-dung and decaying substances.)

A well-marked species, easily recognized by its long clavate head and its very long firm aseptate conidiophore.

A. candidus, Link, in Willd. Gen. Pl., Fung. i, 65 (1824).

Hab.—On Bats' dung, Kew, Nov. 1900.

Not uncommon on decaying plant remains, &c., but not hitherto recorded on dung.

Arthrobotrys superba, Corda (Figs. 53, 54).

A. superba, Corda, Prachtfl. 43, pl. xxi (1839); Sacc. Syll. Fung. iv, 181 (1886).

A. oligospora, Fresen., Beitr. Mykologie, 8, Taf. 3, ff. 1–7 (1850–63).

Snow-white, glistening, densely gregarious and effused, or more or less scattered; fertile hyphae erect, up to 1 mill. high, simple, septate, smooth, 6–7 μ in diam., delicate, bearing in the upper part one to many (12–15) superposed whorls of conidia; conidia arising from minute blunt teeth on slight swellings of the conidiophore, crowded, one-septate, obovate or oblong, lower cell usually the smaller and terminating below in a minute point, 17–23 × 10–12 μ, smooth, hyaline.

Hab.—On dung of Goat, Kew, Mar. 1901; on Horse-dung, Epping Forest, Oct. 1901 (*A. oligospora*). (Distrib.—Germany, France, Italy, Belgium, on dung and damp or decaying substances, and on the earth amongst Fungi.)

A. superba is, as several mycologists have remarked, a very variable species. In its typical form, as it occurred with us on Goats' dung at Kew, and as is well shown in Corda's figures, the Fungus develops an effused growth of densely crowded erect fertile hyphae, which is snow-white and glistening with the crowded whorled conidia. In this form, the whorls of conidia, which may be as many as fifteen in number, are frequently so closely approximated as to appear almost continuous under a lens. The conidiophores are very delicate, and soon become flaccid and then collapse on being removed from the humid air in which the Fungus thrives. Intermixed with this luxuriant form—or more commonly preceding it on the same substratum—are found conidiophores which bear only a few whorls of conidia, or even only a single terminal whorl. This form, which is represented at Figs. 53, 54 of our Plate, was called *A. oligospora* by Fresenius, but Coemans (Bull. Soc. Roy. Bot. Belg. ii. 177 (1863)) is undoubtedly right in considering it merely 'une forme appauvrie' of *A. superba*. Fresenius, it may be noted, describes his *A. oligospora* as having usually only one terminal whorl, but states that occasionally several whorls (up to six) occur. Coemans, in the paper mentioned above, gives instances of the great variability of *A. superba*. Fine illustrations of the various forms of *A. oligospora* are given by Woronin (De Bary and Woronin, Beitr. z. Morph. u. Physiol. der Pilze, Bd. i, Reihe iii, Tab. vi, ff. 8–10, 16 (1870)). It may be noted that the present Fungus in its most reduced form, when it bears only a single terminal whorl of conidia, presents the characters of the genus *Cephalothecium*.

Trichothecium inaequale, sp. nov. (Fig. 61).

Late effusum humillimum subvelutinum album; hyphis fertilibus erectis parce vel haud septatis circ. 150 μ altis 4–5 μ crassis apice saepe noduloso-denticulatis; conidiis obovatis vel subpyriformibus apice rotundatis basi acutis vel plus minus minute apiculatis, septo excentrico, cellula superiore inferiore 4–5-plo longiore, ad septum haud constrictis, 24–30 × 15–20 μ.

Hab.—In fimo equino, Reigate, Nov. 1900; in fimo cuniculorum, Kew, Dec. 1900.

The present species forms a delicate effused bloom on dung, and is at once known by the very unequal size of the two cells of the conidium. It appears to be related to *T. piriferum* (Berk.), Sacc., from which it differs in its larger conidia. The conidiophores in *T. inaequale* are frequently somewhat nodulose towards the apex, and slightly denticulately branched; in this character the present species seems to resemble *T. griseum*, Speg.

DEMATIEAE.

Amerosporae. Trichosporium insigne, sp. nov. (Fig. 33).

Caespitulis minutis atris; hyphis vage ramosis intertextis septatis hyalinis 4–5 μ crassis, conidiis apice ramulorum oriundis perfecte globosis verrucosis ex hyalino aterrimis opacis 25–35 μ diam.

Hab.—On Pigeons' dung, Kew, Nov. 1900.

Allied to *S. sphaericum*, Sacc., from which the present species is distinguished by the hyaline hyphae and the larger warted conidia.

Trichocladium asperum, Harz (Fig. 69).

T. asperum, Harz, in Bull. Soc. Imp. Nat. Moscou, xliv, 125, Tab. 2, f. 1 (1871); Sacc. Syll. Fung. iv, 376 (1886).

Forming minute patches; mycelium creeping, colourless, sparsely septate, branched; conidiophores very short, suberect or decumbent, simple, each bearing a single conidium at the apex; conidia didymous, oblong, rounded at the apex, 18–22 × 12–13 μ, slightly constricted at the septum, cells about equal, or the lower one slightly smaller, when young colourless and smooth, becoming dark brown and subopaque, with the epispore of both cells covered with minute scattered warts.

Hab.—On Rabbit-dung, Kew, Jan. 1901. (Distrib.—Austria and Germany, on wood.)

The upper cell of the conidium, which is usually, at any rate in the young stage, the larger, becomes warted first. Harz (l. c.) suspects that the present Fungus may be the *Sporidesmium asperum* of Corda, Ic. Fung. ii, 6, Taf. 8, f. 27 (1838).

Cladosporium herbarum, Link; Sacc. Syll. Fung. iv, 350 (1886); Mass. Brit. Fung. Fl. iii, 394 (1893).

Hab.—On Goose-dung, Kew, Jan. 1901.

Marchal (in Bull. Soc. Roy. Bot. Belg., xxiv (1), 67 (1885)) makes a *forma fimicola* (raised to varietal rank by Saccardo in the 'Sylloge') of this species when growing on dung, but our specimens differed in no way from the type.

Dictyosporae. Sporodesmium piriforme, Corda (Fig. 52).

S. piriforme, Corda, Icon. Fung. i, 7, f. 116 (1837); Sacc. Syll. Fung. iv, 502 (1886); Mass. Brit. Fung. Fl. iii, 426 (1893).

Hab.—On Rabbit-dung, Mulgrave Woods, Yorks., Sept. 1900.

The conidia are variable in size and form, but always more or less piriform, and attached by a broad truncate base. There are usually three transverse septa, and at a later stage a few vertical septa appear. This species has only previously been recorded as occurring on rotten wood.

Stemphylium asperosporum, Cke. and Mass.; Sacc. Syll. Fung. x, 672 (1892); Mass. Brit. Fung. Fl. iii, 430 (1893).

Hab.—On the dung of Burrhel Wild Sheep (*Ovis burrhel*), Kew, Feb. 1901.

An interesting occurrence, as the species has hitherto been met with only on damp wall-paper.

HYALOSTILBEAE.

Amerosporae. **Stilbum erythrocephalum**, Ditm.

Hab.—On Hares' dung, Kew, June, 1901; on Sheep-dung, Kew, July, 1901.

Isaria sulphurea, Fiedl.

Hab.—On Birds' dung, Kew, Nov. 1901 and Jan. 1902.

PHAEOSTILBEAE.

Amerosporae. **Stysanus Stemonitis** (Pers.), Corda (*non* Karst.).

S. Stemonitis, Corda, Icon. Fung. i, 22, t. 6, f. 283 B (1837); Sacc. Fung. Ital. t. 945 (1881); Sacc. Syll. Fung. iv, 621 (1886); Mass. Brit. Fung. Fl. iii, 458, p. 397, f. 28 (1893).

Hab.—On the dung of Argali Sheep (*Ovis ammon*), Ural Wild Sheep (*O. vignei*), and Burrhel Wild Sheep (*O. burrhel*), Kew, Feb. 1901; on Pigeons' dung, Kew, Feb. 1901.

S. Stemonitis has not apparently been hitherto recorded on dung. The present species is not the *S. Stemonitis* of Karsten (Symb. Myc. Fenn. xix, 93 (1887)), which, according to the description given, is distinct in the slightly shorter, differently shaped, asperous spores. In *S. Stemonitis* (Pers.), Corda, the spores are quite smooth.

S. fimetarius (Karst.) (Fig. 62).

S. Stemonitis, Karst. (*non* Pers.), var. *fimetarius*, Karst., Symb. Myc. Fenn. xix, 93 (1887); Sacc. Syll. Fung. x, 697 (1892).

Stems scattered or more or less densely gregarious, simple or variously branched, 1–1½ mill. high, straight or slightly flexuose, head subcylindrical or lanceolate, at first pale, becoming dark; conidia in long chains, ovoid to broadly ovoid, subverruculose, $6–7 \times 4–4{\cdot}5\,\mu$.

Hab.—On the dung of Sinaitic Ibex (*Capra sinaitica*) and Common Camel, Kew, Feb. 1901. (Distrib.—Finland, on dung of Field-mouse.)

The differently shaped spores, furnished with distinct warts, appear important enough characters to separate the above specifically from *S. Stemonitis* (Pers.), Corda. As mentioned above, Karsten's '*S. Stemonitis*,' under which the present plant was originally described as a variety, is not Persoon's species as described by Corda and other authors. The spores of *S. fimetarius* under a high magnification are seen to bear short raised lines or ribs, which give them a warted appearance.

TUBERCULARIEAE.

Amerosporae. Chaetostroma, Corda, in Sturm's Deutschl. Fl., i, 122 (1829); Sacc. Syll. Fung. iv, 749 (1886).

Sporodochium discoid or pulvinate, becoming black, with a marginal fringe of long, dark-coloured setae; conidiophores filiform, simple, closely crowded side by side; conidia elliptical or subglobose, continuous, coloured, solitary and acrogenous.

The present genus is very closely allied, morphologically, to *Volutella*, Tode, differing only in the blackish colour of every part. The last-named genus in turn is scarcely distinct from *Vermicularia*, Fries, in which the most highly organized species have a distinct peridium covered with bristles and furnished with a definite opening or ostiolum at the apex, through which the conidia escape at maturity. From this type there is a gradual reduction of the wall of the peridium through several species, until finally the peridium is reduced to a mere spinose rim surrounding the fertile disc as in *Chaetostroma*, from which such species of *Vermicularia* differ only in the colourless conidia. It is to be noted, also, that the reduced type of *Vermicularia* just described only differs from typical species of *Volutella* in having the spines black instead of colourless.

C. fimicolum, sp. nov. (Figs. 67–68).

Sporodochiis gregariis superficialibus discoideis planis primo pallidis dein atris, setulis inaequalibus 300–400 × 9–12 μ sursum attenuatis septatis caeruleo-nigris dense vestitis; conidiophoris filiformibus dense confertis pallidis 40 × 3 μ; conidiis acrogenis ellipsoideis continuis olivaceis 5–6 × 2·5–3 μ.

Hab.—In fimo cuniculorum, Reigate, England, Nov. 1900.

An interesting species, most nearly allied to *C. atrum*, Sacc., from which it differs in the smaller spores and the much longer and more numerous marginal setae.

Volutella ciliata, Fr.; Sacc. Syll. Fung. iv, 682 (1886); Mass. Brit. Fung. Fl. iii, 473 (1893).

Hab.—On Hares' dung, Kew, Mar. 1891.

This species, which does not appear to have hitherto been noticed on dung, appeared in some profusion on Hares' dung after it had been kept for some weeks under a bell-jar.

Graphium Comatrichoides, sp. nov. (Figs. 89–91).

Caespitosum, 1–1½ mill. altum, totum aterrimum; stipitibus gracilibus filiformibus erectis basi circ. 20 μ crassis sursum vix attenuatis ex hyphis fuligineis fasciculatis compositis, apice penicillato-expansis, capitulo globoso majusculo primum muco obvoluto, conidiis in hypharum apice pallidiore insertis numerosissimis hyalinis oblongis utrinque obtusis circ. 7 × 2·5 μ.

Hab.—In fimo *Lamae guanaco* (Llama), Kew, Oct. 1901.

In habit agreeing with *G. stilboideum*, Corda (Ic. Fung. ii, f. 69; Sacc. Fung. Ital. Tab. 14), but differing in the black capitulum. The present species much resembles in general appearance species of *Comatricha* in an immature condition.

G. stercorarium, March. (Figs. 124–126).

G. stercorarium, March., in Bull. Soc. Roy. Bot. Belg. xxxiv, 143, pl. 1, f. 5 (1895); Sacc. Syll. Fung. xiv, 1111 (1900).

Gregarious, stems rigid, erect, about 30 μ in diam., ½–1 mill. high, blackish, paler towards apex, surmounted by a subglobose head; conidia very numerous, hyaline, oblong to subcylindrical, rounded at both ends, 8 × 3 μ.

Hab.—On dung of Monkey, Gold Coast, Africa (W. H. Johnston, Oct. 1901). (Distrib.—Belgium; on dung of Hare and Goose, and on cloth covered with dung.)

Examples of this *Graphium* in a dried condition occurred on some Monkeys' dung sent by Mr. W. H. Johnston from the Gold Coast; and the species afterwards appeared in great plenty at Kew on the same dung after it had been kept damp for a week or two. The above description, which agrees in all essential points with that given by Marchal (l. c.), was drawn up from the living Kew examples.

G. subulatum, Sacc., Syll. Fung. iv, 612 (1886); Mass. Brit. Fung. Fl. iii, 455 (1893).

Hab.—On Birds' dung, Kew, Jan. 1901.

Not hitherto recorded on dung.

Didymosporae. Gymnodochium, gen. nov.

Sporodochia subglobosa vel irregularia, superficialia, convexa, nuda, i. e. setis destituta; conidiis catenulatis 1-septatis hyalinis in conidiophoris distinctis acrogenis.—Genus *Endodesmiae* inter *Tubercularieas mucedineas* sectionis *Didymosporae* solum comparandum; ab hoc setarum defectu longe recedens.

G. fimicolum, sp. nov. (Figs. 49–51).

Sporodochiis minutis subglobosis vel irregularibus sparsis vel subgregariis albis; conidiophoris distinctis cylindricis septatis circ. 30 × 3·5 μ; conidiis in catenulis longis flexuosis ordinatis, ellipsoideis, didymis, medio vix vel non constrictis, hyalinis, laevibus, 9–10 × 4·5–5 μ.

Hab.—In fimo *Ovis vignei* (Ural Wild Sheep), Kew, Feb. 1901.

The conidia are borne—fifteen or more in a chain—at the apex of cylindrical conidiophores, which remain for some distance distinct from one another, until they merge into the tissue of the sporodochium. The spores, as they arrive at maturity and fall off the ends of the chains, are slightly pointed at one end, and minutely truncate at the other.

Myxomyceteae. Dictyostelium mucoroides, Brefeld, in Abhandl. d. Senckenb. Naturf.-Gesellsch. vii, 1–21, Taf. 1–3 (in sep.) (1869); Sacc. Syll. Fung. vii, 452 (1888); A. L. Smith in Trans. Brit. Myc. Soc. 1898–99, p. 114.

Hab.—On Hares' dung, Kew, March, 1901; on dung of Rabbit, Epping Forest, Oct. 1901.

Smith (l. c.) has already recorded the occurrence of this species in Britain; it is remarked there that the Fungus 'can only be seen under the microscope'; in our specimens, however, the plants were clearly visible to the naked eye, the stalks being 1 mm. high.

Arcyria albida, Pers.

Hab.—On dung of the Flying-fox (*Pteropus medium*, Temm.), Calcutta, India (I. H. Burkill, Aug. and Sept. 1901).

Exactly agreeing with European examples of the species. Mr. I. H. Burkill supplied us with the following notes: 'The dung on which this Fungus grew is that of *Pteropus medius*, Temm., the Indian fruit Bat, or Flying-fox. The dung was deposited about August 1. At this time the Jamun tree (*Eugenia Jambolana*) was in ripe fruit, and this forms the favourite food of the Bat; the faeces were composed of it alone. The dung was placed in water under a glass. The Fungus was gathered on Aug. 24. On Sept. 10 there was a fresh crop of the Fungus on the surface of the "broth" (i.e. the water in which the dung had been standing), and two *Eugenia* seeds had germinated. There is little doubt that the medium of the Fungus was the fleshy part of the fruit half-digested by the Bat.'

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EXPLANATION OF FIGURES IN PLATES IV AND V.

Illustrating Messrs. Massee and Salmon's paper on Coprophilous Fungi.

Figs. 1–5. *Magnusia nitida,* Sacc.; Fig. 1, perithecium, × 52; Fig. 2, cells of outer wall of perithecium, × 400; Fig. 3, apex of an appendage, × 400; Fig. 4, asci and spores, immature, × 400; Fig. 5, ripe ascus and spores, × 400.

Figs. 6, 7. *Chaetomium bostrychoides,* Zopf; Fig. 6, perithecium, × 45, ascus and spores, × 400; Fig. 7, a terminal appendage, × 400.

Figs. 8, 9. *C. simile,* sp. nov.; Fig. 8, perithecium, × 52, ascus and spores, × 400; Fig. 9, apex of two terminal appendages, × 255.

Fig. 10. *C. crispatum,* Fckl.; apex of a terminal appendage, × 255, and two ascospores, × 400 (from Fckl. Fung. Rhen. nr. 2022).

Figs. 11, 12. *Arachniotus candidus,* Schroet.; Fig. 11, hyphae and groups of ascospores, × 400; Fig. 12, ascus, × 670; ascospores, × 1000.

Figs. 13–17. *Ascodesmis Volutelloides,* sp. nov.; Figs. 13, 14, two ascophores, × 95; Fig. 15, one of the seta-like hairs from same, × 400; Fig. 16, asci and spores, × 400; Fig. 17, spore, × 670.

Figs. 18–22. *Gymnoascus setosus,* Eidam; Fig. 18, part of vegetative mycelium, showing spine-like branches and branchlets, × 400; Fig. 19, single spine-like branch with branchlets, × 400; Fig. 20, ditto, with whorled branchlets, × 1000; Fig. 21, spores, × 400; and ascus and spores, × 670; Fig. 22, two asci and spores, × 1000.

Figs. 23–26. *Syncephalis intermedia,* van Tiegh.; Fig. 23, conidiophore and conidia, × 25; Fig. 24, apex of conidiophore, showing swollen vesicle, which is covered in its upper half with warts, from each of which basidial cells bearing chains of conidia arise, × 150; Fig. 25, basidial cell (basal) with portions of two chains of conidia, × 400; Fig. 26, four basidial cells, showing variation in shape, × 400.

Figs. 27, 28. *Anixiopsis stercoraria,* Hans.; Fig. 27, portion of wall of perithecium, × 400; Fig. 28, asci and free ascospores, × 400 and 670.

Figs. 29–32. *Nectria ornata,* sp. nov.; Fig. 29, ascophore, × 40; Fig. 30, structure of one of the scales from surface of ascophore, × 400; Fig. 31, ascus, × 400; Fig. 32, free ascospores, × 400.

Fig. 33. *Trichosporium insigne,* sp. nov.; fertile hypha with conidia, × 400.

Fig. 34. *Cephalosporium succineum,* sp. nov.; two conidiophores with conidia, × 750.

Figs. 35–37. '*Myxotrichum coprogenum,* Sacc.' (*Gymnoascus Reessii,* Baran.); Figs. 35, 36, branched hyphae and ascospores, from the specimen in Saccardo's herbarium labelled '*M. coprogenum* typicum,' × 400; Fig. 37, spores from the specimen labelled '*f. malaccense,*' × 400.

Figs. 38–43. *Sphaeronaemella fimicola,* March.; Fig. 38, perithecium showing the long subulate beak surmounted at the apex by a mucilaginous drop, containing the ejected spores, × 95; Fig. 39, a perithecium with two beaks, × 95; Fig. 40, apex of beak, showing the penicillate mouth, × 400; Fig. 41, spores, × 400; Fig. 42, spores, × 670; Fig. 43, cells of outer wall of perithecium, × 400.

Figs. 44–46. *Sordaria neglecta,* Hans.; Fig. 44, a perithecium enveloped up to the papilliform neck in white floccose mycelium, × 20; Fig. 45, groups of perithecia, nat. size; Fig. 46, spore, × 400.

Figs. 47, 48. *S. neglecta,* Hans.; *small form* (see p. 74); Fig. 47, perithecium, × 25; Fig. 48, spore, × 400.

Figs. 49–51. *Gymnodochium fimicolum,* gen. nov. sp. nov.; Fig. 49, sporodochium, × 95; Fig. 50, two spores, × 670; Fig. 51, conidiophore with its chain of spores, × 400.

Fig. 52. *Sporodesmium piriforme,* Corda; two conidia, × 400.

Figs. 53, 54. *Arthrobotrys superba,* Corda, reduced form; conidiophore and conidia, × 500.

Figs. 55–60. *Arachnomyces sulphureus,* gen. nov. sp. nov.; Fig. 55, perithecium with appendages, × 25; Fig. 56, cells of wall of perithecium, × 400; Figs. 57, 58, apex of two appendages, × 255; Fig. 59, ascus and spores, × 400; Fig. 60, ditto, × 670.

Fig. 61. *Trichothecium inaequale,* sp. nov.; conidiophore and conidia, × 400.

Fig. 62. *Stysanus fimetarius* (Karst.); sporodochium, × 80; conidiophore and conidia, × 400; two conidia, × 1000.

Figs. 63–66. *Myxotrichum spinosum,* sp. nov.; Fig. 63, entire Fungus, × 75; Fig. 64, sterile hyphae forming peripheral network, with radiating spines, × 400; Fig. 65, ascus and free ascospores, × 400; Fig. 66, ditto, × 1000.

Figs. 67, 68. *Chaetostroma fimicolum,* sp. nov.; Fig. 67, sporodochium, × 40; Fig. 68, marginal seta and conidiophores with conidia, × 400.

Fig. 69. *Trichocladium asperum,* Harz; conidiophore and conidia, × 400.

Fig. 70. *Sepedonium niveum,* sp. nov.; fertile hypha with conidia, × 400.

Figs. 71–75. *Botryosporium foecundissimum* (Sacc. and March.); Fig. 71, portion of fertile hypha, × 400; Fig. 72, head of conidia and free conidia, × 400; Fig. 73, head of conidia, × 1800; Fig. 74, conidiophore showing two subglobose asperulate heads at its apex, from which the conidia originate, × 1800; Fig. 75, conidiophore with a single globose head at its apex, × 1800.

Figs. 76–79. *Myxotrichum aeruginosum,* Mont.; Fig. 76, entire Fungus, × 75; Fig. 77, ascus and free spores, × 400; Fig. 78, ditto, × 1000; Fig. 79, portion of peripheral network of sterile hyphae with radiating spines, × 400.

Figs. 80–82. *M. deflexum,* Berk.; Fig. 80, portion of sterile indurated hyphal covering, × 400; Fig. 81, asci and free spores, × 400; Fig. 82, spores, × 1000.

Figs. 83–85. *Oedocephalum ochraceum,* sp. nov.; Fig. 83, Fungus on Rabbit-dung, nat. size; Fig. 84, two conidiophores, × 400; Fig. 85, free conidia, × 400.

Figs. 86–88. *Arachniotus citrinus,* sp. nov.; Fig. 86, showing pulvinate habit of the Fungus, × 25; Fig. 87, ascus with spores, and sterile hypha, × 800; Fig. 88, ascospores, seen from the front and side, × 1000.

Figs. 89–91. *Graphium Comatrichoides,* sp. nov.; Fig. 89, conidiophore, × 40; Fig. 90, apex of same, × 95; Fig. 91, conidia, × 400.

Fig. 92. *Acremonium fimicolum,* sp. nov.; portion of fertile hypha, × 400.

Figs. 93–96. *Mucor racemosus,* Fresen.; Fig. 93, terminal portion of a sporangiophore, showing group of sporangia, × 50; Fig. 94, basal portion of a sporangium, showing the columella, × 400; Fig. 95, spores, × 400; Fig. 96, portion of a hypha from the substratum, showing interstitial chlamydospores, × 500.

Figs. 97–103. *Chaetomium arachnoides*, sp. nov.; Fig. 97, perithecium at a very young stage (magnified); Fig. 98, Fungus at maturity, consisting of mass of free ascospores and the upper portion of the perithecial wall bearing the appendages, × 10; Fig. 99, portion of wall of upper part of perithecium, × 400; Fig. 100, bent apex of one of the appendages, × 400; Fig. 101, apices of two appendages, × 400; Fig. 102, portion of an appendage in its lower half, × 400; Fig. 103, ascus and free ascospores, × 400.

Fig. 104. *Aspergillus clavatus*, Desmaz.; conidiophore, × 40; conidia, × 400.

Figs. 105–108. *Helicostylum piriforme*, Bain.; Fig. 105, sporangiophore, with whorled clusters of sporangiola, × 95; Fig. 106, ripe sporangiolum and spores, × 400; Fig. 107, young sporangiolum, × 400; Fig. 108, part of a sporangiophore, showing the mode of branching (from Bainier) (magnified).

Figs. 109–112. *Circinella umbellata*, van Tiegh. and Le Monnier; Fig. 109, three plants, nat. size; Fig. 110, portion of a sporangiophore, with a group of young sporangiola, × 120; Fig. 111, ripe sporangiolum, burst and showing the columella, × 400; Fig. 112, spores, × 400.

Figs. 113–118. *Myxotrichum Johnstoni*, sp. nov.; Fig. 113, Fungus on Rat-dung, nat. size; Fig. 114, three tufts, showing pulvinate habit of the Fungus (magnified); Fig. 115, part of network of sterile hyphae, showing free ends, × 400; Figs. 116, 117, two of the long delicate, flexuous branches, or appendages, × 400; Fig. 118, ascus and free ascospores, some of the latter seen from the front, others from the side, × 400.

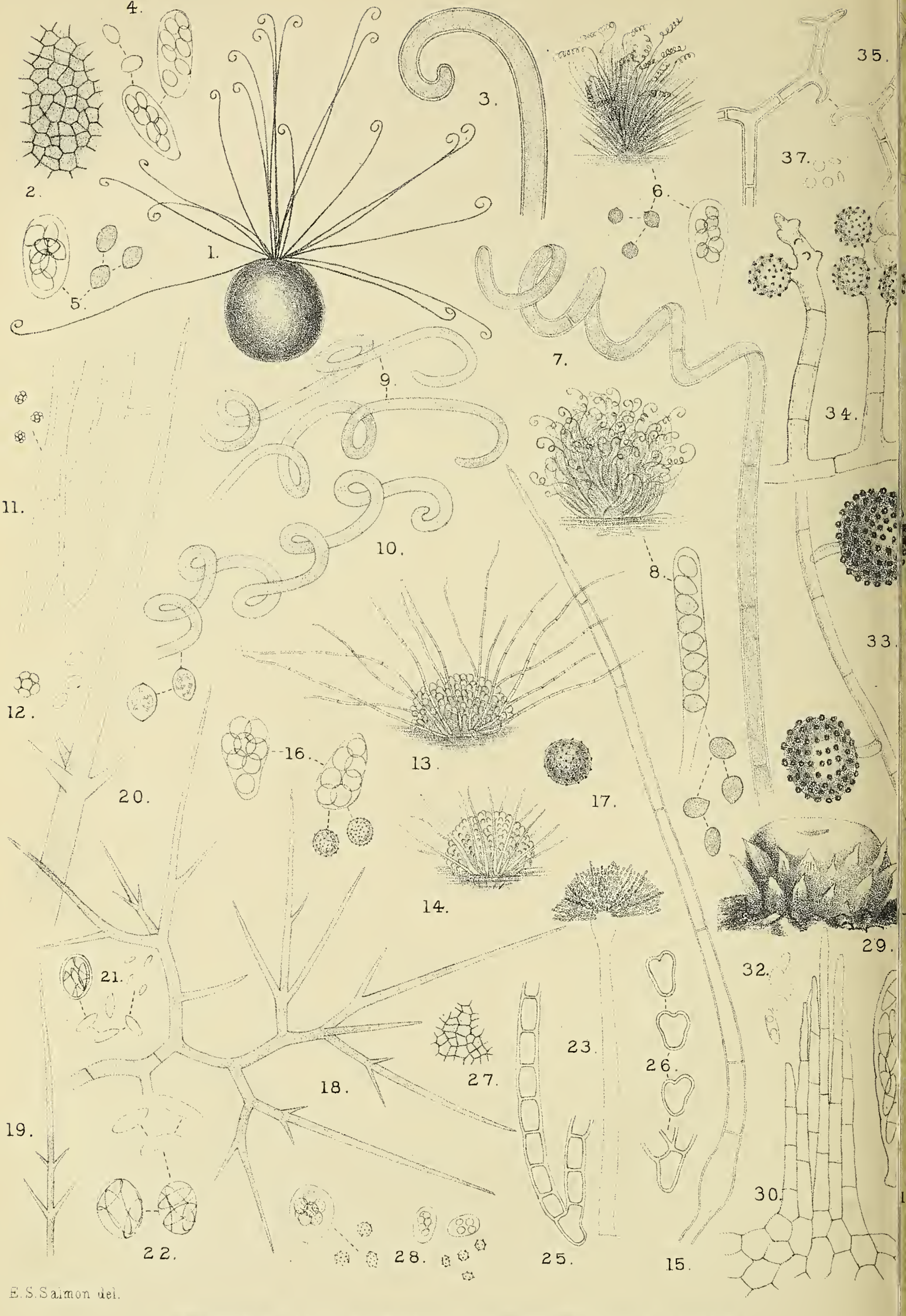
Fig. 119. *Oedocephalum glomerulosum*, Sacc.; conidiophore and conidia, × 400.

Fig. 120. *Botrytis pilulifera*, Sacc.; end of a fertile hypha, × 500.

Figs. 121–123. *Poronia leporina*, Ell. and Everh.; Fig. 121, vertical section of stroma (slightly magnified); Figs. 122, 123, ascus and ascospores, × 400.

Figs. 124–126. *Graphium stercorarium*, March.; Fig. 124, conidiophore, × 95; Fig. 125, apex of same, × 400; Fig. 126, conidia, × 400.

Figs. 127–131. *Arachnomyces nitidus*, sp. nov.; Fig. 127, perithecium with appendages, × 25; Fig. 128, portion of wall of perithecium, × 400; Fig. 129, circinate apex of one of the appendages, × 400; Fig. 130, portion of an appendage in its lower half, × 400; Fig. 131, ascus and free ascospores, × 400.



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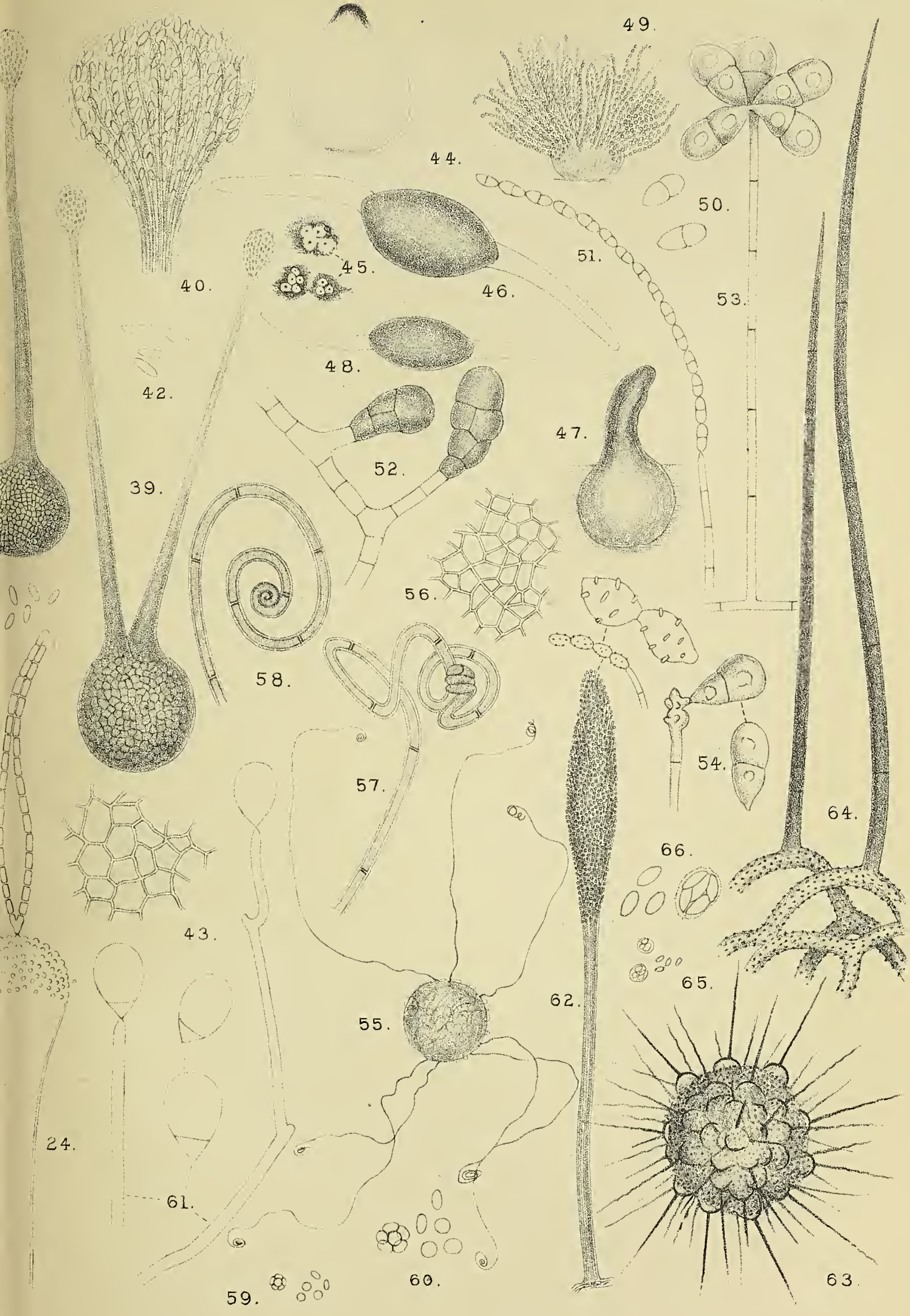

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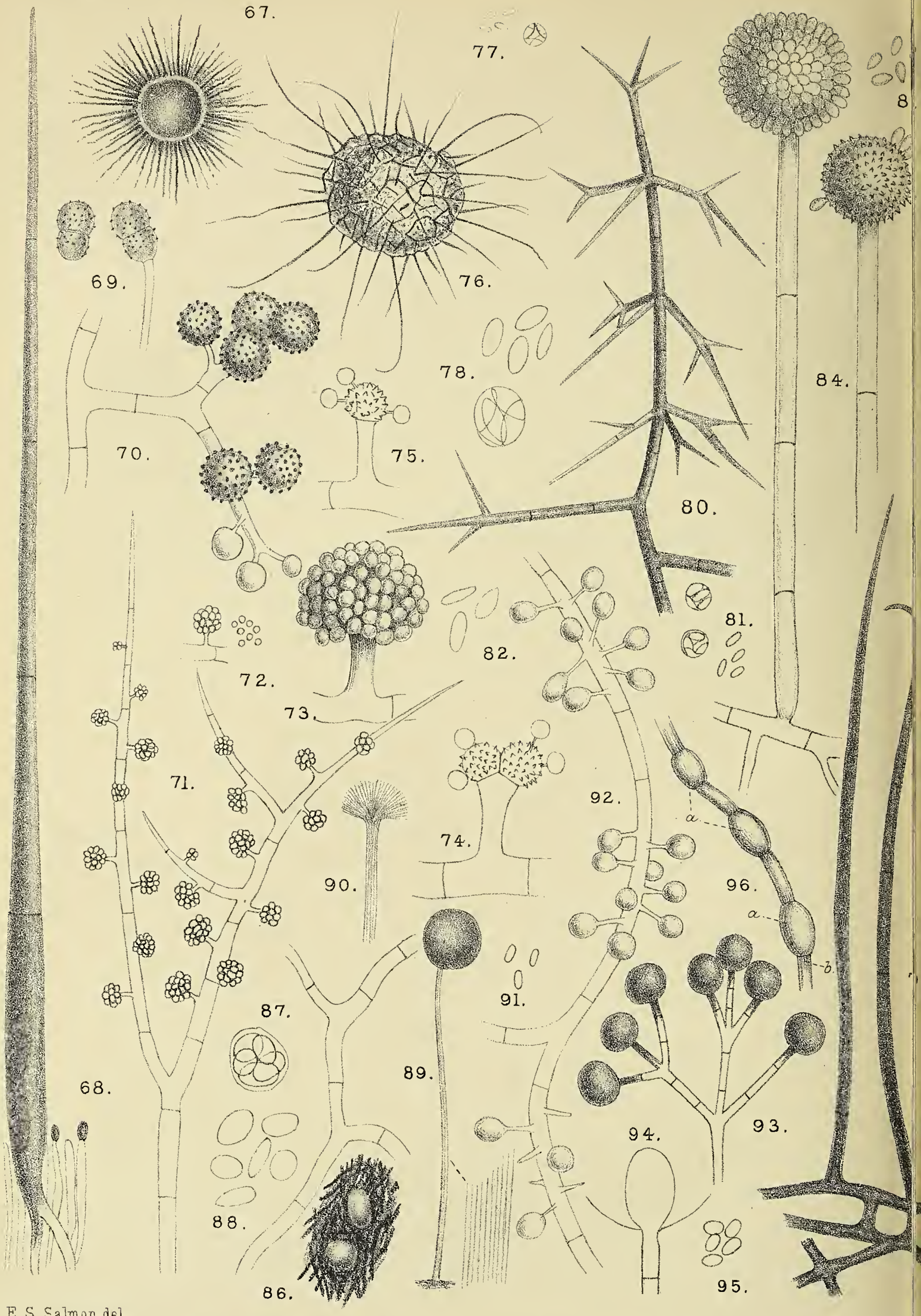

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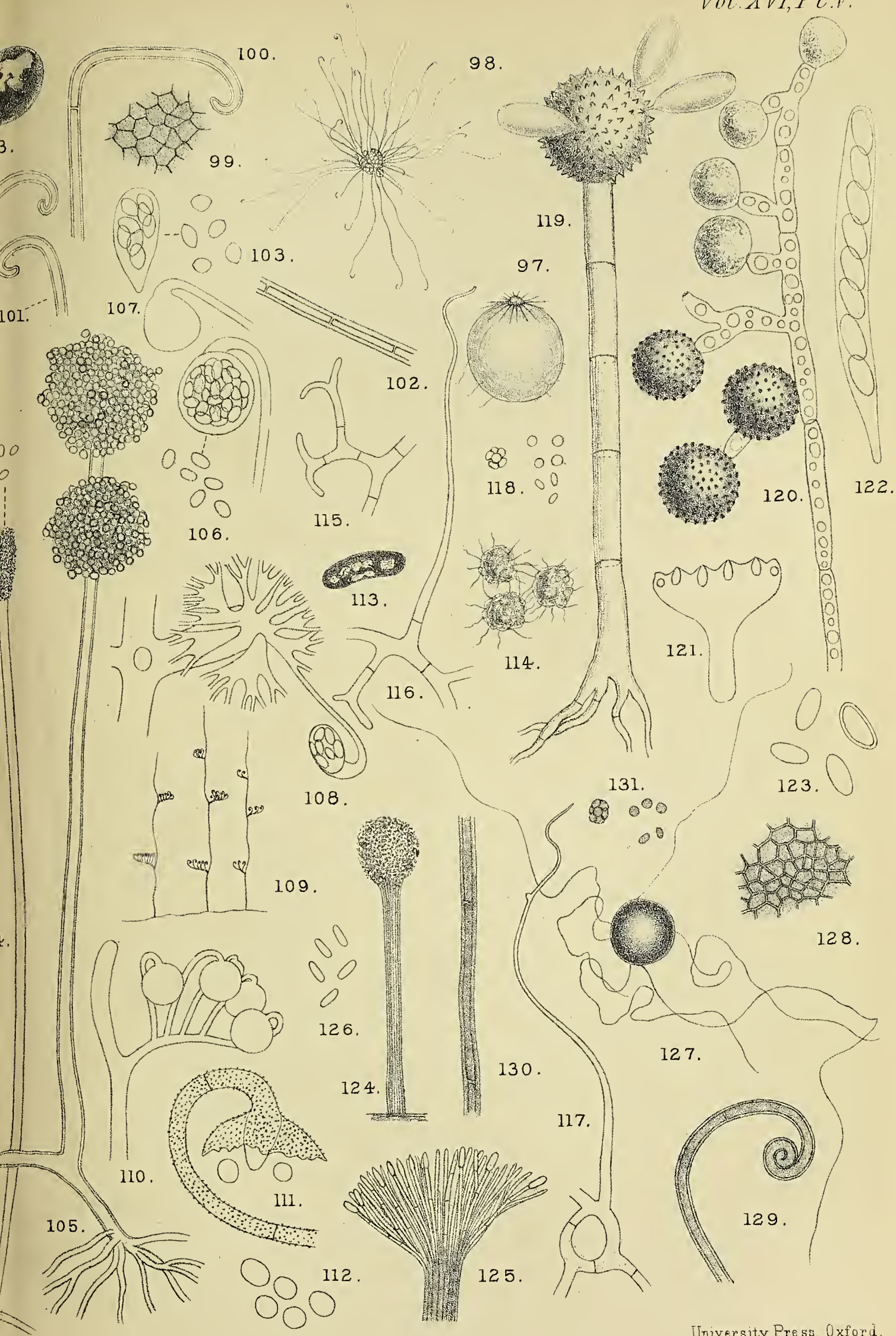

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The Anatomy of Ceratopteris thalictroides, (L.)

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With Plate VI, and eight Figures in the Text.

CERATOPTERIS thalictroides has been known in the past by several other names. The name *Ceratopteris* itself, however, has according to Hooker[1] priority over the rest, having been given to the plant by Brongniart[2] in 1821. Before this date it had been termed *Pteris thalictroides* by Linnaeus[3], and amongst other names Hooker mentions the following: *Teleozoma* by Brown in 1823, *Pteris cornuta* by Beauvois in 1825, and *Ellobocarpus oleraceus* by Kaulfuss in 1824.

The Parkeriaceae are generally regarded as a sub-order of the Polypodiaceae, though some botanists raise them to the rank of a distinct order. The Parkeriaceae contain the single genus *Ceratopteris*, though at one time a second genus, *Parkeria*, was included in it, and in Hooker's[4] 'Genera Filicum' published in 1842, two separate coloured plates are found representing two almost similar Ferns, viz. *Ceratopteris thalic-*

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[1] Hooker, W. J., 1858, p. 234.

[2] Brongniart, 1821, p. 184.

[3] Linnaeus, 1757, p. 1527.

[4] Hooker, 1838, pp. 12 and 50.

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troides and *Parkeria pteroides*. The name *Parkeria* was given by Hooker and Greville[1] to a Fern in 1824, at a time when very little was known of the genus *Ceratopteris*. The plant examined by Hooker and Greville was characterized by the reduction or complete absence of the annulus on the sporangium, and this feature, together with the fact that the Fern which had been named *Ceratopteris* three years before was practically unknown to them, induced the investigators to create a new genus *Parkeria*. In Hooker's 'Species Filicum,' however, published in 1858[2], the genus *Parkeria* is omitted, and the author states in a note at some length, that since the publication of the 'Genera Filicum' he has modified his former views, a detailed comparison of the two Ferns having shown him conclusively that they must be regarded as belonging to the same genus, and must for the future be included under the single genus *Ceratopteris*.

Ceratopteris thalictroides is an annual aquatic Fern, which is found growing in the Tropics in marshes, pools, and running streams. In shallow water the plant roots in the mud at the bottom; in deeper water, however, it is found floating freely. In some rivers it is reported as being exceedingly abundant, almost blocking up the stream with its growth. The plant has a wide geographical distribution, being found practically in all tropical regions of the globe. It has been reported from Mexico and southwards as far as Brazil, from the West Indies, the West Coast of tropical Africa and Madagascar, and from the Punjaub southwards to tropical Australia. In the Indian Archipelago the plant is cooked and eaten by the natives as a vegetable.

I. EXTERNAL MORPHOLOGY.

Owing to the great reduction of the stem, the most noticeable part of the mature plant lies in the leaves. These are of two kinds, the sterile and the fertile, the latter bearing on their under-side numerous scattered sporangia. Hooker, in

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[1] Hooker and Greville, 1824.

[2] Hooker, 1858, p. 236.

his 'Species Filicum [1],' describes the sterile leaves as being simple or more or less divided when young, the older ones being bi-tripinnate and much dissected. All the first leaves which are borne by a young *Ceratopteris* plant are sterile, the fertile leaves do not arise until much later. The leaves on a young plant have been described and figured by Kny [2], the first being simple and spatulate in shape, whilst somewhat older ones are irregularly trilobed. At a later stage the first compound sterile leaves are found (Pl. VI, Fig. 1). The individual leaflets, which vary in number from three upwards, are sessile on each side of the main rachis, and are themselves irregularly trilobed. The fertile leaves arise at a much later stage than the sterile, but both kinds are present at the same time. The fertile leaves are generally taller than the sterile, their lamina is reduced, the leaves being much dissected with narrow linear segments. The sporangia are scattered singly on the under surface, and are never united into sori. No true indusium is present, but the edges of the leaves curve over and enclose the sporangia, forming a false indusium. The sporangia are spherical with a short stalk, and are always situated over a vein.

Large numbers of vegetative buds are found occurring on the sterile as well as on the fertile leaves. These buds arise at the angles of the leaf-segments, and sometimes grow to a considerable size before becoming detached from the parent plant. In some material from the Botanical Gardens at Cambridge, vigorous young plants of *Ceratopteris* with several well-developed leaves were found still attached to a dead and blackened leaf of the original parent plant (Fig. 2). These vegetative buds are found on the sterile leaves of quite young and immature plants; on one measuring 3–4 inches in height three were counted on a single leaf.

The leaves of a mature *Ceratopteris* plant are furnished with stout petioles, which surround and often completely hide the reduced and, comparatively speaking, insignificant stem. In looking at a plant from below, a curious tri-radiate arrange-

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[1] Hooker, 1858, p. 235.

[2] Kny, 1875, pp. 42 and 43.

ment is seen (Fig. 3). The leaves seem to come off in whorls of three, but sections of the stem show that the leaves in question do not issue at the same level, the somewhat deceptive whorled appearance being due to the reduction of the stem and the consequent crowding together of the leaves with very small internodes. In a mature specimen the petioles at first run horizontally for a distance of about 1–2 inches after leaving the stem. They then bend upwards through an angle of 90° and stand erect round the stem in the centre, resembling in a curious manner a number of pillars ranged concentrically round a central axis.

The outline of the petioles varies with the age of the plant. In young specimens it is triangular, with a vascular bundle at each angle. Later the outline becomes circular, and in the mature plant it is convex on the outer side, i. e. on the side turned away from the stem, whilst the inner side is flattened. The main mass of the tissue of which the petioles are composed consists of spongy parenchyma with large air-spaces, and in this parenchyma the vascular bundles lie embedded and stand out as conspicuous dark lines on the sides of the petioles (Fig. 3). The young leaves are all circinately coiled, and are covered, together with the stem apex, with numerous ramental scales. These scales are very scarious in texture.

The roots in the mature plant arise from the base of the petioles, and are given off as a fringe just above that region where the upward bend occurs, which has been already described, when the petiole, from running horizontally, turns upwards and becomes erect.

In the mature plant the roots seem to be confined to the convex outer side of the petiole. In younger plants, however, which possess only sterile leaves, petioles are found furnished with a fringe of roots extending all round the circumference; whether this is the case in all petioles and only those roots on the side turned away from the stem finally persist, the rest dying off at an early age, I have been unable to determine, though this seems very probably to be the case.

The first roots which are formed in a young plant do not arise from the base of the petioles, but directly from the stem; their connexion with the latter will, however, be dealt with later.

Goebel[1], in his 'Biologische Schilderungen,' has given a short account of the differences which he observed between the young floating and the young rooted plants of *Ceratopteris*. He found young swimming plants in British Guiana, and these, he states, were very different in appearance from the young plants which, instead of floating freely in the water, were rooted in the mud. The leaves of the young swimming plant are, according to his observations, very broad and are spread out on the top of the water. The petioles of the fertile leaves are, moreover, much swollen at their bases. The roots are well developed, but instead of acting as fixing organs they hang down freely into the water in a tuft-like manner. I have been unable to investigate any plants of *Ceratopteris* which show these features, for I have only been able to examine young and mature specimens in which the roots are used as organs of fixation. I cannot therefore say whether the differences of appearance between these two forms of *Ceratopteris*, which have been described by Goebel, are accompanied by any marked differences in regard to histological and other details.

II. ANATOMY.

A. Leaf.

1. *Petiole*. In his paper on 'Die Blattstiele der Farne,' Thomae[2] gives a description and figure of a petiole and of a single vascular bundle of *Ceratopteris thalictroides*. In regard to the number and position of the vascular bundles in a section taken through a whole petiole, Thomae states that two rows are present. The upper row, i. e. that on the flattened side turned towards the stem, consists of a single large bundle in the centre, with two or three smaller bundles

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[1] Goebel, vol. ii, p. 281.

[2] Thomae, 1886, p. 151.

lying on each side of it. On the under or convex side four or five bundles only are present. In Engler and Prantl's 'Pflanzenfamilien[1]' it is stated that the number of bundles present in the petiole of *Ceratopteris* varies considerably with its age and development. In a mature plant two concentric rings of bundles are present, an inner and an outer, each ring containing from one or two up to forty steles. In young and immature petioles a single ring (the outermost) may alone be present, and the numbers may be as low as four or five. I have examined a large number of petioles of all ages, and I have always found the arrangement of the bundles to be in accordance with the description given by Engler and Prantl. Even in small petioles, measuring only 2–3 mm. in diameter, I have found a fairly regular ring of bundles towards the periphery, whilst only one or two, sometimes none at all, of the inner ring are present. The single large median bundle described by Thomae is certainly not a constant feature. It is true that at some levels bundles larger than the rest are found, but these may occur in *any* position in the outer ring, and are only found when a bundle is about to divide. Sections taken a few millimetres above and below the level of such a bundle show either two strands instead of one or a single strand of ordinary size. I cannot help thinking, therefore, that Thomae has taken a petiole in which there has been, by chance, a single median bundle about to divide in this way, and lying towards the upper side, and has described this arrangement as being constant and typical of all *Ceratopteris* leaf-stalks.

Secondly, in regard to the structure of individual bundles: Thomae states that they are all collateral, but in the majority of the bundles that I have examined the arrangement is markedly bicollateral, sieve-tubes being well developed on both sides of the xylem. In the bundles forming the inner ring, and in any immature vascular strand, it is often difficult to state definitely whether the arrangement is concentric or bicollateral, for it is not easy to distinguish between the

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[1] Engler and Prantl, 1900, p. 341.

imperfectly differentiated sieve-tubes on the one hand and ordinary parenchymatous cells on the other.

In the mature steles, the sieve-tubes in transverse sections are unmistakable, for they are large elements, and have characteristic granules adhering to their walls. Each bundle (Fig. 4) is surrounded by a ring of brown thick-walled cells (Fig. 4, *scl*). The walls of those cells which lie immediately next to the bundle are fairly thick, but in the cells of the succeeding layers the thickening becomes less until the tissue gradually merges into the surrounding parenchyma. The endodermis (*e*) is easily distinguished by the thickening of the radial walls. This thickening of the radial endodermal walls is a very constant feature in *Ceratopteris*, for it is found in the bundles of the stem, roots, and leaves of young, as well as of mature, plants.

Within the endodermis a single layer of cells is found (Fig. 4, *pe*), the individual cells of which are large and are superposed with great regularity on those of the endodermis, the radial walls of the two layers being in direct continuation with each other. This arrangement, which is not an uncommon one in other Ferns, e. g. in *Loxsoma*[1], is found in a large number of the bundles of *Ceratopteris*. I have been unable to determine definitely whether this relation between the endodermis and the pericycle is due to the fact that they have had a common origin, though this seems highly probable. If this be the case, then the inner layer must be regarded as a false and not as a true pericycle.

The xylem occupies the centre of the bundle and consists of a group of scalariform tracheids, the number varying with the age and size of the bundle. In the larger steles small areas of parenchymatous cells are found scattered among the tracheids; in the smaller bundles these are absent. The protoxylem consists of a small group of spirally thickened elements. In some of the smaller bundles, and especially in those in a young plant where the individual elements are very small, it is often almost impossible to make out the proto-

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[1] Gwynne-Vaughan, 1901, p. 78.

xylem. When present it is in a more or less median position, and on the outer edge of the xylem. In a few cases, but these are very rare, the xylem seems to touch the pericycle directly; as a general rule small parenchymatous cells are interposed between the two tissues.

Scattered parenchymatous cells are also found lying round the tracheids between these elements and the sieve-tubes (Fig. 4, *pa*). On the side of the xylem which is away from the protoxylem, and on this side only, Thomae has figured and described the sieve-tube zone. Beyond this again, and between this zone and the pericycle, he has figured a layer of protophloem-elements, though he has not described them in his account of *Ceratopteris*. He does however mention and describe protophloem-elements in his general description of the vascular elements in the petioles of Ferns. This layer of protophloem he figures as being made up of conspicuous thick-walled elements, and the sieve-tubes in his drawing also give one the impression of being thick-walled. The sieve-tubes are however essentially large thin-walled elements (Fig. 4, *st*) and are present on both sides of the xylem. A layer of small crushed elements are found (Fig. 4, *pp*) on one side of the xylem only, viz. on the side turned away from the protoxylem, the individual cells being inconspicuous and not particularly thick-walled. This inconspicuous layer probably represents the protophloem, which forms so noticeable a feature in Thomae's figure[1].

In regard to the structure of the young petiole there is not much to be said. The petioles of the first two or three leaves are more or less circular in outline, and contain a single central stele. Petioles produced at a later stage are reniform in shape with two steles—one at each corner. A third and still older stage shows petioles with a triangular outline, the steles, three in number, being found at the angles. As the plant increases in age the individual bundles divide frequently and anastomose, this being the case in the petioles of quite old plants.

2. *Lamina.* The leaves of *Ceratopteris thalictroides* are

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[1] Thomae, 1886, p. 151.

composed mainly of spongy parenchyma with large air-spaces. The epidermis is made up of large thin-walled cells which have a sinuous outline when seen in surface-view. Stomata are present on both sides of the leaf in the sterile forms ; they are also present on the fertile leaves on the upper side in fairly large numbers, but they are less numerous on the under surface. Seen in transverse sections of leaves (Fig. 5) the stomata have a very curious appearance. A large air-space lies immediately below the opening and the guard-cells have a curious beak-shaped projection. This is found on the inner face of the guard-cells, i. e. the side which is turned towards the other guard-cell, and at the topmost corner of this side. The neighbouring epidermal cells which border immediately on the stoma are somewhat smaller in size. As in *Salvinia* and *Azolla* the guard-cells are but feebly cuticularized, but in regard to their shape and beak-shaped projection there is a strong resemblance to those figured and described by Haberlandt[1] in *Lemna.*

The steles in the sterile leaves are very numerous and anastomose largely, forming a conspicuous network which is easily seen. Trabeculae of parenchyma are found bridging over the air-spaces between the vascular bundles and passing across from the epidermis on the upper side of the leaf to that on the lower. The bundles in the fertile leaves are five in number and are comparatively small. Where a bundle occurs, more parenchymatous tissue is found surrounding it on all sides. Each stele consists of a group of tracheids 4–8 in number, the xylem frequently abutting directly on the pericycle. The phloem is feebly developed and cannot be distinguished from ordinary parenchymatous cells. The endodermis and pericycle are again very conspicuous.

B. The Stem.

a. The mature Plant. The steles in the stem are of two kinds, a ring of large conspicuous steles (Fig. 3, b_1) being ranged round the periphery, and within this ring a number of

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[1] Haberlandt, 1896, p. 401.

small inconspicuous steles (Fig. 3, b_2) are irregularly scattered in the parenchymatous tissue. The large outer bundles vary much in shape, some being circular in outline, others oval or long and narrow, or slightly S-shaped. Both the large and small steles anastomose with each other at different levels.

The bundles run more or less obliquely in the stem, and it is only at some levels that really transverse sections can be obtained, and this again is generally a matter of chance. Fig. 6 represents a photograph taken of one of the large outer steles. The structure is roughly the same as that met with in the petiolar vascular strands, but everything is on a much larger scale and no surrounding ring of sclerenchymatous tissue is present. The xylem lies in the centre, and is made up of scalariform tracheids with small islets of parenchymatous cells scattered among them. The protoxylem (*px*) is found on the outer edge of one side of the xylem, lying between the latter and the sieve-tubes. Owing to the small size of the individual elements of the stele, the protoxylem is often difficult to identify, but its position, as stated above, is clearly seen in sections of steles near the apex. At this level none of the tracheids are differentiated but those composing the protoxylem, and these, in consequence, stand out conspicuously. The bundle is very markedly bicollateral, the large sieve-tubes (Fig. 6, *st*) forming conspicuous elements on each side of the xylem; the characteristic granules on the walls of the tubes are also clearly seen. Beyond the sieve-tubes some ordinary parenchymatous cells are found, amongst which elements are present which probably represent the protophloem (Fig. 6, *pp*). The cells have slightly thickened walls which are darker in colour than those of the ordinary parenchymatous tissue, and some have a more or less crushed appearance. This tissue is the only one present which can in any degree be compared to the protophloem, and if it be regarded as such then the stem-bundles differ from those in the petiole by having this tissue developed on both sides instead of one side only of the xylem. Parenchymatous cells are scattered about irregularly, separating the sieve-tubes from the xylem in some places and from the pericycle in others. They are always present at the two ends of the bundle, lying between the xylem and the pericycle (Fig. 6, *pa*).

The pericycle and endodermis are easily distinguished.

The small strands of the stem (Fig. 7) are often very feebly developed. In passing through a series of transverse sections from the apex downwards towards the base of the stem, it is found that at some levels individual bundles suddenly end somewhat abruptly. At other levels again these small bundles are seen to be uniting with each other or dividing. Their arrangement, where this can be determined with any certainty, seems to be bicollateral, but the phloem is often indistinguishable.

β. The young Stem. The structure of the young stem can only be studied in microtome sections. A transverse section, taken from the middle or near the base of the stem of a young plant 2–4 inches in height, shows that the main mass of the stem-tissue consists of loose large-celled parenchyma, in which the vascular bundles lie embedded. As in the case of the mature stem, the younger one is polystelic, each strand being furnished with a separate endodermis and pericycle. The number of strands present varies from two to five, and no clearly marked difference in size is met with, as in the case of the older plants; the division into an outer ring of large steles and an inner group of small ones does not occur in the young stem. Each stele is bicollateral, but here again, owing to the incomplete differentiation of the tissues, the sieve-tubes have often not yet acquired their characteristic appearance.

γ. The Course of the Vascular Strands in the Stem. I have attempted to make out the course and fate of the steles in the stem of *Ceratopteris* plants of different ages, but it is only in the young stems that it has been possible to find any degree of regularity in the behaviour of individual strands. The result given in text-figure 1 was arrived at by tracing the course of each bundle in the stem of a young plant in a series of transverse sections from the base upwards and towards the apex. From this diagrammatic figure it will be seen that there is a certain amount of regularity in the behaviour of the different strands. The shaded strands represent the bundles of roots, the unshaded ones the bundles of the stem. The triangular areas mark the points at which the petioles leave the stem. The stem-bundles anastomose frequently with each other, union between two adjacent strands being however generally followed by a re-division of the single strand which has resulted from this union. The roots in the young plant do not arise in the same manner as in the mature Fern, and a definite relation exists between the stem, petioles, and roots. Kny[1], in his work on the germination and development of the Parkeriaceae, states that in the young plant a primary root arises a little below each of the primary leaves. He does not, however, describe in any detail the course of the steles of the root, stem, and petiole in connexion with this relation, which seems to be a very constant one. In tracing a series of sections from the base upwards and towards the stem-apex it is seen that a young root, which has a single vascular strand, and is at first quite distinct from the stem, gradually approaches the latter until the spongy parenchyma of the two unite though the root-bundle remains as yet distinct and unchanged. Further up the series, some connexion is seen to take place between the root-stele lying in the stem

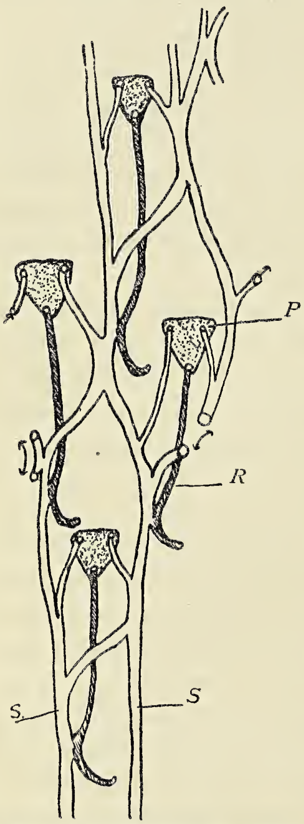

FIG. 1. Illustrating the course of the Vascular Bundles in the stem of a young *Ceratopteris*. *P* = petiole with three bundles leaving the stem. *S* = stem-bundle. *R* = root-bundle.

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[1] Kny, 1875, p. 48.

and a neighbouring stele of the latter ; the two apparently unite and then almost immediately afterwards separate again or re-divide, a stele resulting from this division occupying the same place as the original root-stele, and continuing on its upward course as before. Very soon, however, a petiole leaves the stem containing three vascular strands ; of these two are given off from the stem, the third being the one which has, lower down in the stem, formed this curious connexion.

Fig. 8 represents a diagrammatic longitudinal section of a young stem of *Ceratopteris*, showing this relation between these bundles of the petiole, root, and stem respectively.

In the mature stem no such regular arrangement can be made out as has been described in the young plant. The roots arise directly from the petioles and have no connexion with the stem. No definite behaviour can be made out in regard to any of the steles of the stem. The large steles of the outer circle are continually uniting and dividing, and at certain levels pass out to the leaves, each leaf receiving the whole or part of several steles. In tracing a mature petiole downwards and into the stem, it is seen that the bundles composing the two rings become fewer in number owing to the union of adjacent petiolar strands. From these larger strands numerous small branches are given off, which form a network in the centre of the entering petiole, and finally pass inwards to the centre of the stem. These are the small inner bundles of the stem which have been already described as ending abruptly at varying levels lower down in the stem. In other words, the small, inner and feebly developed bundles of the stem seem to arise as branches of the large steles of the outer ring on the passage of the latter out to a leaf. Since in the young plants steles of one size alone are found, and these, as in the case of the large outer bundles of the mature stem, pass out either as a whole or in part to the leaves, the two systems must be regarded as corresponding to each other. The large outer bundles may therefore be regarded as primitive, the small inner bundles, which are derived from these as branches, being of secondary development.

Jeffrey[1] has described in detail the development of the steles in the rhizome of *Pteris aquilina*, and has found that the large central strands are not primitive as is generally thought, for they are given off as small branches from the true primitive axial steles which can be traced into the rhizome from the primary root. These large, secondary, axial strands are therefore regarded by this author as medullary bundles.

It seems possible to compare these secondary axial strands of *Pteris aquilina* with those found in *Ceratopteris*. In both cases they are given off from the primary steles and come to lie in the centre of the stem. In *Pteris*, however, they increase considerably in size until they are equal to, or larger than the steles from which they have been derived, whilst in *Ceratopteris*, on the other hand, they decrease and finally die away.

δ. *The Apex of the Stem.* The apex of the stem of *Ceratopteris* is surrounded by the young leaves, which enclose it on all sides, completely hiding it from view. Large numbers of ramenta are also present, and these cover the immature and developing leaves as well as the apex itself. These ramenta are but one cell thick; when seen in surface view the individual cells have a sinuous outline.

The structure of the apical region of the stem is best studied in a median longitudinal section taken through the apex. Transverse sections through the same region also show interesting points. Fig. 9 is reproduced from a photograph of a median longitudinal section. In the centre lies the actual apex of the stem itself, in the form of a curious cone-shaped prominence, at the summit of which the three-sided apical cell is found. The cells composing this apical cone are large and have conspicuous nuclei which stain deeply. On each side of the cone the young leaves are found, arching over towards the apical cone which stands erect. This cone-shaped apex reminds one very strongly of that found in

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[1] Jeffrey, 1899, p. 605.

Salvinia and *Azolla*, but in these forms the apical cell, which is found at the summit of the cone, is two-sided and not three-sided as in the case of *Ceratopteris*. The cells of which the young leaves are composed are arranged in a markedly regular manner when seen in longitudinal sections; towards the apex they are in horizontal layers, a single cell occupying each layer. Lower down and farther away from the leaf-apex vertical walls make their appearance in the individual cells, but for a considerable length of time the arrangement remains very regular. Near the apex the vascular strands of the stem are undifferentiated into their different tissues, but consist of masses of parenchymatous cells. The tissue is however readily distinguished from the ordinary parenchyma by the closeness with which the cells are arranged and by the conspicuous and deeply staining nuclei.

The ramenta are made up of cells which, when seen in section, have a shrunken appearance: they are generally destitute of nuclei and cell-contents.

Fig. 10 shows a transverse section through the apical region of a stem of *Ceratopteris*. In this it is seen that the cone-shaped apex (*st*) is circular in outline, lying amongst the young leaves, which are cut across in different planes.

C. The Root.

According to Kny[1], the secondary roots, which are developed from the bases of the petioles, are exogenous in origin. A root arises, according to his investigations, from a single mother-cell lying immediately below the epidermis. Van Tieghem and Douliot[2], however, maintain that this is not the case, for each root arises from a single mother-cell which originates within the endodermis itself. The roots are therefore endogenous and not exogenous, and in this respect *Ceratopteris* resembles the rest of the Filicineae. The mature root is traversed by large air-spaces, generally six in number, which are separated from each other by strands of tissue or

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[1] Kny, 1875, p. 48.

[2] Van Tieghem and Douliot, 1888, p. 540.

trabeculae, which run across from the central cylinder to the outer peripheral layer. The root-apex is occupied by a well-marked apical cell (Fig. 11) which is three-sided, the apex being covered by a root-cap of 2–3 layers. The apical cell cuts off segments in the three planes with great regularity; vertical walls soon appear in these segments, then horizontal walls, and at a short distance below the apex the air-spaces are developed. These arise as splits between the cells. Fig. 12 represents a transverse section of a root just below the region of the apical cell, showing the regular arrangement of the cells and six developing air-spaces.

Numerous lateral roots arise from the adventitious roots. These, according to Poirault[1], are arranged in two rows; each root arising from a single endodermal cell. Poirault also states that in *Ceratopteris* these rootlets do not always reach the exterior at once, for having made their way as far as one of the air-spaces of the mother-root, they grow for some time obliquely downwards before passing through the cortical parenchyma to the exterior. The material I have examined, however, did not show any of these internal rootlets.

D. The Development of the Vascular System.

The development of the vascular system in *Ceratopteris thalictroides* agrees, up to a certain point, with that found in many other Ferns. The later stages seem, however, to differ somewhat markedly from those described and figured in other cases by Leclerc du Sablon[2]. Figs. 2 to 8 represent the various stages met with in the development of the vascular system of *Ceratopteris* from the root upwards. Figs. 2 and 3 are taken from the primary root of a young plant about a month old. Figs. 4–8 are from an older plant about three inches in height, in which the primary root had died away, numerous secondary roots having arisen to take its place.

A little distance below the apex of the root the vascular tissue is differentiated. The xylem arises as two minute groups of tracheids (Fig. 2, *x*) on each side of the bundle.

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[1] Poirault, 1894, p. 121.

[2] Leclerc du Sablon, 1890, p. 5.

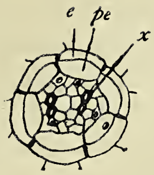

FIG. 2

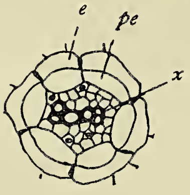

FIG. 3

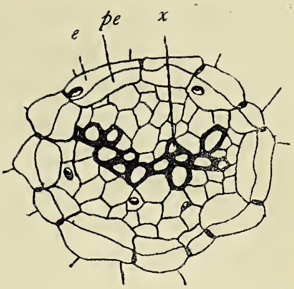

FIG. 4

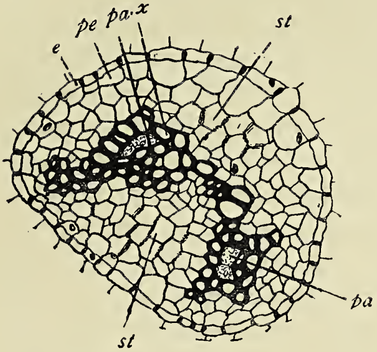

FIG. 6

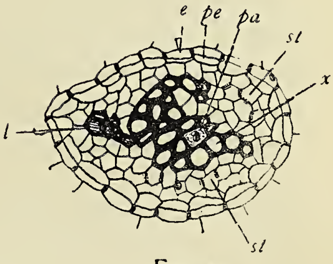

FIG. 5

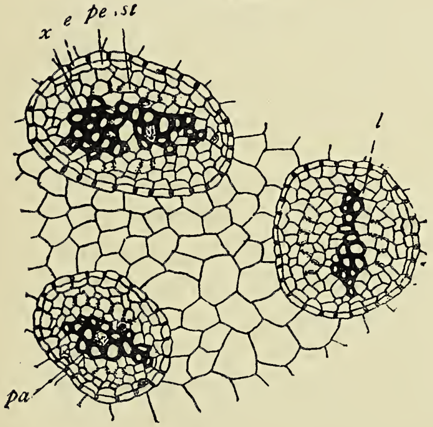

FIG. 8

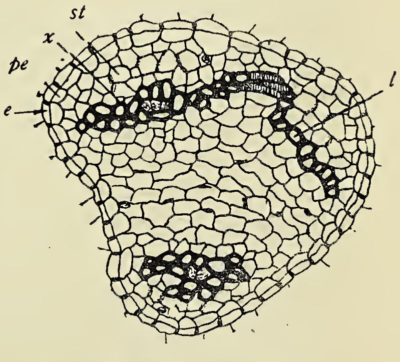

FIG 7

FIGS. 2–8. Stages illustrating the development of the Vascular System in *Ceratopteris thalictroides*. Figs. 2 and 3 from a young plant. × 360. Figs. 4–8 from an older plant. × 120. *e* = endodermis, *pe* = pericycle, *x* = xylem, *st* = sieve-tubes, *pa* = parenchyma, *l* = leaf-trace.

The endodermis and pericycle are clearly seen (Fig. 2, *e*, *pe*) and the protoxylem-groups may or may not touch the pericycle. By the further differentiation of tracheids between the two original groups, a solid band of xylem is formed (Fig. 3, *x*). The phloem, which in a later stage is found on each side of the band of xylem, is as yet undifferentiated, and cannot be distinguished from ordinary parenchyma. In the young plant from which Figs. 2 and 3 were obtained, no further stages of development were found, but in Fig. 4, which was taken from the base of a considerably older plant, a stage is seen corresponding in arrangement with that already described in Fig. 3, though everything is on a larger scale. Following a series of transverse sections of this stem from the base upwards, it is seen that, by the further development of tracheids, a more or less solid central xylem-strand is found with phloem (Fig. 5, *st*) lying on both sides, the sieve-tubes showing, as a rule, the characteristic dots on their walls. One or more ordinary parenchymatous cells (Fig. 5, *pa*) are generally mingled with the tracheids, but their presence is not constant. In some cases the xylem-strand becomes horse-shoe-shaped before reaching the stage represented by Fig. 5, but this again is not a constant feature. In other plants, younger than the one under consideration, the stem remains monostelic throughout, the single solid strand giving off leaf-traces at intervals.

In the plant in question, however, the single stele divides into two, and throughout the remaining portion of the stem more than one stele is always present. In Fig. 6 the xylem of the stele is about to divide into two strands which are seen in Fig. 7, still enclosed by a common endodermis. The two strands are separated by large thin-walled cells containing somewhat disorganized nuclei; this tissue is very similar in appearance to that seen in the main mass of parenchyma of the stem in which the bundles lie embedded. One of the two xylem-strands resulting from this division gives off almost immediately a leaf-trace (Figs. 7 and 8, *l*). The endodermis breaks and unites very rapidly round each strand.

Comparing the above results with those given by Leclerc du Sablon [1] in the case of *Pteris aquilina*, *Trichomanes alatum*, *Osmunda regalis* and *Angiopteris evecta*, we find that *Ceratopteris* agrees with the above Ferns as far as that stage in development which is represented by Fig. 5. No resemblances are found beyond this point, for in *Ceratopteris* the solid stele divides directly into two, whilst in the Ferns described by Leclerc du Sablon a ring of xylem is formed by the appearance of pith or phloem in the centre of the solid xylem-strand. No such ring can be detected in *Ceratopteris*, for the xylem is always present as a solid central mass, and the parenchymatous cells which may or may not be scattered irregularly amongst the tracheids can hardly be regarded in the light of phloem or medullary tissue.

Van Tieghem [2] has described polystely as a modification of the original pithless monostele, which by repeated bifurcations gives rise to several steles. Jeffrey [3], in his work on the morphology of the central cylinder of Angiosperms, states that polystely does not arise in this way. According to this author, the primitive condition is represented by the type found in the young stages of all polystelic Ferns and Angiosperms examined by him, viz. a tubular stele with an inner and an outer endodermis. In no case has he found this bifurcation of a pithless monostele described by Van Tieghem. In *Ceratopteris*, however, Van Tieghem's description of polystely seems to hold good, for no trace of a tubular stele is found.

A certain amount of consideration must, however, be given to the fact that *Ceratopteris* occupies a somewhat isolated position amongst the Filicineae owing to its aquatic or semi-aquatic manner of life. The reduction of the stem, the absence of sclerenchyma, and, above all, the small size of the individual vascular elements, can all be traced to this cause, and it seems possible that this comparatively simple type of arrangement in the development of the polystelic stem may

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[1] Leclerc du Sablon, 1890, p. 5.

[2] Van Tieghem, 1886, p. 282.

[3] Jeffrey, 1899, p. 613.

be also correlated with its manner of life. In this case *Ceratopteris* can hardly be regarded as typical, and the development of its vascular system cannot form any basis for investigation as to the origin of the polystelic condition met with in the Vascular Cryptogams.

III. THE SPORANGIA.

The development of the sporangia, together with the germination of the spores and formation of the embryo, have been very fully worked out and described by Kny[1]. In his Plate VIII, Figs. 1–19, he has figured the various stages met with in the development of a sporangium: the sporangium arises from a single cell; walls arise in this, forming a triangular cell in the centre surrounded by a single layer of cells. The central one cuts off a two-layered tapetum and itself forms the archesporium; this by division gives rise to four spore-mother-cells, each of which forms four spores. At a later stage the tapetal layers are absorbed and the spores lie freely in the cavity of the sporangium. In the figures given by Kny none of the earlier stages show the presence of an annulus, though this is frequently present in sections of young sporangia where the archesporium has not yet divided into the four spore-mother-cells. In Fig. 13 the annulus is shown in a sporangium containing the four mother-cells at a stage before the absorption of the two tapetal layers. The sporangia are scattered irregularly over the leaves; as a rule, near the apex of the leaf younger ones are found, but this is not constant, and sections of leaves often show a mature sporangium side by side with a very young one.

IV. THE VEGETATIVE BUDS.

Ceratopteris reproduces itself largely by means of vegetative buds. These arise at the angles and at the lobes of all the leaves, the sterile as well as the fertile producing them in large numbers. Hofmeister[2] states that each bud arises from

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[1] Kny, 1875, p. 49.

[2] Hofmeister: see Sachs, 1882, p. 433.

a single epidermal cell. Heinricher[1] has shown, in his researches on the origin of vegetative buds, that the bulbils of some of the Polypodiaceae (*Asplenium bulbiferum*) also arise in the same way from a single epidermal cell. I have been unable to verify Hofmeister's statement in regard to *Ceratopteris,* though everything seems to point to the buds being developed in this manner. I have however been able to obtain stages in the development of the vegetative buds themselves, by cutting numerous series of sections through leaves at whose angles or lobes bulbils were present. Fig. 14 shows a longitudinal section through the centre of a very young bud; the whole bulbil is surrounded by young ramenta which act as a protection to the young apex and leaves. The apex of the bud lies in the centre; it consists of a broad prominence, at the summit of which the three-sided apical cell is found. The apex is much broader and flatter in the young bud than it is in the mature stem, where the curious cone-shaped structure is present; the cells too are smaller, but the apical cell is well marked. Sections of the same bud, taken either before or after the median one, show the beginnings of the young leaves as little protuberances of tissue. The whole bud itself is always situated over a vein of the leaf. Sections taken through a leaf bearing a somewhat older bud show a more advanced stage in the structure of the apex (Fig. 15). This has become much narrower; in fact, it is on a small scale a repetition of the apex of a mature stem which has already been given in Fig. 9. The cone-shaped apex is shorter and the young leaves are also on a smaller scale, but they arch over towards the apex in a similar way, and in both cases the arrangement of the cells is the same.

CONCLUSION.

The position of *Ceratopteris* amongst the Leptosporangiate Ferns is not altogether clear; it has, on the whole, marked affinities with the Polypodiaceae, and this is more especially

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[1] Heinricher, 1881, p. 115.

the case in regard to the gametophyte. Many of the differences seen in the structure of the mature plant are due of course to its manner of life; thus, for example, the reduction of the stem and of the elements composing the vascular tissue throughout the plant, the very small amount of sclerenchyma found, and the presence of the large air-passages are all correlated with its aquatic life. The sporangia are larger than in most Ferns; they are scattered singly on the leaves and are not aggregated into sori. In regard to the development of the spores, their germination, the formation and subsequent growth of the prothallus, no important differences are seen between *Ceratopteris* and the Polypodiaceae as a whole. According to Kny[1] and Van Tieghem[2], in regard to the formation of the antheridia, *Ceratopteris* resembles *Aneimia* and *Pteris*, though, when mature, the antheridium projects somewhat less from the surface of the prothallus. In regard to the archegonia, Campbell[3] states that they are developed independently of the original growing apex, the archegonial meristem being lateral. In the embryo Kny[4] has pointed out that both the two anterior quadrants form the first leaf, and from this the stem arises laterally at a later stage. Kny has laid some stress on this point in his discussion as to the origin of Dicotyledons and Monocotyledons. These groups have, in his opinion, originated independently of each other from the Vascular Cryptogams; he brings forward this point in regard to the formation of the young stem as a resemblance between Monocotyledons and the Filicineae, both of which are furnished with but one cotyledonary leaf. Campbell[5], on the other hand, is of opinion that the line of descent of the Angiosperms as a single group passes through the Eusporangiate Ferns and possibly through the Isoetaceae. *Ceratopteris*, which he describes as an 'aberrant genus,' may form the connecting link between the Polypodiaceae and *Marsilia*. He compares

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[1] Kny, 1875, p. 15.

[2] Van Tieghem, 1891, p. 1382.

[3] Campbell, 1895, p. 375.

[4] Kny, 1875, p. 58.

[5] Campbell, 1895, p. 518.

the fertile leaves of *Ceratopteris*, which curl over the sporangia forming a kind of pod, to the sporocarp of *Marsilia*. The leaves which are formed first in the young plants of both are also very similar, being simple and spatulate in shape. In both plants the stem grows by a three-sided apical cell, though in *Ceratopteris* the actual apex is much narrower than in *Marsilia*, and in general appearance is much more like the apex of the stem in *Salvinia*. In *Salvinia*, however, the apical cell is two- not three-sided, though Leitgeb[1] states that in the very early stages a three-sided apical cell is found. The vascular system again in *Ceratopteris* is polystelic, in *Marsilia* it is tubular with an inner and an outer endodermis. Taken as a whole *Ceratopteris* has much stronger affinities with the Polypodiaceae than with the Marsiliaceae, but in any case it is a divergent form, though many of its peculiarities can be directly traced to its manner of life.

The differences met with in the anatomical structure are not enough to place the Parkeriaceae as an order distinct from the Polypodiaceae, but the resemblances on the other hand are strong enough to admit of their being ranked as a sub-order of this group of Ferns.

SUMMARY.

The chief points of interest may now be summarized.

1. *Ceratopteris thalictroides* is an annual aquatic Fern with marked anatomical modifications in correlation with its aquatic manner of life.

2. The stem is much reduced, fertile and sterile leaves are present, and the later roots are developed from the bases of the petioles.

3. The steles in the stem and leaves are markedly bicollateral.

4. In the stem an outer circle of large steles is found, within which small, feebly developed steles are scattered irregularly.

5. The vascular bundles of the stem and of the first few

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[1] Leitgeb: cf. Schenk, 1881, p. 216.

leaves and roots of young *Ceratopteris* plants are in close connexion with each other.

6. The apex of the stem is in the form of a cone, at the summit of which a three-sided apical cell is found.

7. The stem of the young plant is monostelic, at a later stage the monostele divides directly into two, and further division of the two resulting steles gives rise to the polystelic condition of the older stem.

8. The sporangia are large and scattered. They are spherical in shape, with a short stalk, and the annulus may be much reduced.

9. Large numbers of vegetative buds are found. Each bud arises at the angle of a leaf and grows by a three-sided apical cell. Buds are borne by both sterile and fertile leaves.

10. *Ceratopteris* shows stronger affinities with the Polypodiaceae than with any other group of the Leptosporangiate Ferns. It has somewhat slighter affinities with the Marsiliaceae, and may possibly be intermediate in position between these two orders.

In conclusion I must add that this work was undertaken at the suggestion of Mr. A. C. Seward, and my best thanks are due to him, not only for the material, but also for the many suggestions and advice that he has given me throughout.

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EXPLANATION OF FIGURES IN PLATE VI.

Illustrating Miss Ford's paper on *Ceratopteris.*

Fig. 1. Compound sterile leaf of *Ceratopteris,* showing vegetative buds (*b*) at the angles of the leaves. ($\frac{2}{8}$ nat. size.)

Fig. 2. Young vegetative bud still attached to parent plant, showing young simple leaves. (Nat. size.)

Fig. 3. View of stem and petioles of a mature *Ceratopteris* plant from below. *r.* = roots, *vb.* = bundles of the petioles, *s.* = stem, b_1 = larger stem-bundles of outer ring, b_2 = smaller inner bundles. (Nat. size.)

Fig. 4. Transverse section of a petiole bundle. *scl.* = sclerenchymatous sheath, *end.* = endodermis, *p .* = pericycle, *pa.* = parenchyma, *st.* = sieve-tubes, *pp.* = protophloem, *x.* = xylem, *p.x.* = protoxylem. (× 455.)

Fig. 5. Transverse section of a stoma. (× 335.)

Fig. 6. Transverse section of a large bundle from the stem. Lettering as in Fig. 4. (From a photograph.)

Fig. 7. Transverse section of a small inner bundle of the stem. Lettering as in Fig. 4. (× 455.)

Fig. 8. Longitudinal section of young stem, showing the relation between the bundles of the stem, root, and petiole. *r.* = root, *st.* = stem, *pl.* = petiole, *x.* = xylem, *p.* = phloem.

Fig. 9. Longitudinal section through apex of the stem. *st.* = stem, *l.* = leaf, *sl.* = ramenta. (From a photograph.)

Fig. 10. Transverse section through apical region of stem. *st.* = stem, *l.* = leaf, *sl.* = ramenta. (× 75.)

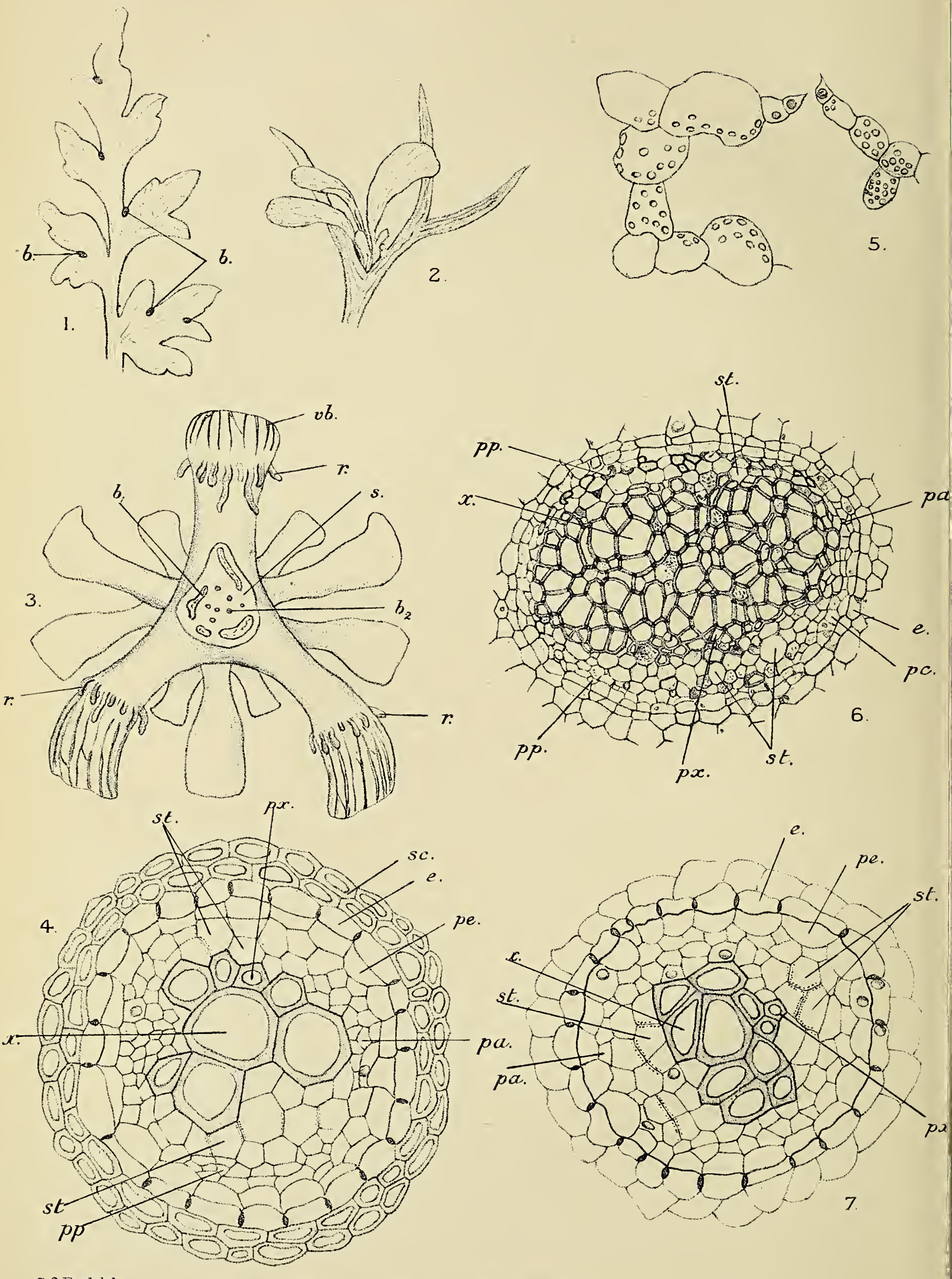
Fig. 11. Longitudinal section through apex of young root. *a.* = apical cell, *l.* = air-passages.

Fig. 12. Transverse section of root below the apex. *l.* = air-passages. (× 455.)

Fig. 13. Section of young sporangium. *an.* = annulus, *sm.* = spore-mother-cells. (× 300 times.)

Fig. 14. Longitudinal section through young vegetative bud. *vb.* = vascular bundle of leaf, *a.* = apical cell, *sl.* = ramenta. (× 75.)

Fig. 15. Ditto through older bud. (× 75.)



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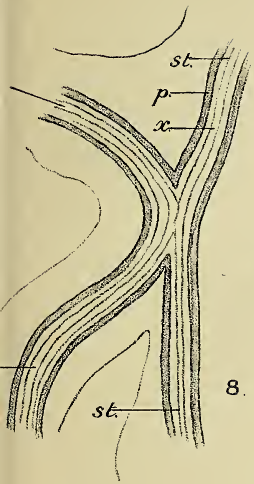
FORD.—CERATOPTERIS.



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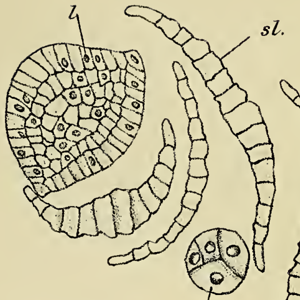

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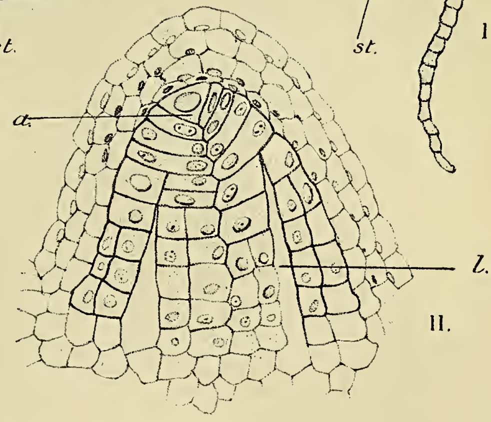

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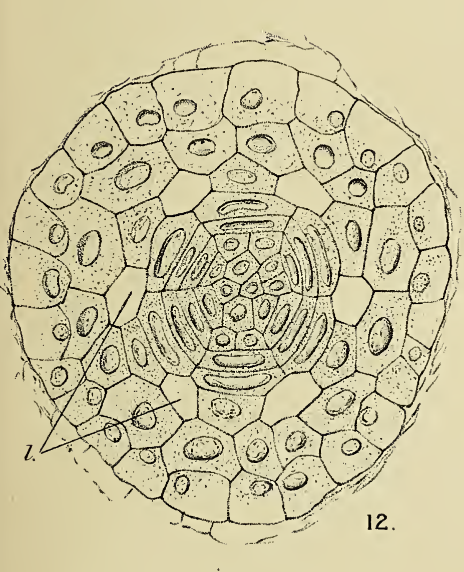

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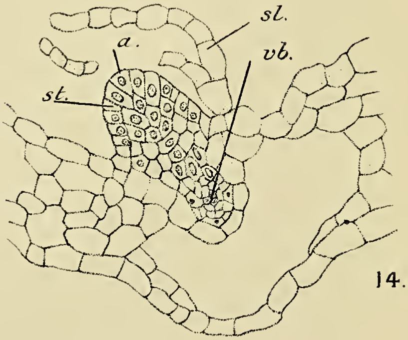

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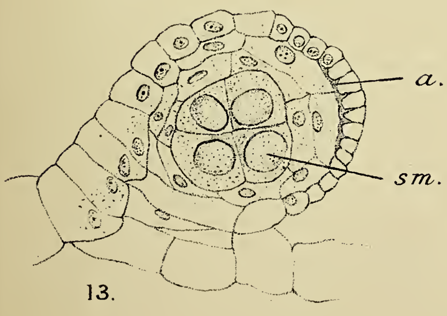

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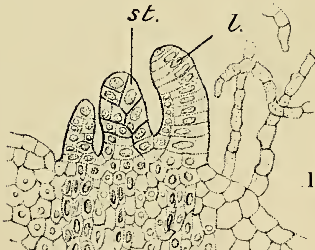

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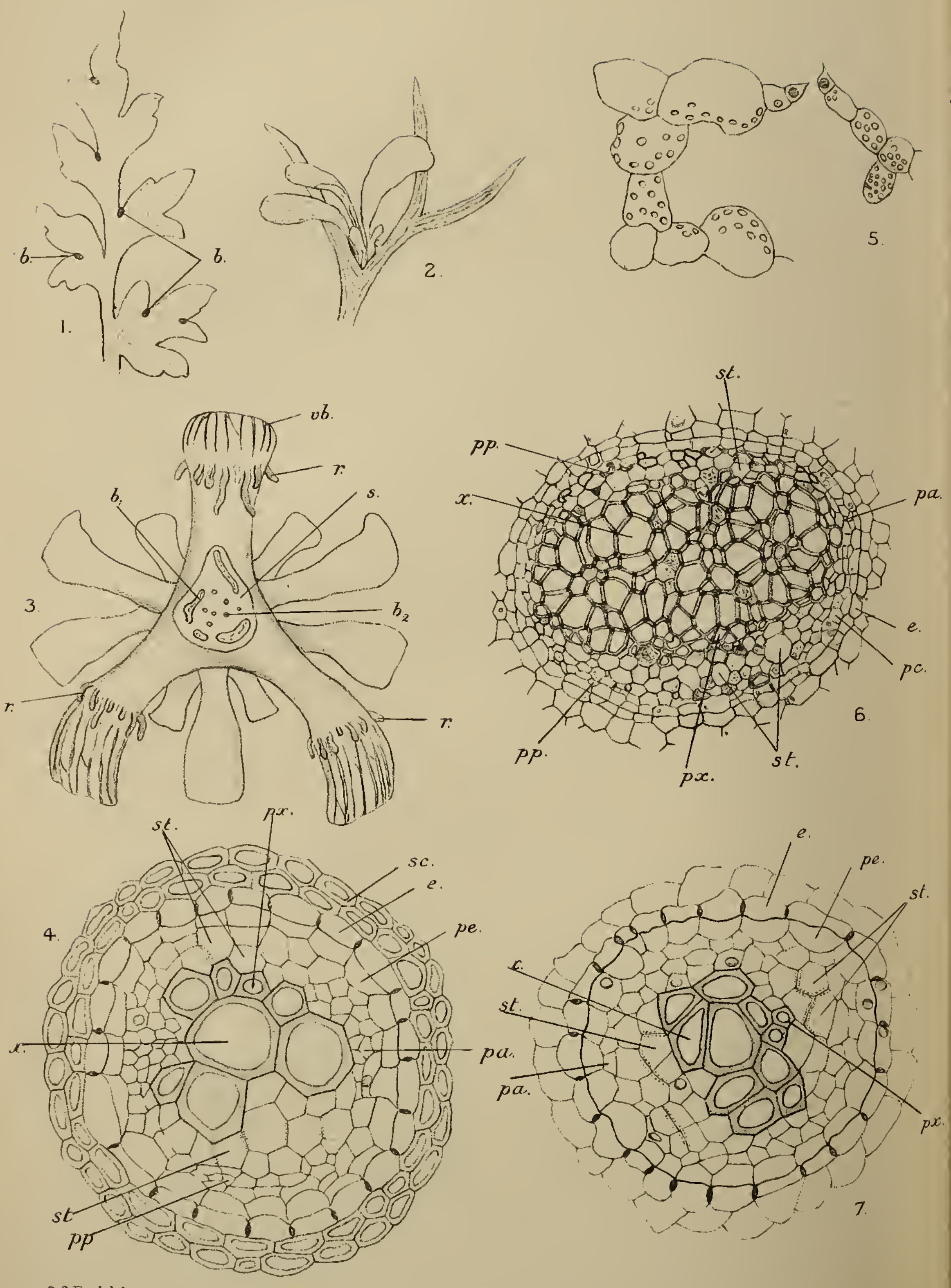

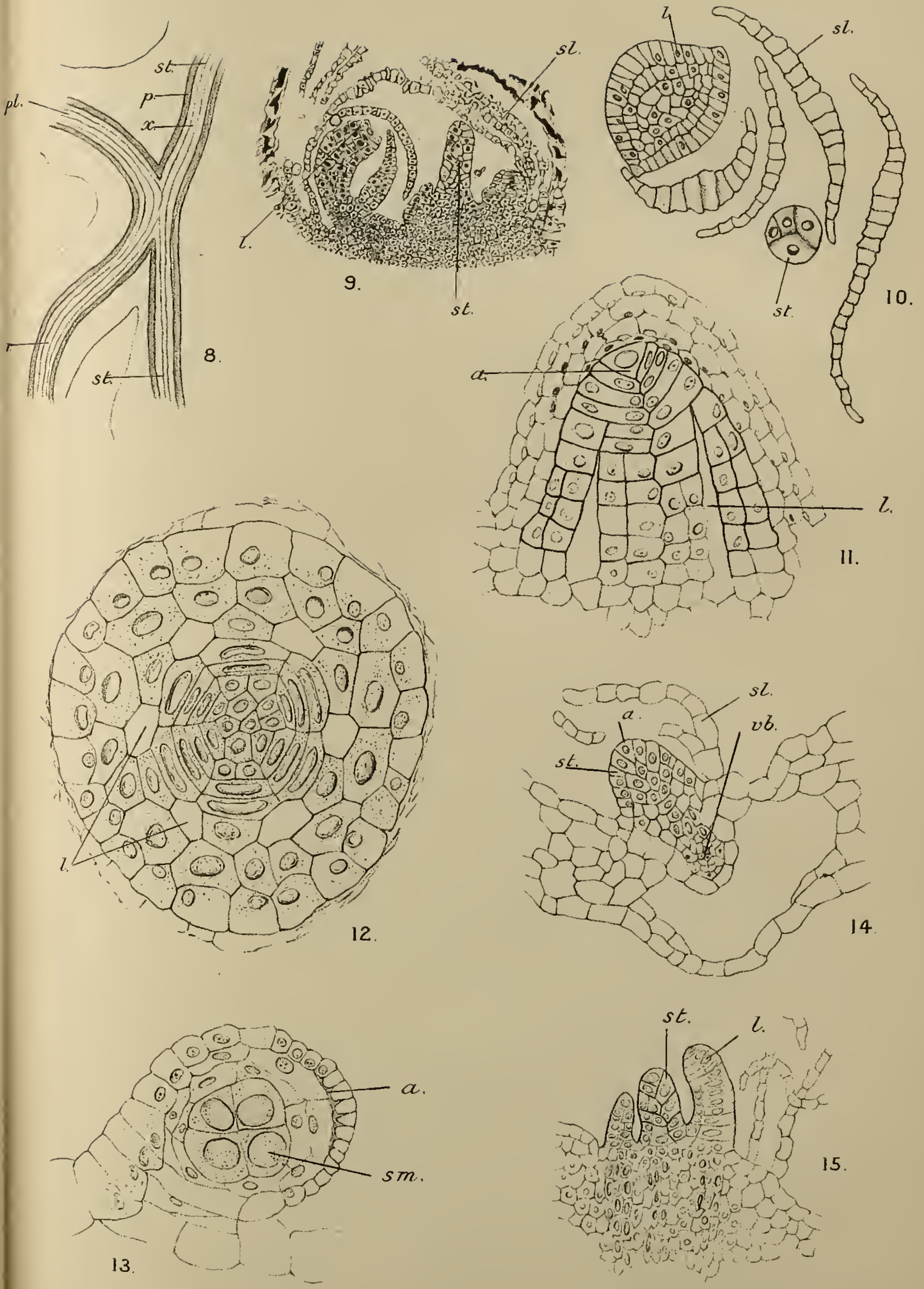

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FORD.—CERATOPTERIS.

University Press, Oxford

The Development of the Pollinium and Sperm-Cells in Asclepias Cornuti, Decaisne.

BY

C. STUART GAGER.

With Plate VII.

INTRODUCTION.

THE flower of *Asclepias* has always been of interest to botanists. It was studied as early as 1763 by Adanson, and later by Gleichen (1779) and by Sprengel (1793)[1]. The mode of occurrence of the pollen has been especially interesting. Loew (1895) mentions a paper by Kölreuter in which the 'hangenden Beutelchen,' later known as pollinia, are described as the 'male genitals' of the plant, and these organs have also been similarly described by Baron Jacquin (1811).

In 1831 Brown, who separated (1867) the Asclepiadeae as a Natural Order of plants from the Apocyneae of Jussieu, made the first serious study of their pollinia. His first paper on this subject appeared in 1809, but he failed to observe the grains of pollen, and thought that the pollinium consisted of one individual cavity filled with minute granular matter mixed with an oily fluid. In 1831 Bauer, an artist, offered to Brown for publication drawings of several Asclepiadeae, made in

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[1] Referred to by Brown, 1833.

[Annals of Botany, Vol. XVI. No. LXI. March, 1902.]

1805, and representing 'the internal structure of the pollen-mass as cellular; each cell in the flower-bud just before expansion being filled with a grain of pollen, . . . while in the expanded flower this grain is exhibited as shrivelled, having discharged its contents, which consist of a mixture of an oily fluid and minute granules[1].'

Link considered the pollen-mass as 'composed either of a cellular tissue, or manifestly of grains of pollen: the former part of the description being no doubt meant to apply to true Asclepiadeae, the latter to the Periploceae[2].'

In 1827 Treviranus described the pollen-mass of *A. curassavica* as 'filled with compressed, nearly round but obtusely angular, colourless, simple grains, containing minute granules; the pressure of the external grains, or those in contact with the general covering, giving it the appearance of being cellular[2].'

Ehrenberg[3] (1829) describes the pollen-mass as 'consisting of a proper membrane bursting in a regular manner, the cavity being not cellular but filled with grains of pollen, each grain having a cauda or cylindrical tube often of great length, and all the tubes being directed towards the point or line of dehiscence.' This appendage he considers analogous to the 'boyau' of Amici (1824) and Brongniart (1827), differing, however, in its forming an essential part of the grain in Asclepiadeae; whereas in other families the application of an external stimulus is necessary for its production. Later, Ehrenberg[3] (1831) believes that the grains of pollen are in their earlier stages without the 'boyaux,' which make their appearance subsequently at the period of impregnation.

In 1833, as a result of further researches on the Asclepiadeae, Brown describes the pollen-mass in several species of *Asclepias*, particularly in *A. phytolaccoides* and *A. curassavica*, the figures being drawn by Bauer. According to the description and figures, the pollen-mass consists of cells disposed in three series parallel to its sides, the middle series being often more

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[1] Brown (1831), p. 719.

[2] Brown, loc. cit., p. 720.

[3] Quoted by Brown (1831).

or less interrupted. The membrane of the pollen-grain is described[1] as made up of two united coats, and the cavity filled with spherical granules of nearly uniform size. These granules were not often found in the pollen-tubes, nor were the tubes branched or jointed. The figures accompanying this paper are excellent. Brown, without doubt, considers the cells of the pollinium as true pollen-grains.

In 1840 Jussieu figured the pollinia with pollen-tubes projecting, and considered the pollinia as masses of pollen-grains. Schleiden (1849) also considers the pollinia as masses of pollen, clothed with a special membrane.

In his work on the Microscope (1853), Schacht gives directions for the microscopic study of the flower of *A. syriaca*, and describes (Chapter 4) and figures correctly for the first time (Fig. 15) the pollinium mother-cells for this plant. I find no mention of Schacht's work by later writers on this subject. Schacht, however, derives all of the pollen-grains of a single anther-locule from a single 'primary mother-cell,' which he figures (Fig. 21 *a*)[2]. Engler (1876)[3] states that this is not true for *Asclepias*, though it is the mode of development in *Albizzia lophantha*, Benth. The writings of Sprengel (1793) and others I will only mention, as they are concerned with fertilization in the old sense of the term, i. e. pollination[4].

In 1886 appeared Wille's paper on the development of the pollen-grains in Angiosperms. The first part of this paper deals with the mode of formation of the membrane or coats of pollen-grains. In the Orchidaceae he traces 'a successively retrograde developmental process.

1. Free pollen-grains in *Cypripedium*.

2. Free tetrads with a new membranous structure on the exterior in *Epipactis*.

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[1] Loc. cit., p. 724.

[2] The same writer in his later paper (1860) refers to the cells of the pollinium as pollen-grains.

[3] p. 298.

[4] Meyen (1838), Delpino (1865), Hildebrand (1866), Robertson (1886–7), and Ule (1897).

3. Tetrads held together by the middle lamellae, which have been dissolved into mucilage (*Schleim*) without any special membrane structure for the individual pollen-grains in *Orchis*. It is a step further in the same direction when the middle lamellae between the tetrads remain unaltered. Whether this results in some Orchidaceae I know not, still one finds such a condition in several Mimosae (Rosanoff) and Acaciae (Engler), e. g. *Acacia pulchella*. In Asclepiadaceae (*A.* spec.) the reduction has proceeded still further, for here I have not succeeded in finding a single tetrad division, but the whole mass of apparently undivided pollen-mother-cells were surrounded by an exine-like membrane[1].'

Strasburger (1889), referring to Wille's paper, also states that the pollen-mother-cell of *Asclepias* never divides. In *A. syriaca*, he says, one finds the single locule of each half of the anther filled with a row of large, radially oriented cells, rich in content, the primary mother-cells (*Urmutterzellen*) of the pollen. These cells afterwards divide transversely, the longest lying in the middle of the locule, always dividing into four cells, those adjacent to its two walls into fewer cells, in some cases not at all[2].

Wille, then, seems to have been the first to suggest this interpretation of the structure of the pollinium in *Asclepias*. Vines (1895) gives the same idea, stating that the pollen-mother-cells 'develop directly, without division, into a cell of the pollinium, each such cell being, at any rate physiologically, equivalent to a microspore.'

Later, Strasburger (1900) confirms Raciborski's (1897) account of centrosome-like bodies in the pollen-mother-cell of *Asclepias*, but from the context it is not clear whether he there refers to the individual cells of the pollinium, or to the cell that gives rise to them, and, from the state of our knowledge on the subject at the time Raciborski wrote, we cannot

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[1] 'Hier ist es mir nicht einmal gelungen, irgend eine Tetradentheilung zu finden, sondern ganze Massen scheinbar ungetheilter Pollenmutterzellen werden hier von einer eigenartigen Membran umgeben.' Wille (1886), p. 41.

[2] 'Diese Zellen entsprechen den Pollenmutterzellen anderer Objecte, theilen sich aber nicht mehr.' Strasburger (1889), p. 80.

be sure to just what cells he refers as pollen-mother-cells. From his comparison of the large size of the cells relative to their respective nuclei, it seems as if he must refer to the cells which give rise to the individual cells of the pollinium, for this comparison does not apply very well to any of the other cells of the pollinium. Juel (1900) says that the manner of tetrad division in Asclepiadaceae is still a question.

Neither Juel nor Strasburger (1900) mention Stevens's (1898) paper, nor is any reference made in the latter to Wille's work or to Strasburger's statement. Stevens figures and describes in part the division of the cells from which the pollinium units originate, and calls them pollen-mother-cells.

The general appearance and structure of the pollinium suggest that the cells which compose it are pollen-mother-cells rather than pollen-grains, and this, doubtless, lent ready acceptance to Wille's interpretation of them. The development of these cells, four in a row, from the large primary cells, accompanied by a reduction of the number of chromosomes, as described by Stevens[1], suggests that the cells of the pollinium are pollen-grains. If this is the correct interpretation of them, the arrangement of the cells in a row, rather than at the corners of a tetrahedron, differs, so far as our present knowledge goes, from the mode of formation of pollen in all other plants.

If these cells which develop the fertilization (pollen) tube are pollen-mother-cells, we would expect to find the subsequent nuclear phenomena and the number of cell-divisions to be different from those in the development of the nuclei and sperm-cells in pollen-grains, that is, that there would be a shortening of the process from the mature archesporial cell to the sperm-cells if the microspore were cut out, which would be the case if Wille's interpretation proved to be correct. This has already been suggested by Atkinson (1901). It was for the purpose of determining the course of events in the development of these cells and of the pollen-tube, and the

[1] Loc. cit., p. 81.

nuclear phenomena in the formation of the sperm-cells, that this study was undertaken, for it is clear that the proper interpretation of the structures depends upon a complete knowledge of these phenomena.

METHODS.

Asclepias cornuti was chosen for the basis for the work, but comparisons were made with *A. phytolaccoides*, *A. incarnata*, *A. quadrifolia*, and *A. tuberosa*. The material was collected at frequent intervals during the months of June, July, and August in the summers of 1899 and 1900. Some of it was put up in the field and the rest in the laboratory at different times during the day, from 7 a.m. to 7 p.m. After the removal of the perianth, the buds were halved to ensure more rapid penetration, and placed in Flemming's chromosmic-acetic acid solution for twenty-four hours. The material was then washed in water for twelve hours, dehydrated, bleached, infiltrated, and imbedded in paraffine in the usual manner. The sections were cut of various thicknesses, but those thirteen and one-half microns thick proved best for study. Some of the slides were stained with iron-alum haematoxylin, but the safranin-gentian-violet-orange combination gave the better results.

In order to facilitate the handling of the small pollinia they were placed in tiny bags of cheese-cloth, closed at the top by a small piece of copper wire, one end of which was allowed to project as a handle. The pollinia were placed in these bags after dehydrating.

Pollinia were germinated in a 5 per cent. cane-sugar solution and placed in the Flemming at intervals of from five to thirty minutes during germination. In addition to this, pollinia were examined that had germinated on slices of sugar-beet kept moist in a Petri dish, and also those that had germinated on the stigma. Their behaviour seemed to be the same under each of the above conditions. A rather vigorous circulation of protoplasm was noticeable in freshly germinated pollen-tubes.

THE ARCHESPORIUM.

Sections through young buds about 3 mm. in diameter showed the five young anthers around the central axis of the flower, each having two well-defined oval areas containing a varying number of large, long cells, arranged radially, and having comparatively large nuclei (Pl. VII, Fig. 1). These areas occupy the position of the pollen-masses in older buds, and so, evidently, locate the locules.

Much younger buds were then sectioned until a stage was reached where there was no marked indication of differentiation of cells in the anther. Such a stage is shown in Fig. 2, where cell-division is taking place in various directions throughout the tissue. Soon, however, these divisions cease, and a row of sub-epidermal cells in each end of the anther on the proximal side appear larger and richer in protoplasmic content. They are usually straight, but at a later age some of them have a slightly sigmoid form. Division in these cells is always in periclinal planes, cutting off a sub-epidermal cell from an inner cell, which is later seen to give rise to the cells of the pollinium, and which will be referred to as the primary pollinium-cell (Fig. 3). The division is shown complete in Fig. 4. This process varies from that described by Schacht (1853), who derived all the cells of a single pollinium from one primary mother-cell.

THE TAPETUM.

The sub-epidermal cells undergo many divisions in different planes, as shown in Fig. 5. Parallel with these changes the other tissue-cells immediately surrounding the primary pollinium-cells become altered, until finally a well-defined tapetal layer surrounds the primary pollinium-cells (Fig. 7). It is thus seen that in *Asclepias* the tapetum is a morphological composite, as described by Coulter (1898) for *Ranunculus*, by Caldwell (1899) for *Lemna minor*, and by Fulmer (1899) for *Hemerocallis fulva.* Frequently some of the primary pollinium-cells appear to disintegrate and function as tapetal cells, as described by Caldwell (1899). The multiplication of nuclei characteristic of tapetal cells takes place in this layer as shown in Fig. 7. After the pollinium becomes mature, the cells of the tapetum disintegrate.

THE PRIMARY POLLINIUM-CELLS.

The young primary pollinium-cells now pass through an extended period of growth, elongating greatly until they are from four to six times as long as broad. They are oriented with the long axis radial as described by De Mirbel[1] (1833) for *Cucurbita*, by Juel (1900) for *Carex acuta*, and as first described by Schacht (1853) and later by Stevens (1898) for *Asclepias*. The nuclei increase in size and the nucleolus, which often occupies over one-half of the nuclear cavity, stains deeply with gentian-violet.

About this time also, from one to two little wart-like bodies appear at the edge of the nucleolus, similar to those described and figured by Wiegand (1899) for *Potamogeton*, and interpreted by him as probably the true nucleoli. I could not make out any constant difference in the staining reaction of these little bodies and the large one to which they are adjacent, as described by him. In Fig. 9 two of these bodies are shown for each nucleolus, and in Fig. 10 there is only one, while in Fig. 11, which is a later stage, there are none. Figs. 13 and 14, which represent sections through the nucleolar structure of the pollen-mother-cell, suggest that in *Asclepias*, at least, these wart-like bodies are a stage in the fragmentation of the nucleolus. Fig. 13 suggests that five bodies have been given off from the large one, and, if this is the correct interpretation of the condition there figured, it is probable that Figs. 13 and 14 represent successive stages in this division. From the later condition shown in Figs. 12 and 16, it seems probable that this fragmentation of the nucleolus does not always take place. Associated with this phenomenon of growth and fragmentation, is a more or less vacuolated

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[1] Quoted by Nägeli (1842), p. 7.

condition of the nucleolus as shown in Figs. 10 and 12–16 When there is no fragmentation there are usually no vacuoles present, though this is not always the case.

Fragmentation of the nucleolus has been described by Farmer (1893) for *Lilium Martagon*, and (1895) for *Pellia epiphylla*, where the particles into which it breaks up are found usually on young chromosomes or close to them. Farmer suggests that this proximity is due to 'mechanical' causes. From the staining reactions in *Asclepias*, the suggestion is very strong that it functions as a reservoir for chromatin or for some allied substance, as Farmer (1895) and Pfitzner have suggested.

Miss Sargant (1896), in her studies on *Lilium Martagon*, thinks that the nucleolar substance serves as material for the spindle-fibres, or at least to solder them to the chromosomes. This may be its function in *Asclepias*, as the spindle-fibres seem to be of nuclear origin. Other facts, however, argue against this interpretation.

Zimmermann (1893) believes that the nucleoli are thrust out into the cytoplasm, and then in the metaphase taken up again into the daughter-nuclei, '*omnis nucleolus e nucleolo*.' But if this were true in *Asclepias*, then it becomes more difficult than ever to explain the loss of nucleolar substance, as such, after the first division of the primary pollinium-cell, for Stevens (1898), by careful measurements, has shown that the volume of the nucleoli of the daughter-nuclei of the first division is only about one-tenth of the volume of the nucleoli of the primary pollinium-cell nucleus.

After the pollinium-cells are formed they contain prominent rod-shaped bodies which will be referred to later. These bodies stain very deeply with the gentian-violet, and it is possible that this fact may be associated with the disappearance of the nucleolar substance, as such. Stevens[1] argues for the nutritive function of the nucleolus, but thinks that its substance goes to form 'the kinoplasmic spindle and the cell-plate.' On this supposition, however, large nucleoli would be

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[1] Loc. cit., p. 83.

as necessary an antecedent to the second division as to the first. If the interpretation suggested above should prove to be correct for *Asclepias*, it could not be considered as the function of the nucleolus in all plants, for the nucleolus is sometimes present after the spindle-fibres are formed[1].

The mature primary pollinium-cell is shown in Fig. 10. In this stage the nucleolus stains very slightly, if at all, with the gentian-violet, while the nuclear reticulum takes a deep blue colour. There is a well-defined nucleolar membrane, and the slightly vacuolated cytoplasm contains many granules evenly distributed throughout and stained with the gentian. These granules first appear at a much earlier stage (Fig. 9), but disappear as division approaches.

THE FIRST DIVISION OF THE PRIMARY POLLINIUM-CELL.

After attaining the maximum size, the primary pollinium-cell passes a comparatively long period during which it undergoes no visible changes. Stevens refers to this as a period of rest. The first indication of approaching nuclear division is the contracted condition of the linin network to one side of the nucleolus, first described by Moore (1894) and later by others, and known as synapsis. The network does not appear to be wrapped about the nucleolus either in whole or in part during this stage. Immediately preceding this condition, the granules on the linin network are more prominent and stain more deeply with the gentian-violet, while the nucleolus takes the gentian only slightly, if at all. During synapsis the network does not takes the gentian, while the nucleolus stains a deep blue. There is no reason for considering synapsis in *Asclepias* as other than a normal condition.

The nucleus is too small for an accurate determination of the finer cytological phenomena at this or at later stages of division. After synapsis the reticulum opens out (Fig. 12), and stains deeply with the gentian, while the nucleolus stains less deeply than during synapsis. Fig. 16 shows what is

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[1] e. g. in the generative cell of *Pinus*. Ferguson (1901).

probably an early stage in the segmentation of the spireme, but the details of this process could not be accurately followed.

Before the formation of the nuclear spindle, the nucleus elongates in the direction of the long axis of the mother-cell as described by Strasburger[1] for *Senecio vulgaris.*

The mode of disappearance of the nucleolus and of the nuclear membrane, and the origin of the nuclear spindle, were not observed, though careful search was made for them. The nuclear plate stage of the division is shown in Fig. 17. The long axis of the spindle is always parallel to the long axis of the cell, and does not vary as described by Juel (1900) for *Carex acuta.*

Fig. 17 *a* is a detail of this division. Here the U-shaped chromosomes at the equator of the spindle are shown to be twelve in number. Fig. 8 represents a tissue-cell in which twenty-four chromosomes are shown in the nucleus. After careful and extended counting, this has been determined to be the full complement for *Asclepias,* as Stevens also states. Fig. 3 *a* is a detail of the division cutting off the tapetal cell from the pollen-mother-cell. Here there are fifteen chromosomes shown, indicating that reduction in number does not take place in this division. It thus becomes evident that numerical reduction takes place in the division figured in Fig. 17.

Cell-division follows directly upon the division of the nucleus. The two daughter-nuclei form at the poles, and the cell-plate appears well defined. The daughter-nuclei become separated from the spindle-fibres very early, and the development of the cell-plate into a cell-wall takes place without any connexion with the daughter-nuclei (Fig. 18). This has been described by Stevens (1898), who showed its significance in the light of Haberlandt's[2] (1887) declaration that the influence of the daughter-nuclei propagated along the connecting fibres is necessary for the development of the cell-plate into the cell-wall.

Inspection of Figs. 18 and 20 shows delicate kinoplasmic

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[1] 1879, p. 9.

[2] Quoted by Stevens.

radiations at the poles of the nuclear spindle. These radiations have been described for *Asclepias* by Raciborski (1897), and by Strasburger[1] as centrosomes. Raciborski says that if the sections are very thin and the lens strong enough, the supposed spherical centrosomes appear only as centres of radiating plasma-threads. My own slides agree with Raciborski's description.

THE SECOND DIVISION OF THE PRIMARY POLLINIUM-CELL.

The daughter-nuclei resulting from the first division of the primary pollinium-cell enter upon the resting stage (Fig. 19), with the chromatin distributed upon a linin reticulum. Gradually they take up a position at the centre of their respective daughter-cells, and in the meantime the spindle-fibres, which at first took a violet stain from the gentian-violet, lose this colour, and take on the yellowish brown colour of the cytoplasm. They gradually shorten and finally disappear (Fig. 20).

The nucleoli of the daughter-nuclei are very much smaller, relative to the size of the nucleus, than in the nucleus of the primary pollinium-cell. Stevens suggests from this fact that the substance of the nucleolus has gone to form the new structures in the cell. The writer found no direct evidence on this point.

The second division (Figs. 21, 22) is quite similar to the first. Synapsis was not observed and probably does not occur here. The divisions result in four cells, the structural units of the pollinium, arranged normally in a radial row. No exception to this was observed. The cytoplasm of the young pollinium-cell is much more fibrous in appearance than that of the mother-cell.

In no case were less than four pollinium-cells developed from each primary pollinium-cell, as Strasburger (1899) describes. In every instance each primary pollinium-cell divided and gave rise to four pollinium-cells arranged in a radial row (Fig. 23).

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[1] 1900, p. 166.

The outer wall of the pollinium-cells consists of part of the wall of the mother-cell together with the cross walls formed by the division of the mother-cell. Neither the pollinium-cells nor the tetrads (as in Orchidaceae[1]) ever become free, but form the pseudo-tissue known as the pollinium, a condition similiar to that described by Rosanoff (1865) for Mimoseae. As they enlarge, these cells press upon each other and thus assume various shapes (Figs. 24–26, 32, 34), and the radial arrangement also becomes obliterated at last (Fig. 34). At places where the cytoplasm has shrunken slightly from the outer wall it is easy to see that a delicate inner membrane has been formed (Figs. 23–25).

At a very early stage, there appear in the cytoplasm clearly defined circular areas of rod-shaped bodies which stain very densely like chromosomes (Figs. 24, 25). In older pollinium-cells these bodies become more and more distinct (Fig. 26) and the oval spaces containing them seem to be delimited by a distinct membrane, though whether or not this is more than the surface film of the cytoplasm may be a question. Such a condition as that shown in Figs. 28–31 seems to indicate that there is a true membrane developed here about a vacuole in which are the rod-shaped bodies. These areas suggest the nuclear-like bodies described by Juel (1900) for *Syringa rothomagensis*, but of course it can be only a similarity in appearance, for Juel's interpretation is not at all probable for the condition found in *Asclepias*. These rod-shaped bodies gradually disappear as the pollinium-cells develop, and this suggests that their function is nutritive. They often descend into the pollen-tube, but have never been found to travel as far as the micropyle. It is possible that the disappearance of so large a percentage of the nucleolar substance of the primary pollinium-cell may have some connexion with the appearance of these bodies. The writer purposes to study them further as soon as fresh material again becomes available.

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[1] Guignard (1882), p. 35.

THE FIRST DIVISION OF THE POLLINIUM-CELL.

The nucleus of the young pollinium-cell occupies an approximately central position in the cell. As the cell increases in size the nucleus enlarges considerably, and the nucleolus especially becomes relatively very large, and stains strongly with the gentian-violet. The chromatin granules are distributed evenly and apparently in a single row on the threads of the linin reticulum and stain deeply with the gentian.

As the time for division approaches, the nucleus migrates to the cell-wall of the pollinium-cell and becomes closely appressed to it, flattening out at the place of contact (Fig. 26). The nuclear membrane seems to disappear along this region, and the nucleus gives every indication of being firmly fixed to the cell-wall. Previous to the formation of the spindle, the nucleolus frequently fragments (Fig. 27), as in the case of the nucleolus of the mother-cell, but no wart-like bodies could be determined, and there was no suggestion as to the mode of fragmentation. There was no evidence that the nucleolus always fragments previous to this division.

The karyokinetic spindle is oriented at right angles to the cell-wall (Fig. 28), as described by Caldwell (1899) for *Lemna minor*, and Duggar (1900) for *Symplocarpus foetidus* and *Peltandra undulata*. It is probably of the 'multipolar diarch' type described by Strasburger (1900), though, on account of its minute size, this fact could not be determined with certainty. The spindle never becomes bipolar at either end as Caldwell and Duggar found, but the twelve chromosomes in the late anaphase stage are arranged at the ends of the spindle in rows parallel to the cell-plate (Fig. 29).

The formation of the cell-wall separating the two daughter-cells presents a very interesting figure. As the cell-plate lengthens, the ends of it bend toward the wall of the pollinium-cell in a manner similar to that described by Guignard (1882) for *Neottia Nidus avis*, by Duggar (1900) for *Symplocarpus*, and by Chamberlin (1899) for *Pinus Laricio*, forming an arc which cuts off a small lenticular cell. As the cell-plate curves back, the spindle-fibres spread out and radiate in all directions from the cell-plate. The ends of the fibres, except those attached to the nucleus, are free in the cytoplasm of the larger cell. These fibres shorten and finally disappear as the cell-wall develops, and the smaller cell is cut off quite completely from the larger one, though it does not become entirely free at first, as it is held by the wall of the pollinium-cell at the two points where this is joined by the newly formed wall (Fig. 31 *a*). Eventually this connexion disappears, and the smaller cell, surrounded by its own cell-wall, lies, as it were, in the little pocket of its sister-cell. The development of this cell-wall from the cell-plate seems to take place here much as described by Mottier[1]. By some unexplained process the smaller cell finally becomes completely surrounded by the larger one. It seems as if the larger cell grew around the smaller one, the cell-walls of the former breaking down at the point where they come in contact, for later, the smaller cell lies more deeply within the larger cell, and is surrounded by a membrane distinct from itself. No conclusive evidence, however, was found in support of this theory. The membrane is shown around the spindle in Fig. 32.

The nucleoli of both cells are relatively large and prominent objects, staining deeply with the gentian-violet (Fig. 31). No characteristic difference could be observed in the staining reaction of the two nuclei.

THE ORIGIN OF THE SPERM-CELLS.

The nucleus of the smaller cell divides in the pollinium-cell and, so far as observed, this division is accomplished before the germination of the pollinium-cells, as described by Schaffner (1896) for *Alisma Plantago*, Wiegand (1899) for *Potamogeton*, Merrell (1900) for *Silphium*, and others.

The nuclear spindle in this division is different from those observed in any of the other divisions. It is rather sharply

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[1] Mottier (1897), p. 192.

pointed at both ends, and much longer and more acuminate at one pole than at the other (Fig. 32). The more tapering pole appears to be somewhat bent to one side, but this was doubtless caused by the shoving of the microtome knife, or by some other mechanical injury. The difference in the length and manner of tapering of the two ends does not seem to be due to the way the section was cut, as the poles seem well defined and pointed at both ends, and not truncate at one end as would be expected had the microtome knife cut off one pole. Here also the nucleus was too tiny to permit of the details of spindle-formation, &c., being clearly made out.

The nucleus of the larger cell at this period possesses a rather conspicuous, vacuolated nucleolus, with a well-defined membrane, and a prominent nuclear reticulum. It would seem as if this division takes place rather rapidly, for in over ten thousand pollinium-cells examined, at a time when this division would be expected, only the single instance figured was found.

Cell-division follows the division of the nucleus of the smaller cell, each daughter-nucleus organizing about itself a portion of protoplasm, forming two cells, which later prove to be the sperm-cells. These cells remain enclosed by the delicate wall which originally surrounded their mother-cell (Fig. 33). No instance was found where any of these pollinium-cells failed to develop, as Schleiden (1849) has described.

GERMINATION OF THE POLLINIUM-CELLS.

When the pollinia are deposited on the stigma, or placed in a suitable germinating medium, the outer wall bursts after a time, and the fertilization-tube protrudes (Figs. 34, 35). Brown (1833) states that this tube does not branch, but the writer found rare instances of the branching of the tube in the tissue of the style.

The nucleus of the larger cell enters the fertilization-tube in advance of the sperm-cells, and the latter remain close together. Faint traces of the delicate wall that originally surrounded the smaller cell remain, even after the sperm-cells have advanced some way down the tube (Fig. 36), but finally the membrane completely disappears. Eventually the sperm-cells pass the tube-nucleus (Fig. 37), and are carried through the micropyle to the cavity of the ovule by the pollen-tube, which penetrates as far as the synergids. The fate of the tube-nucleus was not determined.

CONCLUSION.

There now remains the question first raised by Wille as to the true nature of the structures referred to above as pollinium-cells, and the homologies of the primary pollinium-cells. Juel's work on *Carex* has shown us that it is possible to have in the higher plants a structure physiologically a pollen-grain but morphologically something quite different. In fact, three alternatives may be stated as possible in the development of the sperm-cells in Angiosperms.

1. The normal development as described for most genera where the pollen-mother-cell, by two divisions at right angles to each other, gives rise to four pollen-grains, situated at the corners of a tetrahedron. Each grain ultimately develops two sperm-cells and a vegetative cell.

2. Division of the nucleus of the pollen-mother-cell into four nuclei, three of which abort, as in *Carex*. In this case only one pollen-grain develops from each mother-cell.

3. The development of the sperm-cells from the pollen-mother-cell without the so-called tetrad division of the latter, as suggested by Wille and others for *Asclepias*. This would be analogous to the development of the embryo-sac directly from the mother-cell in *Lilium*, but has not yet, so far as the writer knows, been demonstrated for any plant.

The second case is at once ruled out for *Asclepias*, since abortion of cells was not found at any stage in the development of the sperm-cells. Which of the two remaining cases, then, obtains here? Are the pollinium-cells pollen-mother-cells, as Wille and others have held, or true pollen-grains, as is to be inferred from Stevens's statement? The answer to this question is found in the history of their development. In the case of the development of true pollen-grains, and of the spores of Bryophytes and Pteridophytes, numerical reduction of the chromosomes takes place in the mother-cell. In *Asclepias* this reduction occurs in the primary pollinium-cell, the two successive divisions giving rise to four cells, each of which eventually develops two sperm-cells and a larger cell which germinates into a tube through which the sperm-cells pass to the ovule. The course of development, so far as the number of nuclear divisions, the place of the numerical reduction of the chromosomes, and the mode of formation of the sperm-nuclei are concerned, agrees precisely with what takes place in other plants that form pollen-grains. We must conclude, therefore, that the primary pollinium-cells are pollen-mother-cells, and that the pollinium-cells are true pollen-grains.

The chief peculiarity in the division of the primary pollinium-cell is in the arrangement of the spindles of the successive mitoses. Two different orientations have hitherto been described in Angiosperms. First, spindles at right angles to each other; second, spindles parallel but not in the same line[1]. In *Asclepias* we find a third variation, where the axes of the spindles are in the same line, resulting in the disposition of the four daughter-cells in a radial row. The only other instances of a similar arrangement are exceptions in the plants where they occur[2]. This arrangement, however, would not affect the homology of the structures.

The close union of the pollinium-cells, each surrounded by a firm cellulose wall, and the fact that neither they nor the tetrads are ever set free, would be misleading in attempting to homologize them. Brongniart's sections of the pollen-mother-cells of *Cucurbita maxima* suggest in appearance the cross sections of the pollinium of *Asclepias*, yet Rosanoff has shown for Mimoseae a similar condition of pollen-grains.

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[1] Coulter (1898) for *Ranunculus*; Fullmer (1899) for *Hemerocallis fulva.*

[2] Wimmel (1850) for *Fuchsia*; Wille (1886) for *Orchis mascula.*

SUMMARY.

1. The individual cells of the pollinium of *A. Cornuti* are true pollen-grains which never become free.

2. The divisions of the pollen-mother-cell are successive, and the spindles of the two divisions are oriented with their long axes radial and in the same line, so that each pollen-mother-cell gives rise to a row of four pollen-grains radially arranged.

3. The outer membrane of each pollen-grain is composed of the wall of the mother-cell (which does not dissolve), plus the cross walls formed by the two divisions of the mother-cell.

4. Each pollen-grain possesses an inner membrane which it develops about itself.

5. The generative cell divides, before the formation of the pollen-tube, into two sperm-cells, each of which travels down the pollen-tube, passing the vegetative nucleus on the way.

The above investigation was carried on in the Botanical Laboratory of Cornell University, and the writer wishes to express his best thanks and sincere appreciation to Professor G. F. Atkinson for exceptional opportunities offered by him, and for his constant encouragement and helpful suggestions.

ITHACA, N. Y.

Addendum :—Since the above paper was completed, Dr. Scott has called my attention to Corry's work on *Asclepias* (1883, 1884)[1]. This writer agrees with Schacht in considering the archesporium as unicellular. From the archesporial cell are derived by successive divisions in different planes the pollen-mother-cells ('primitive mother-cells'). The pollinium is composed of the special mother-cells, which are formed by

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[1] Corry, T. H., On the Mode of Development of the Pollinium in *Asclepias Cornuti*, Decaisne. Trans. Linn. Soc., London, 2nd Ser., Bot., vol. ii, p. 75, 1883.

—— On the Structure and Development of the Gynostegium, and the Mode of Fertilization of *Asclepias Cornuti*, Decaisne (*A. syriaca*, L.). Trans. Linn. Soc., London, 2nd Ser., Bot., vol. ii, p. 175, 1884.

the division of the primitive mother-cells in three planes at right angles to each other.

Corry also observed two nuclei in the pollen-grain, but considered the smaller one the vegetative nucleus, and the larger one the 'active' nucleus. No mitotic figures are given by him, and he does not trace in detail the steps in the development of the pollen.

There have also appeared two other papers on *Asclepias* since my own paper was completed, one by Fry (1901)[1], and the other by Strasburger (1901)[2].

Fry considers the archesporium as multicellular, and states that the primary sporogenous cells become spore-mother-cells without further division. All the spore-mother-cells of a sporangium divide into four, but the exact number of chromosomes in any division was not determined. The generative and tube nuclei are figured, and the author considers that the generative nucleus moves to the wall of the pollen-grain before division, and is cut off by a cell-wall. The fact that this nucleus was formed at its lateral location as a result of the position assumed by the nucleus of the young microspore before division was not observed. Fry also mentions and figures the rod-shaped bodies in the pollen-grain that stain like chromatin, but tests with several reagents failed to reveal their nature.

Prof. Strasburger's paper is especially interesting from the fact that in 1889 he stated that the pollen-mother-cells never divide. In the first part of the paper is briefly discussed the literature concerning the homology between the pollen-mother-cell and the embryo-sac mother-cell, and the author refers to the fact that a shortening of the ontogeny, similar to that which takes place in the development of the embryo-sac of some plants, has never been observed in the development of pollen.

Strasburger then takes up the case of *Asclepias* and reviews

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[1] Fry, T. C., Development of the Pollen in some Asclepiadaceae. Bot. Gaz., vol. xxxii, p. 325, 1901.

Strasburger, E., Eine Bemerkung zu der Pollenbildung bei *Asclepias*. Ber. d. deut. bot. Gesell., vol. vii, p. 450, 1901.

the literature, speculating on the probable development of the pollen-grain directly from the mother-cell. Then follow the results of his own researches. He considers the phenomenon of numerical reduction as the criterion for the pollen-mother-cell, and on this basis he considers the long cells which give rise to the individual cells of the pollinium as the mother-cells of the pollen. The full complement of chromosomes in *Asclepias* is held to be twenty, but the author states that he was unable to count them exactly. 'About ten' chromosomes were counted on the equatorial plate of the first division of the pollen-mother-cell.

The daughter-nuclei resulting from the first division of the pollen-mother-cell come to the full resting condition. The second division the author considers as 'homotypical,' but states that this cannot be proved on account of the smallness of the elements on the nuclear plate. Rod-shaped bodies are not figured, but the contents of many of the pollen-grains are described as especially coarse-grained, and eagerly devouring the stain. Possibly the rod-shaped bodies are here referred to.

The fact that the young pollen-grain divides into a larger vegetative and a smaller generative cell is mentioned and the completed division shown, but the karyokinesis is not figured.

Centrosomes were not found, and the author inclines very strongly to the opinion that they do not exist at all in the higher plants.

The above three papers all leave the identity of the pollen-grain and its ontogeny in *Asclepias* an open question, since the peculiarities of the division are so different from those observed heretofore in other types, and have led many to believe that a shortening of the process takes place in the members of this genus. It would remain an open question until it was proved that all the divisions concerned, up to and including the formation of the sperm-cells, are exactly the same in all essential points in *Asclepias* as those which occur in other Angiosperms. This identity is established for the first time by the developmental history as traced in the foregoing paper.

The full number of chromosomes was determined only after several hundred counts had been made, and Fig. 8, Plate VII, showing twenty-four elements on the division spindle seems almost conclusive evidence that the characteristic number for *Asclepias* is at least twenty-four.

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EXPLANATION OF FIGURES IN PLATE VII.

Illustrating Mr. Gager's paper on the Pollinium of *Asclepias.*

All the figures are drawn with the aid of a camera lucida, at 140 mm. projection. Tube length 160 mm. Nos. 1 and 34 with Zeiss 8 ocular, and Bausch and Lomb 2–3 objective. Nos. 2, 3, 4, 5, 9, 17, 18, 20, 21, 22–25, 35, 37, with Zeiss 4 ocular, and 2 mm. hom. imm. Nos. 3*a*, 8, 17*a*, 21*a*, with Zeiss 18 ocular, and 2 mm. hom. imm. No. 6 with Zeiss 4 ocular, and Bausch and Lomb 2–3 objective. No. 7 with Zeiss 12 ocular, and Bausch and Lomb 2–3 objective. Nos. 10–16, 19, 26–32 with Zeiss 12 ocular, and 2 mm. hom. imm. Nos. 33, 36 with Zeiss 8 ocular, and 2 mm. hom. imm.

Fig. 1. Cross section of bud about 1 mm. in diameter, showing the five young anthers and the young primary pollinium-cells radially arranged in the developing microsporangia. × 85.

Fig. 2. Cross section of portion of anther much younger than Fig. 1. Developing archesporium. × 450.

Fig. 3. Cross section of portion of anther older than in Fig. 2. Division of archesporium to cut off tapetal cell. × 450.

Fig. 3 *a*. Detail of division figure in Fig. 3. Fifteen chromosomes on equator of spindle. × 1525.

Fig. 4. Cross section of end of anther. Division complete, cutting off tapetal cell. × 450.

Fig. 5. Cross section of end of anther. Young primary pollinium-cell with characteristic large nucleoli. Tapetal layer developing peripherally from the sister-cells of the primary pollinium-cells, axially from the parenchymatous cells. × 450.

Fig. 6. Cross section of nearly mature anther. Primary pollinium-cells in first division. × 45.

Fig. 7. Cross section of microsporangium. Tapetal layer well differentiated. Primary pollinium-cells in first division. × 120.

Fig. 8. Tissue cell showing twenty-four chromosomes, the full complement for *Asclepias cornuti.* × 1525.

Fig. 9. Young primary pollinium-cells, showing vacuoles in cytoplasm and in nucleolus, wart-like bodies, and first appearance of the small granules in the cytoplasm staining like chromatin. × 450.

Fig. 10. Mature primary pollinium-cell. Fibrous character of the cytoplasm, and the small granules staining like chromatin. Nucleolus vacuolated and having a distinct membrane. Chromatin distributed on the threads of the nuclear reticulum. × 1225.

Fig. 11. Synapsis preceding the first division of the primary pollinium-cell. × 1225.

Fig. 12. Nucleus of the primary pollinium-cell soon after synapsis. Nucleolus vacuolated and having one wart-shaped body. × 1225.

Figs. 13, 14. Nucleoli of primary pollinium-cells showing stages that suggest fragmentation and a possible connexion between fragmentation and the wart-like bodies. The nucleoli have each one large vacuole. No. 14 had already given off one fragment. × 1225.

Fig. 15. Nucleus of primary pollinium-cell showing six nucleoli. The larger one suggests a possible origin of the wart-like bodies. × 1225.

Fig. 16. Nucleus of primary pollinium-cell showing early spireme. Two vacuoles in the nucleolus. × 1225.

Fig. 17. First division of the primary pollinium-cells. × 450.

Fig. 17 *a*. Detail of first division of primary pollinium-cell, showing the reduced number (twelve) of chromosomes. × 1525.

Fig. 18. Later stage in first division of the primary pollinium-cell. Cell-plate and kinoplasmic radiations from the daughter-nuclei. × 450.

Fig. 19. Nucleus after completion of first division of primary pollinium-cell. × 1225.

Fig. 20. Still later stage than Fig. 19 in first division of primary pollinium-cell. Cell-plate complete; daughter-nuclei moving to centre of daughter-cells. × 450.

Fig. 21. Second division of primary pollinium-cell. × 450.

Fig. 21 *a*. Detail of second division of primary pollinium-cell, showing the reduced number of chromosomes, twelve at the lower pole, eleven at the upper. × 1525.

Fig. 22. Second division of primary pollinium-cell, cell-plate stage. Kinoplasmic radiations from daughter-nuclei. × 450.

Fig. 23. Second division of primary pollinium-cell complete, showing the four radially arranged tetrads. × 450.

Fig. 24. Four tetrads from the same mother-cell, rounded, showing the delicate inner membrane and the early appearance of the rod-shaped bodies. × 450.

Fig. 25. Young microspore showing further development of rod-shaped bodies. × 450.

Fig. 26. Young pollinium-cell. The nucleus appears affixed to the cell-wall previous to the first division. The inner cell membrane and the rod-shaped bodies are prominent. × 1225.

Fig. 27. Fragmentation of nucleolus before first division of the pollinium-cell. Cf. Fig. 15. × 1225.

Figs. 28–31. The first division of the pollinium-cell. × 1225.

Fig. 32. Division figure in the formation of the two sperm-cells. × 1225.

Fig. 33. Division complete, forming the two sperm-cells. × 858.

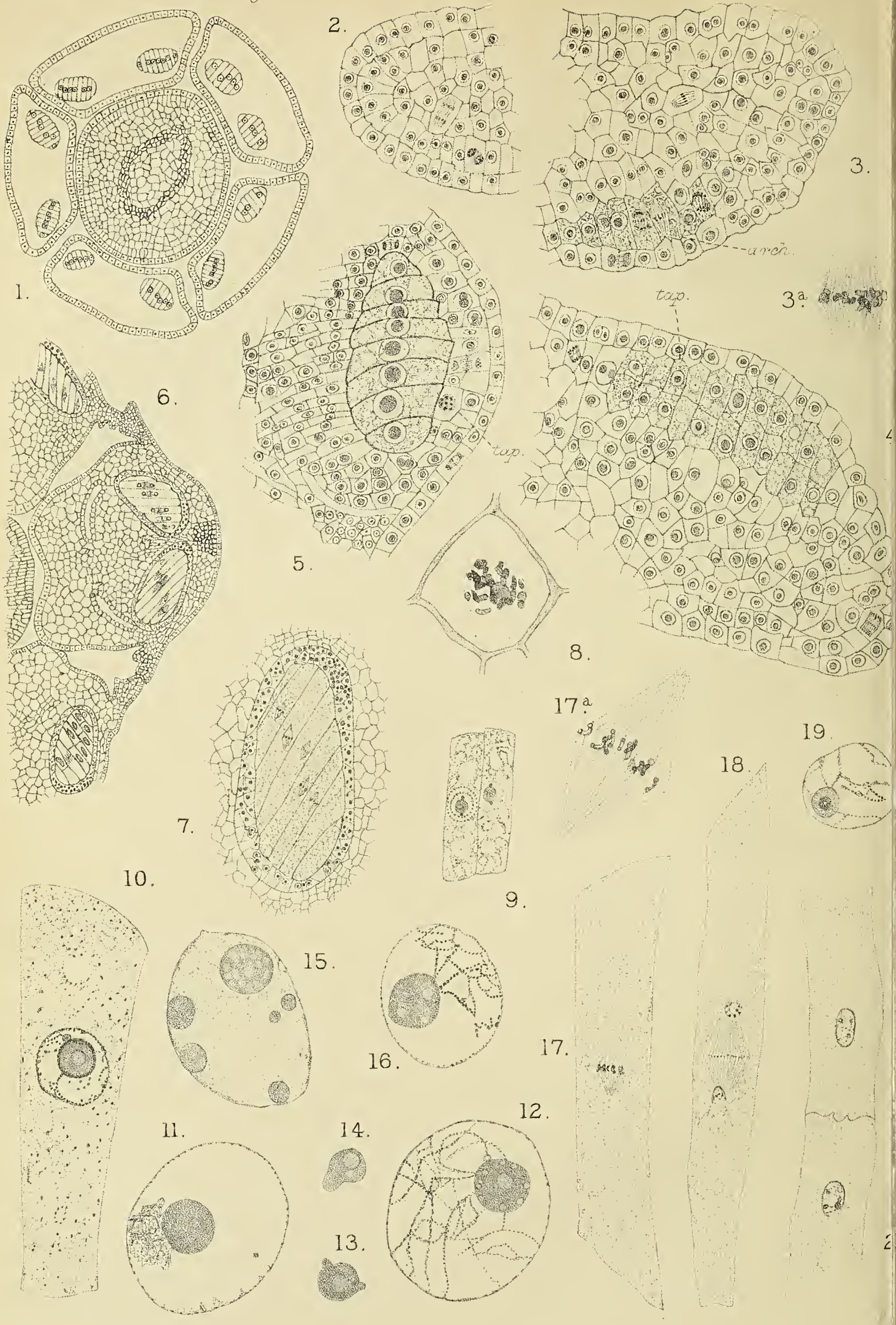
Fig. 34. Cross-section of pollinium. The pollinium-cells at the left have begun to germinate. × 85.

Fig. 35. Germination of mature pollinium-cell. × 450.

Fig. 36. Fertilization-tube germinated on the stigma. The tube-nucleus is in advance of the two sperm-cells. × 858.

Fig. 37. Fertilization-tube about to enter the micropyle. The two sperm-cells have passed the tube-nucleus. Two synergids and oosphere in the embryo-sac. × 450.

Annals of Botany.



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GAGER.— POLLINIUM OF ASCLEPIAS.

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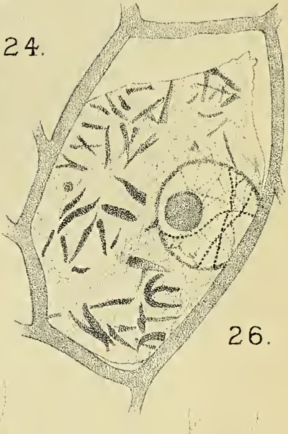

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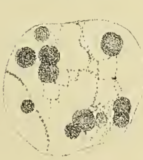

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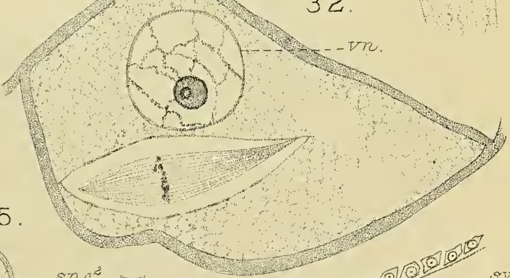

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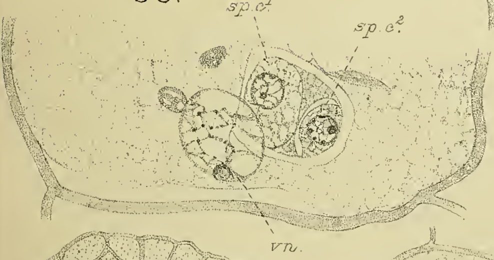

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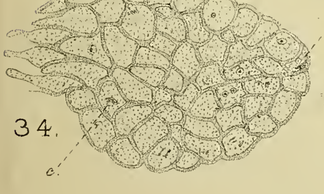

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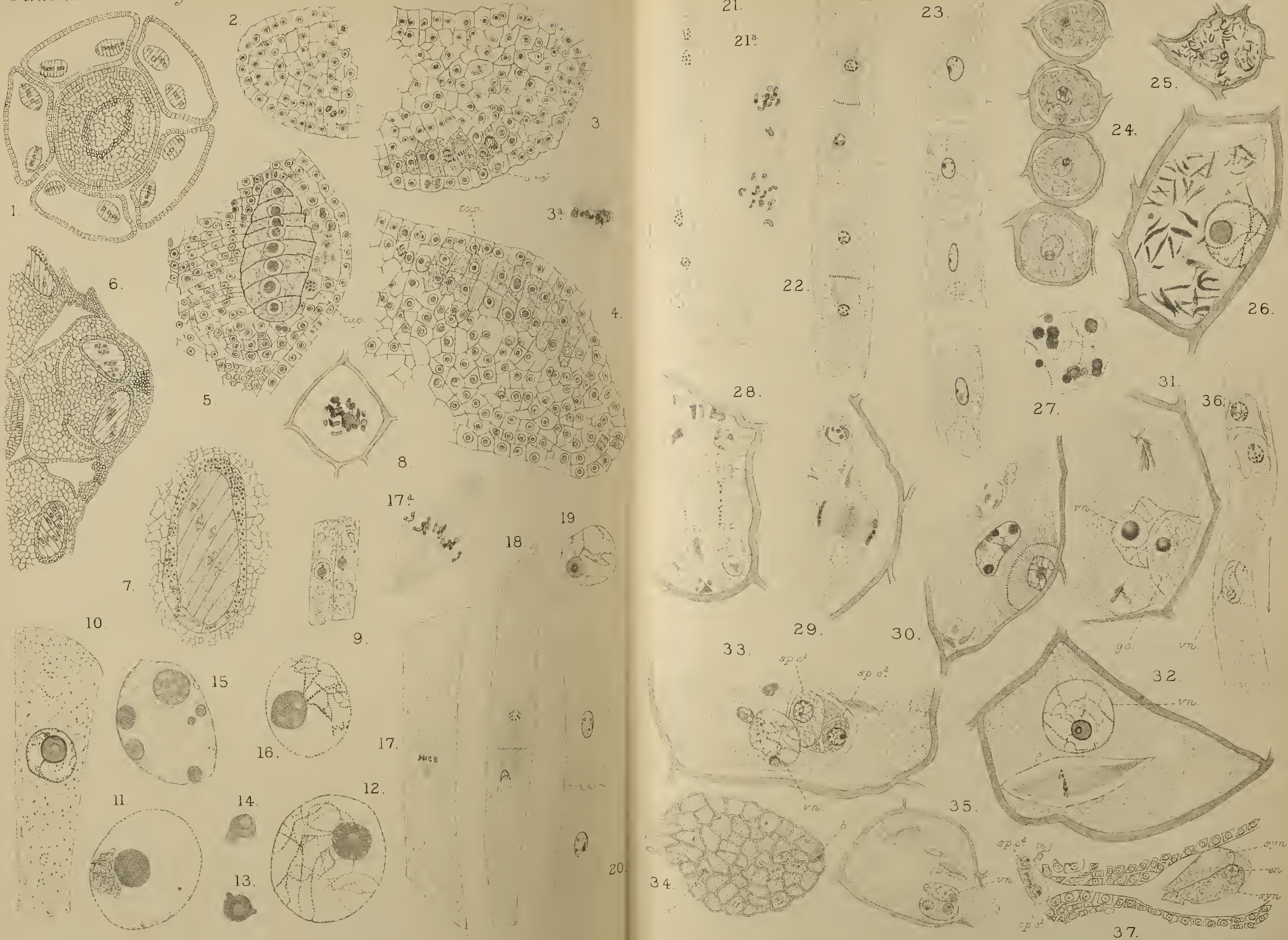

C. Stuart Gager del.

GAGER.— POLLINIUM OF ASCLEPIAS.

University Press, Oxford.

Morphological Notes.

BY

SIR W. T. THISELTON-DYER, K.C.M.G., C.I.E., F.R.S.

Director, Royal Botanic Gardens, Kew.

With Plates VIII and IX.

V. ABNORMAL FRUITS.—PRECOCIOUS GERMINATION IN A MELON.

THE melon figured in Plate VIII was kindly sent to me in July, 1898, by General, the Right Honourable Sir Dighton Probyn. It had been grown at Sandringham in the gardens of H.R.H. the Prince of Wales, now H.M. the King, and when cut open on the table at Marlborough House, the interior was seen to be filled with well-developed seedlings, as shown in the figure.

The specimen was so striking that it was eventually preserved in spirit and placed in the Kew Museums. Sir Dighton Probyn, however, kindly supplied me with two other examples from the same source, and exhibiting the same condition; these were submitted to careful examination by Mr. Horace Brown, F.R.S., who was working in the Jodrell Laboratory.

The whole interior of the melon when received at Kew was filled with well-developed young plants. Some of these were removed with the section of the fruit which had been cut away. The first point was to ascertain whether the young plants originated from intra-ovarian buds or from seeds. As

[Annals of Botany, Vol. XVI. No. LXI. March, 1902.]

will be seen, it was conclusively shown by the cases represented in Pl. IX, Figs. 1–3, that the young plants were the result of precocious germination.

Mr. Horace Brown kindly allows me to make use of the following notes which he drew up at the time:—

'The cotyledonary leaves of several plantlets measured 1½ in. long and 1¼ in. across, and were of a light-green colour. The hypocotyls were about 2 in. long and ¼ in. in diameter. The roots were well developed, with secondary root-fibres up to ½ in. in length.

'The plants had undoubtedly been produced from seeds, since in some cases the two halves of the testa were still attached to the cotyledons, and a few seeds were found in the early stages of germination. In one instance a tap-root was found to have actually penetrated the solid parenchyma of the pericarp to a depth of about ½ in., considerable force being required to withdraw it. This root is shown in Pl. IX, Fig. 2, the point to which it had penetrated being indicated by a dotted line. Penetration of the pericarp by the roots seemed to have occurred only in exceptional cases: for the most part they ramified amid the placentas and the broken-down ovarian tissue, from which they seem to have derived their nourishment.

'The dry weight of the plantlets far exceeded that of the seeds from which they were produced. Sixteen perfect seeds, after washing and drying, were found to weigh 0·1560 gram., or an average of ·0097 gram. for each seed, including the testa.

'The dry weight of one of the plantlets was 0·1929 gram., or about *twenty times* the weight of the seed from which it sprang. Hence there can be no doubt that the plant had availed itself of a large amount of nutriment which could only have been derived from the fruit.'

It is obvious that the physiological problem is one of considerable interest. The seedlings would speedily have exhausted the nutriment stored up in the seed, and their further development would have been arrested if there had been no external supply available. It is well known that the placental tissues in the melon break down into a copious sugary juice as the fruit ripens, and upon this it is perfectly clear that the young seedlings fed. This is not surprising in view of the well-known research of E. Hamilton Acton[1]. What is, however, more remarkable is that they were able to plunge their roots into the fairly resistent and less disintegrated tissues of the pericarp itself. This penetration is clearly shown in the lower part of the section on Plate VIII.

The cotyledons of the seedlings were, as stated by Mr. Horace Brown, distinctly green. He wrote to me:—

'I think the amount of chlorophyll present must be very small. It does not give a strong coloration to the alcohol in which the plants are immersed, and what little green there is fades rapidly on exposure to light.'

Subsequently he wrote to me further:—

'I amused myself by scooping the seeds out of a melon and testing the translucency of the walls of the pericarp. I was quite surprised to find how much light would pass through fully 1½ in. of the walls. In full sunshine there must be quite a respectable twilight in the neighbourhood of the seeds, and as I see Van Tieghem states that the formation of chlorophyll in etiolated seedlings commences in a diffused light which will barely permit small print to be read by the eye, we need not wonder that the ovarian seedlings contained a small amount of chlorophyll.'

Chlorophyll is formed in the cotyledons of Conifers in complete darkness[2] as well as in the precocious germination of seeds of the orange, which occasionally occurs. Such cases are, however, quite exceptional.

Whether the small amount of chlorophyll present in the melon seedlings was effective functionally to an appreciable extent may be doubted. The chemical changes which took place in the interior of the fruit would be accompanied by the evolution of carbonic acid, which would probably be present

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[1] Proc. R. S., Vol. xlvii, pp. 150–175.

[2] Sachs, Textbook, second ed., p. 743.

in any part of the internal cavity not occupied by fluid, in a greater proportion than in atmospheric air. But the illumination of the seedlings would be too feeble to allow of its being fixed and decomposed.

On the whole the nutrition of the seedlings closely approached that of a saprophyte. What is, however, noteworthy is that it must have been practically anaerobic. At any rate, it is evident that the working up of the disintegrated tissues of the parent melon into new living tissue required a minimum amount of oxygen.

Precocious germination in the melon had not previously been unknown, though it is apparently uncommon. Mr. Harry J. Veitch, a well-known authority, wrote that he had 'met with such occasionally before, but not often, but cannot offer any explanation for the occurrence.' The question then arose as to whether it was to be regarded as a case of physiological variation. This point seems disposed of by the following note from Mr. A. Mackellar, who grew the melons at Sandringham, for which I am indebted to Sir Dighton Probyn:—

'I have to-day cut open two melons in which the seeds have germinated and developed into nice-sized seedlings with broad green leaves. Each melon was grown on different plants, but the same variety, and was cut for a fortnight and kept on a shelf in the fruit room; previous to being cut they were kept on the plants for quite a fortnight after being quite ripe.

'No doubt the cause of the seeds germinating and growing in the melons is the unusual length of time the melons have kept fresh. I have seen seeds germinated in a melon before, but not so far developed as in this case. The melon in which the seeds germinated is called "Osberton." Along with it I grew "Hero of Lockinge," but no seeds in this variety germinated, neither did the melons keep quite so long. My reason for keeping the melons so long is that I had two houses in which the melons were ripe almost at the same time, forty in each house. There were no germinated seeds in any of the melons that were cut when first ripe.'

I may add that I subsequently heard of cases occurring elsewhere than at Sandringham in 1898. It is possible, therefore, that there were some conditions in the season of that year that were favourable to their happening.

Precocious germination occasionally happens in the orange and other species of *Citrus*, and appears to be not infrequent in the papaw (*Carica Papaya*); an instance is figured in the 'Gardeners' Chronicle' for December 10, 1887, p. 717. But in the vast majority of cases seeds remain in a dormant condition for a considerable time after maturity. This is no doubt an adaptive character which has been acquired in order to facilitate their dispersion to considerable distances. It might be expected, therefore, that in the case of gregarious plants whose seeds grow where they fall precocious germination might occur. It is actually met with amongst the *Dipterocarpeae*; Blume figures a case in *Dipterocarpus retusus*[1]. It is especially characteristic of the mangroves (*Rhizophoreae*). In the case of *Rhizophora* itself I quote the following from Brandis's 'Forest Flora,' p. 217:—

'Germination takes place in the fruit on the tree, the radicle protrudes soon after flowering as a long cylindrical body, thicker near the end, attains a length of 12 in. or more, and at length roots in the mud when the fruit falls.'

In *Bertholletia excelsa*, which has been described by Mr. Watson[2], the woody pericarp makes it impossible for the seeds to be dispersed before germination. This, therefore, takes place *in situ*, and the surviving seedlings are liberated by the final disruption of the decayed pericarp.

Something of the same kind would probably happen in the case of the melon. Its feral form would have a pericarp less succulent than that developed in cultivation; this would be penetrated by the roots, which would thence reach the soil, and the pressure exerted on the pericarp by the growing seedlings would eventually set them free by its disruption.

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[1] Flora Javae: Dipterocarpeae, tab. ii; reproduced in Engler and Prantl, Pflanzenfamilien, vol. iii. 6, p. 256.

[2] Annals of Botany, vol. xv. pp. 99–102.

VI. ABNORMAL FRUITS.—PLEIOTAXY OF GYNAECEUM IN ORANGE.

I was indebted to a correspondent for the abnormal orange figured in Plate IX. As is well known, the fruit of the orange ordinarily consists of a single row of carpels enclosed in a fleshy rind. In this case the axis has been prolonged and has given rise to another series of carpels forming a smaller fruit, which is entirely immersed in the external one. Although various abnormalities in the fruit of the orange have been figured, I have been unable to find any illustration of a similar one. Masters (Teratology, p. 75) figures a case in which the outer united whorl surrounds a confused mass of free carpels. A similar case is better figured by Risso and Poiteau (Histoire et Culture des Orangers, tab. 56).

A similar state of things to that now described is said to be characteristic of the so-called 'Californian Navel Orange.' This apparently originated as an isolated sport, as the trees in California are said to have been all propagated from one which is still preserved at Washington.

A. P. de Candolle regarded the 'rind' of the orange as developed from the torus or receptacle, which is usually regarded as an axial structure (Organographie, vol. ii. p. 41), and Masters (Teratology, p. 75) favours this view.

In the case now figured (Fig. 4) the external rind had been removed before it came into my hands. The carpels are united below to the prolonged axis, but are separated above to leave an open pit, at the bottom of which is the secondary fruit. The ventral surface of the carpels is clothed with the characteristic glandular 'rind.' This is shown in section in Fig. 5, where the glands are unusually prominent, and crowded together in groups with little intervening tissue. In such a position the 'rind' could hardly be an axial structure. The secondary fruit is shown in section in Fig. 6; except that the number of carpels is fewer than ordinary, there is no deviation from the normal structure.

Fruits with one series of carpels may be regarded as reductions from a more generalized multiseriate type. The interest of a case such as I have described is the proof that a tendency to revert to the more generalized type may still be latent.

THISELTON-DYER — ABNORMAL FRUITS.

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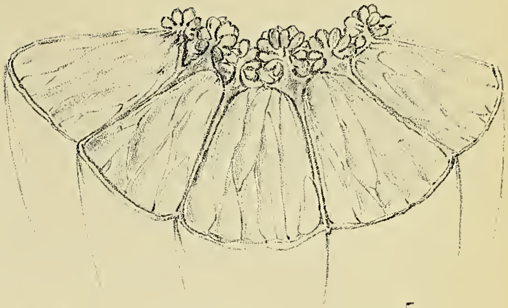

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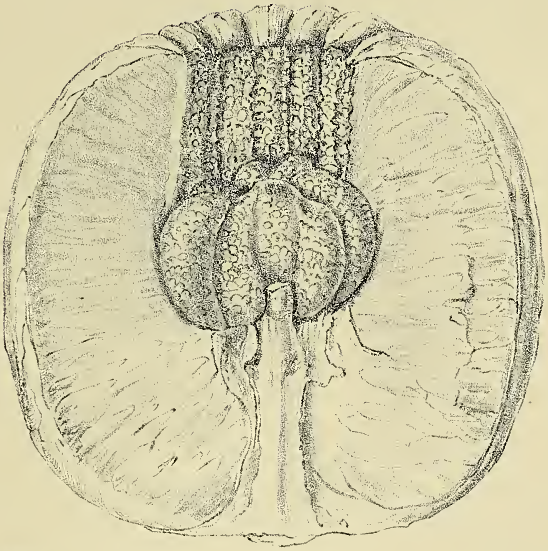

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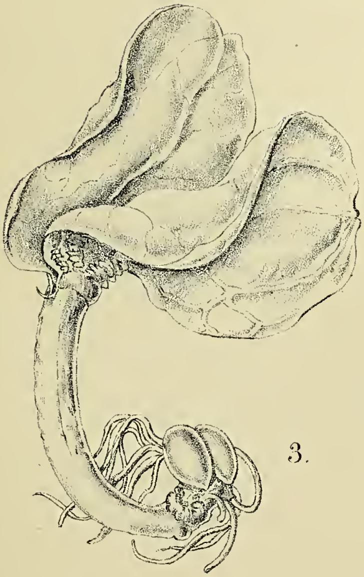

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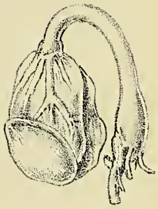

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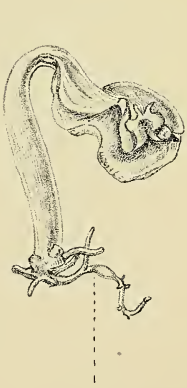

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THISELTON - DYER —— ABNORMAL FRUITS.

NOTES.

ON A NEW TYPE OF FERN-STELE, AND ITS PROBABLE PHYLOGENETIC RELATIONS.—Among the alcohol-material of various Ferns, recently brought home by one of us from the Malay Peninsula with a view to the study of their anatomy, were several species of the genus *Lindsaya*. In all of these, *L. orbiculata* (Lam.), Bed. (=*L. flabellulata*, Dry.), *L. orbiculata*, var. *tenera*, Bed. (=*L. tenera*, Dry.), *L. rigida*, Sm., *L. lancea* (L.), Bed. (=*L. trapeziformis*, Dry.), we found that the rhizome presented a constant type of stele which was entirely new to us, and of such striking interest in relation to the phylogenetic problems which have quite recently become prominent in the province of Fern-anatomy, that we determined to undertake a detailed investigation of all the species of *Lindsaya* that we could obtain. *L. Guianensis*, Dry., from British Guiana, growing in one of the pits at Kew, shows the same structure[1], while *L. retusa*, Metten., on the other hand, has a typical solenostele. The nearest affinities of *Lindsaya*, as determined by soral characters, appear to be with *Davallia* § *Odontoloma*; concerning one species of this section, *Davallia repens*, Desv., a very widely distributed Fern in the Indo-Malayan region and Polynesia, it is remarked in the 'Synopsis Filicum,' p. 93: 'Quite doubtful as between *Odontoloma* and *Lindsaya*.' It was of great interest, therefore, to find that the structure of the stem of this species conformed exactly to what we will call provisionally, for convenience' sake, the *Lindsaya*-type. We have since ascertained that the stele of *Davallia repens* has already been partially described by Trécul[2], who, however, missed the crucial character. The reference to this paper, which we had unfortunately overlooked, was given to us by Mr. Gwynne-Vaughan, who, it appears, is familiar with this type of structure.

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[1] Since the text of this note was written we have obtained fragments of the rhizomes of *L. scandens*, Hk., *L. davallioides*, Blume, and *L.* (*Schizoloma*) *lobata*, Poir. (= *L. nitens*, Blume) from herbarium-material, for which we are indebted to the kindness of Mr. R. H. Yapp, who collected it in Perak. In all these species we find the same type of stele.

[2] Structure du système vasculaire dans le genre *Davallia*, et en particulier dans *Davallia repens*. Comptes Rendus, t. 101, 1885.

[Annals of Botany, Vol. XVI. No. LXI. March, 1902.]

Our object in publishing the present note (pending the preparation of a detailed paper on the anatomy of *Lindsaya*, which, owing to the difficulty of obtaining alcohol-material of other species, must occupy several months) is to call attention to the *primâ facie* inferences to be drawn from the occurrence of this type of stele in the adult stems of these Ferns. The occasion is the more opportune owing to the publication in the last number of this journal of Mr. Boodle's paper on the anatomy of the Gleicheniaceae, in which he gives a detailed account of structures already partially described by Poirault (Ann. Sci. Nat., Bot., 1893), structures having an important bearing on the phylogenetic question which we propose to outline.

The '*Lindsaya*-type' of stele, at present known in the creeping rhizomes of the five species[1] (or four species and one variety) of *Lindsaya* enumerated above, and also in that of *Davallia repens*, is a monostele showing in cross-section a central mass of xylem, consisting of scalariform tracheids intermingled with parenchyma, and surrounded by a complete ring of phloem, pericycle and endodermis, as in *Gleichenia* or *Lygodium*, but differing most strikingly from these Ferns *by possessing, in addition to the external phloem-mantle, a strand of phloem completely embedded in the xylem* near the dorsal surface of the latter. This strand of internal phloem consists of typical sieve-tubes mixed with parenchyma and separated by one layer of similar parenchyma from the surrounding xylem (Fig. 9).

As the node is approached from below[2], the strand of internal phloem forms a dorsal projection on the side corresponding to the leaf-insertion, thrusting up the dorsal 'vault' of xylem, as Trécul calls it, on that side (Fig. 10). An accumulation of parenchyma arises in the phloem-strand immediately ventral to this bay, and in the midst of this accumulation endodermal cells appear which soon come to enclose a few parenchymatous cells (Fig. 10). The dorsal bay of phloem rapidly extends laterally outwards, and at the same time the internal endodermis with its enclosed parenchyma moves up dorsally behind it, so that the phloem of the bay assumes the form of a slightly curved plate lining the inside of the thrust-out xylem arc on one side of the dorsal vault. The vault now breaks at the point near its centre where

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[1] The addition of the three species mentioned in the first footnote on p. 157 raises the number to eight.

[2] The following description is taken from *Lindsaya orbiculata*, but the other species agree in essentials.

this arc joins the unaltered part, placing the internal and external phloem in communication: the free end of the arc rapidly raises itself, at the same time rotating laterally outwards, while its internal phloem (derived from the phloem of the bay) closely follows it, so that a wide gap is formed in the stelar tissues; as the free end of the arc moves away from the stele the internal endodermis approaches the outer one, they touch and open, thus placing the internal strand of parenchyma, which has dilated considerably, in connexion with the cortex (Fig. 11). Meanwhile the arc of xylem, with its internal and external phloem, raises itself further from the dorsal surface of the broken stele, deepens its concavity so as to take on a gutter-shaped form (Fig. 12), finally detaches itself from the

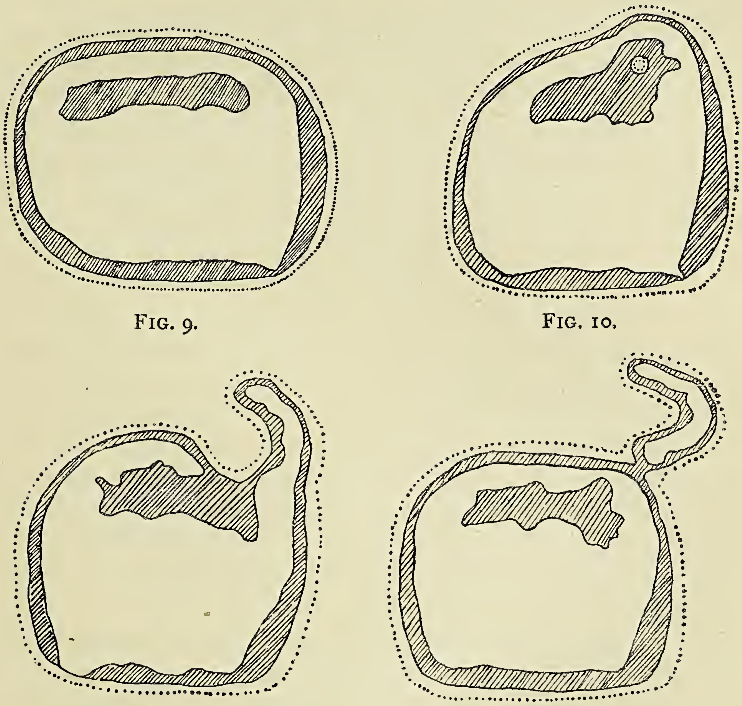

FIG. 9. FIG. 10.

FIG. 11. FIG. 12.

Transverse sections of stele of rhizome of *Lindsaya orbiculata*. The phloem is diagonally shaded, the xylem, pericycle and endodermis left blank. The outer limit of the endodermis is indicated by a dotted line. Fig. 9. Internode. Figs. 10–12. Detachment of leaf-trace.

corner of the stele, and becomes the meristele of the petiole, its plane of symmetry being now parallel with the dorsal surface of the stele. The broken dorsal vault becomes again complete before the meristele is quite detached (Fig. 12), but in such a way that a bay of the internal phloem is left, in the same position as the one below the node. This superior bay gradually dies out, and the stele returns to its internodal condition.

The first point of interest about this type of stele is its correspondence with the condition found by Leclerc du Sablon[1] in the young stems of *Pteris aquilina* (Fig. 15) and *Nephrodium molle*, and the similar condition found by Mr. Boodle in *Anemia Phyllitidis* (Anatomy of Schizaeaceae, pp. 389–390, and Fig. 26, Ann. of Bot., XV, 1901). In these Ferns the central part of the protostele of the first-formed portion of the stem consists of a solid cylinder of xylem as far as the exit of the first leaf-trace. Close above this point there arise in its centre a few sieve-tubes. The appearance of this strand of phloem in the midst of the xylem gives to the stele the same essential character as that of the internodes of the adult rhizome of *Lindsaya* (Fig. 14). At the departure of some later leaf-trace, the hollow cylinder of xylem (together with the mantle of external phloem, pericycle, and endodermis) is broken, and the endodermis dips down into the centre of the now horseshoe-shaped stele. By the closing up of the gap formed by the departure of the leaf-trace, and the inclusion within the stele of a strand of parenchyma surrounded by a layer of endodermis, the solenostelic structure is obtained (Fig. 18). Higher up still the solenostele breaks into two stelar arcs.

By the writings of Mr. Gwynne-Vaughan[2] and of Dr. Jeffrey[3] we have recently been made familiar with the idea that solenostelic and siphonostelic structure may be phylogenetically intermediate between protostelic on the one hand, and dialystelic or astelic on the other. The solenostelic structure in the young stem of *Pteris aquilina* is ontogenetically transitional between the protostelic structure of the base of the first-formed stem, and the dialystelic ('polystelic') structure of the rhizome; and so in the

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[1] Recherches anatomiques sur la formation de la tige des Fougères. Ann. Sci. Nat., Bot., 1890.

[2] Polystely in the genus *Primula*, Ann. of Bot. xi, 1897. Studies in the Anatomy of the Solenostelic Ferns. I. Loxsoma. Ann. of Bot. xv, 1901.

[3] The Morphology of the Central Cylinder in the Angiosperms. Trans. Canad. Inst., 1900.

Type of Stele with internal phloem alone.

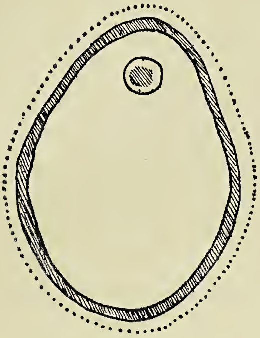

FIG. 13.

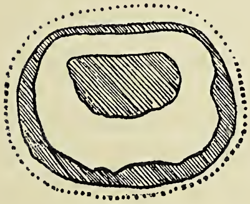

FIG. 14.

FIG. 15.

Type of Stele with internal endodermis enclosing parenchyma or sclerenchyma within the internal phloem.

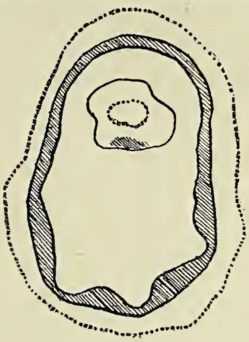

FIG. 16.

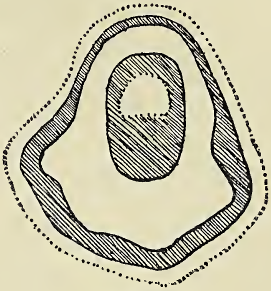

FIG. 17.

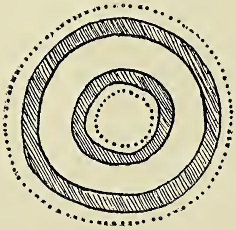

FIG. 18.

FIG. 13. *Gleichenia flabellata* just below node (from Boodle). FIG. 14. *Lindsaya rigida*, internode. FIG. 15. *Pteris aquilina*. Transitional structure in primary stem (from L. du Sablon). FIG. 16. *Gleichenia dichotoma* just below node (from Boodle). FIG. 17. *Davallia* (*Microlepia*) *pinnata* below node. FIG. 18. *Pteris aquilina*. Transitional structure above that of Fig. 7 (from L. du Sablon). Phloem diagonally shaded. External limit of endodermis a dotted line.

adult stems of many Ferns the solenostelic structure (specially predominant in the middle grade—Prof. Bower's Gradatae—of the Fern series) is phylogenetically transitional between the protostelic structure almost certainly primitive for the Ferns, and the dialystelic condition characteristic of the great majority of the higher forms (Polypodiaceae). The young plant of these higher forms (in certain cases at least) starts by laying down the protostelic structure, but very soon this gives place to the solenostelic, which in its turn passes into the dialystelic arrangement characteristic of the adult stem. The great interest of the *Lindsaya*-type of stele is that it appears to furnish a phylogenetic link hitherto wanting in a mature stem (see Boodle, Anatomy of Schizaeaceae, p. 407, Ann. of Bot., XV, 1901) between the protostelic and the solenostelic structure; and this view is distinctly supported by the occurrence of the same type at the same stage in the ontogenetic series of the Ferns already mentioned.

The chief objection to this hypothesis of the morphological position of the *Lindsaya*-stele is the fact that the Lindsayeae are relatively advanced Ferns so far as their sori are concerned, coming into Prof. Bower's highest grade, the Mixtae, with a flat receptacle, no definite order of development among the sporangia, and a nearly if not quite vertical annulus. The great majority of the rest of the Mixtae (Polypodiaceae in the wide sense) have dialystelic structure. There is, however, evidence that the *Lindsaya*-type is not wanting among the more immediate allies of the Lindsayeae, the Davallieae, while the Dennstaedtiaceae, which appear to come immediately below in the series, are predominantly solenostelic; whether they will supply evidence of similar transitions we do not as yet know. It is not to be supposed that all the morphological characters of the Ferns will evolve strictly *pari passu*, and if an anatomical character of a relatively low grade is well adapted to general conditions of habit and the like, there is nothing surprising in its being retained in plants in which evolution of the sorus has advanced considerably. This, however, is a large question, which we hope to treat more fully in our detailed paper. We may expect also a considerable elucidation of the whole of these relations as a result of Mr. Gwynne-Vaughan's extended researches on the solenostele, the second instalment of which, dealing with the Cyatheaceae in the wide sense, and the Davallieae, we may hope to see published within the next few months.

Meanwhile we may point out that there are not wanting indications of the steps by which protostelic structure was changed into the *Lindsaya*-type. Mr. Boodle has described in his last paper[1] the structure of the stele of the node of *Gleichenia* (subgenus *Mertensia*) *flabellata*. As the node is approached from below, a 'nodal island' of parenchyma, in the midst of which are some sieve-tubes, appears in the xylem of the stele near its dorsal surface, so that at this level the structure of the stele in the essential relations of xylem and phloem is identical with that of *Lindsaya*. The description of the arrangement of tissues above this point, involving the detachment of the leaf-trace, strikingly agrees with the facts we have described in the case of *Lindsaya*, the main differences being the much bulkier and sclerotic strand of tissue enclosed by the internal endodermis in *G. flabellata*, and the fact that the two endodermes oin in the latter only after the xylem and phloem of the meristele have become detached from the stele at the other end; in this last respect *G.* (*Eugleichenia*) *dicarpa* is much more like *Lindsaya* (see Boodle, Fig. 22).

The petiolar meristele of *Gleichenia* is, we are inclined to believe, primitively collateral in structure, i. e. with phloem belonging only to its outer (lower) side. The internal phloem, which passes round the incurved ends of the meristelic xylem, as seen in cross-section, and in extreme cases (*G. dicarpa*) becomes almost continuous round the concave side of the dorsal bay of xylem, may be regarded as an inward extension of the external phloem, developed to meet the increasing needs of conduction. But such an extension had to be provided with an attachment to the phloem of the stele. At first its attachment to the ordinary external phloem of the stele seems to have been mediated by the downward extension of the bay of the meristele (*G. dicarpa*, Boodle, Fig. 20), which in its lower part contains phloem alone (cf. our Fig. 11). In other cases we must suppose the downward extension of this bay became completely enclosed in the xylem of the stele, forming a 'nodal island' consisting not only of phloem but also of a downward extension of the central parenchyma or sclerenchyma of the meristele, enclosed by an internal endodermis. Of what precise benefit to the plant this blind downward extension of the internal phloem (or its corresponding upward extension, described by Mr. Boodle in *G. dichotoma*) may be, it is difficult in the present state of physiological anatomy to guess. But if we imagine the

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[1] Boodle, Gleicheniaceae, p. 723.

phloem of the inferior and superior nodal islands continued respectively through the lower and the upper internodes till they meet corresponding extensions from the next nodes below and above, it is clear that we have reached the *Lindsaya*-type, and have obtained an internal stelar phloem-system forming a satisfactory attachment for the internal phloem of the meristele, which has now become completely concentric.

Finally, with regard to the change from the *Lindsaya*-type to that of the solenostele, we have the strand of parenchyma or sclerenchyma surrounded by its own endodermis in the concavity of the meristele, already usually carried down into the 'inferior phloem island' in *Gleichenia*, and into the 'inferior phloem-bay' in *Lindsaya* (Fig. 10). We have only to imagine it continued down in the centre of the internal phloem, till it reaches the next node, and the change is made. In *Davallia* (*Microlepia*) *pinnata* we have found this change apparently in progress. Immediately above the node the stele has the *Lindsaya*-type with internal phloem alone, but a stout strand of sclerenchyma continuous with that lying in the concavity of the horse-shoe-shaped open meristele, and surrounded by an endodermis, penetrates the internal phloem of the stele, ending blindly some little distance above the next node below (Fig. 17). The appearance presented corresponds strikingly with Boodle's Fig. 17, which we have reproduced as Fig. 16, of the node of *Gleichenia dichotoma*, representing a section taken just below the separation of the xylem of the leaf-trace.

The above is a very brief indication of our ideas as to the probable phylogenetic meaning of the new facts. In this preliminary note they are necessarily expressed imperfectly and somewhat dogmatically. Detailed qualification would be out of place, but we may perhaps point out that we do not intend to convey the impression that in our opinion the method we have roughly sketched is necessarily the *only* way in which the solenostele has arisen in evolution. Doubtless in some cases the pith may have come before the internal phloem, and in such a case the stage represented by the *Lindsaya*-type would not be passed through at all.

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February, 1902.

AN ALGA-LIKE FERN-PROTHALLIUM.—The Fern-prothallium, which forms the subject of this note, is so remarkable in character, and presents features of such general biological interest, that I have thought it desirable to offer a preliminary account.

The prothallium belongs to *Schizaea bifida*, a Fern confined to New Zealand and certain parts of Australia[1].

The prothallium is quite unlike the ordinary types of Fern-prothallia, and is strongly suggestive of an Alga. A good specimen has the form of a soft-looking round green cushion, from a quarter of an inch to half in diameter. Erect green filaments can be seen projecting above the general surface even with the naked eye.

Closer examination shows that it is composed of branched filaments. Each filament is a single row of cells, the cells being rather large, about ·25 mm. in length and a third or fourth of this in thickness, but may be longer where less illuminated towards the centre of the prothallium.

Some of the filaments lie on the surface of the ground, and from these erect filaments are given off which usually branch abundantly, and may rise to the height of 3 and 4 mm.

The development of the branches can be readily followed. Each filament has an apical cell, from which segments are cut off behind; these segments do not divide again, though any one may bud out laterally at its upper end to form a branch which repeats the features of the parent filament. Each segment commonly gives rise to but one branch, but at the centre of the prothallium branching may be more crowded. Not all the segments give rise to branches; the last branch formed may be several cells behind the apex of the parent filament. A few filaments spread through the underlying soil, and these are colourless, but otherwise of similar character, except that they bear at intervals distended, bladder-like cells, which carry short, brown root-hairs, usually two to each of the distended cells.

Filamentous prothallia are already known in *Trichomanes*, and, as is well known, small more or less filamentous prothallia occur in many Ferns when spores are sown too quickly. But these starved filamentous prothallia bear male organs only.

The prothallia of *Trichomanes* are incompletely filamentous, for although the antheridia are borne by the filaments, the archegonia

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[1] The filamentous prothallium of another species of the genus is already known; see Elizabeth G. Britton and Alexandrina Taylor, Life History of *Schizaea pusilla*. Bull. Torrey Bot. Club, New York, vol. xxviii, 1901.

occur only on archegoniophores, which are masses of meristematic cells. The prothallia of *Schizaea*, however, are *completely filamentous throughout*, not only the antheridia but also the archegonia being produced on filaments.

Both kinds of sexual organs may be produced on the same prothallium, but are carried on separate branches. The archegonia are produced near the base of an erect filament, and occupy the position of lateral branches at the upper end of a cell. The cell grows out, forming a protuberance which is directed obliquely upwards. This is then cut off as an archegonium mother-cell. A second and a third mother-cell may be produced by the same cell. Often enough these are the only archegonia produced by the upright filament, but I have seen a second group of archegonia produced by the segment above. The filament which thus produces the mother-cells of the archegonia continues to grow upwards, and may be abundantly branched; the cells are not distinguishable from those of the ordinary sterile branches.

The mother-cell cut off in the way described gives rise to the whole of the archegonium. This, when mature, is flask-shaped, the neck is rather thick and of moderate length; it is composed of usually 3 tiers of cells, 4 in each tier. The cells of the terminal tier are longer than the others and diverge widely when the archegonium opens. The neck curves out below into the rather wider venter, which is narrowed a little to the base of attachment of the archegonium.

It will be seen that the archegonium is remarkable amongst Ferns in having a free venter, and in this respect it resembles the archegonia of typical Bryophytes. The neck, however, is short and not of considerable length as in Bryophytes.

Antheridia are produced in considerable numbers; they occur more or less regularly on both sides of an erect filament, which may itself terminate in an antheridium. Rather short cells, which obviously correspond to branches, grow out and curve upwards. Uusually one, but sometimes two such cells are formed from each cell of the filament from the base upwards. At the end of the lateral cell a segment is cut off as the antheridium mother-cell. The development of the antheridium follows the simple type already known in *Anemia*; and the wall which cuts off the cap-cell is nearly transverse, but it is, perhaps, somewhat more primitive. The mature antheridia are ovoid in form, the cap end being the narrower. The spermatozoids are of the usual type in Ferns.

After the first antheridium is formed the basal cell, from which the first antheridium mother-cell was cut off, may swell out laterally, and a second segment is then cut off and develops into an antheridium. Similarly a third antheridium may be formed from the basal segment.

It need hardly be said that the main, though not the sole, biological interest which attaches to the present remarkable prothallium, centres round the question whether its structure is primitive or not. Two different interpretations may be placed on such a filamentous prothallium:—

(1) It may be regarded as directly representing an algoid ancestor in the phylogeny of *Schizaea* and of Ferns generally;

(2) Or the filamentous structure may be considered to be a secondary adaptive character of no phylogenetic import.

Goebel[1] has discussed the question with reference to the filamentous prothallium of *Trichomanes,* and has pointed out that it is not clear why, amongst the Hymenophyllaceae, the species of *Trichomanes* should in general possess a filamentous prothallium, whilst those of *Hymenophyllum* are flattened cellular expansions, for they live under similar conditions. It is difficult to see, therefore, how the filamentous condition can be adaptive. The filmy character of the leaves of the Hymenophyllaceae may be an adaptive character, due to their moist environment. Species of other genera of Ferns, living under similar conditions, show corresponding adaptive modification of their leaves. But so far as is known their prothallia are never like those of *Trichomanes,* but resemble the prothallia of forms to which they are respectively related.

If we now compare *Trichomanes* with *Schizaea bifida* we find that the latter lives under conditions which are quite distinct from those necessary for *Trichomanes.* We can hardly suppose that it is moisture which has called forth the filamentous character, for Fern-prothallia generally can only grow where moisture prevails. Four other species of Fern were found growing with the present prothallia, and all have prothallia of the type common in the Polypodiaceae.

The prothallia of *Schizaea bifida* were found growing, some on damp sandy soil, others on clay soil. The ground was in places bare, but often partly covered with a growth of small Mosses and Hepaticae, and no doubt the filaments are sometimes an advantage to the prothallium in enabling it to rise up to the light between its

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[1] Organographie der Pflanzen, p. 421.

neighbours. But such a growth of Mosses and Hepaticae is of such general occurrence that, if the filamentous condition be an adaptation for this special end, one can only speculate why it has not arisen in a host of other Fern-prothallia to which it would be equally useful.

Again, in *Trichomanes*, although the prothallium is generally filamentous, yet small cellular bodies or even flat expansions, which remind us of other Fern-prothallia, are formed to carry the archegonia. Goebel explains this as due to the need of a better supply of nutriment for the archegonium. On the other hand the existence of such cellular bodies might be quoted as evidence of reduction from the more usual form of prothallium. But if the retention of cellular masses for the nutrition of the archegonia was needful in the case of *Trichomanes*, why, we may ask, is a similar feature absent from the prothallium of *Schizaea*? It is difficult to imagine that the absence of the meristematic archegoniophore is an adaptive feature.

It would seem, therefore, that Goebel's explanation is the correct one, and that the condition of things in *Schizaea* is a primitive condition, even more so than that existing in *Trichomanes*.

The whole vegetative structure of the prothallium of *Schizaea* is eminently suggestive of one of the filamentous Algae. That the Ferns as well as other higher plants have descended from an aquatic ancestor is of course rendered probable by the character of the ciliate spermatozoids. But a specially interesting feature in *Schizaea* is the mode of development of both kinds of sexual organs as morphological equivalents of the ordinary branches of a filamentous prothallium, a mode which explains the character of these organs. Are we not therefore justified in regarding *Schizaea* as a primitive form?

The question, however, is not one which can be decided by the evidence derived from a single form, but must rest on a broad basis of comparison of the development in the different families of Ferns. Nevertheless the probability of the filamentous prothallium being primitive is increased by its occurrence in the separate families of Hymenophyllaceae and Schizaeaceae. When we add to this the frequency of a filamentous stage at the beginning of the development of so many different types of Ferns, and the tendency to form filamentous prothallia when nutrition is inadequate, we have accumulated a weighty body of evidence in favour of the hypothesis.

It may be observed that the characters of the Schizaeaceae show that the family is a relatively primitive one[1]. Bower places it in his group 'Simplices,' which on comparative grounds he regards 'as being relatively primitive and less specialized types of Ferns.' The records of Palaeontology show that the group is an ancient one. *Senftenbergia* from the Carboniferous and *Klukia* from the Jurassic are referred by Potonié [2] to the family, whilst the living genus *Lygodium* dates from the Cretaceous. Apparently the family has undergone but slow modification. Hence, without committing ourselves to the view that gametophyte and sporophyte undergo modification at the same rate, have we not some warrant in looking for primitive characters in the prothallium?

In speaking of the prothallium of *Schizaea* I have preferred to compare it with an Alga rather than with the protonema of Moss, for it has appeared to me more suggestive of the former. But, in any case, the protonema of the Bryophyta is itself, in many respects, comparable with an Alga. The prothallium of *Schizaea* may be compared with the protonema of the Bryophyta, and we have, moreover, an additional point of resemblance to the Bryophyta in the free archegonial venter. But it is to be noted that the archegonium of *Schizaea* is carried upon a filament, whereas this does not appear to be the case in any known Bryophyte. The male plant of *Buxbaumia* makes the nearest approach to *Schizaea* in having the antheridia directly borne on the protonema. But the stalked antheridium is protected by a leaf-like lobe (which is without chlorophyll), so that the filamentous character is not completely retained. In the female plant of *Buxbaumia* the protonema produces a more considerable gametophore, consisting of a small stem with a few simple leaves, which are also without chlorophyll. The archegonium is at the apex of the stem. Goebel (l. c. p. 350) is inclined to consider *Buxbaumia* as a relatively primitive form which has remained at a stage that other Mosses have passed through. He suggests that such a form may have arisen from a filamentous Alga in which the branches that developed the sexual organs have become more complex. If this view be correct and *Buxbaumia* is not a form reduced in accordance with a supposed saprophytic habit (which Goebel regards as still unproved), we have an interesting form for comparison with *Trichomanes*. Even if *Buxbaumia* be reduced, the gametophores of the

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[1] Bower, Philosophical Transactions, 1900, B. Vol. 192, p. 123.

[2] Die natürlichen Pflanzenfamilien, Th. I., Abt. 4, p. 371.

Phascaceae are but little further developed than those of *Buxbaumia*. But what I wish to point out here is that the prothallium of *Schizaea* is at just the same stage of evolution as the hypothetical Alga postulated by Goebel as the ancestor of the Mosses.

Many other points call for consideration, but their discussion would go beyond the scope of such a preliminary account as the present, and must be deferred. I hope, however, to shortly offer a further account of the present prothallium as well as those of other species of *Schizaea*.

It will be seen that, whatever interpretation we place upon it, the prothallium of *Schizaea* is a highly interesting form. But does not the weight of evidence justify its recognition as a relatively primitive type, which probably represents the character of the common Alga-like ancestor of both Ferns and Bryophytes more nearly than any plant hitherto described?

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ON AN UNEXPLAINED POINT IN THE ANATOMY OF HELMINTHOSTACHYS ZEYLANICA.—It has not been, I believe, hitherto recorded that in *Helminthostachys zeylanica* there are a number of small passages or canals running through the cortex from the neighbourhood of the stele to the external surface of the rhizome. These canals bear a definite relation to the leaf-insertion: one being situated in front of each leaf, opening out on to the surface immediately above the insertion of the 'stipule' of the leaf to which it belongs, not in the median line of the rhizome but well down towards the under side. The passage may, in fact, be regarded as a backward prolongation into the cortex of the space that lies between the 'stipule' and the stem as a narrow canal running right up to the stele.

The presence of these canals exercises a considerable influence upon the stele, and occasions certain modifications in structure which, I think, may best be explained by describing the manner of the departure of the leaf-trace, which the woodcut is intended to illustrate. The figure *A* is a diagrammatic longitudinal section of the stele in the neighbourhood of the leaf-gap, while *B* and *C* represent transverse sections taken at the levels *aa* and *bb* respectively. The xylem is represented by dark shading, the phloem by light, the parenchymatous tissue being left unshaded; the dotted line indicates the endodermis. The leaf-trace is supplied with a large arc of xylem which separates off from the stele, leaving a gap in it which affects the whole of the vascular ring, endodermis, phloem, and xylem; so that the parenchyma in the centre of the stele becomes continuous with that of the cortex. Passing towards the apex of the stem the xylem ring soon becomes complete again, and shortly afterwards so does the (external) endodermis, but the phloem ring remains for a considerable time interrupted by a ridge or strand of parenchyma continuous with that which forms the leaf-gap, lying on the outside of the xylem ring, and eventually covered in externally by the endodermis. The strand consists of cells similar to those of the pith, and easily distinguished from the elements of the phloem by their greater size, rounded outline, and dense starchy contents.

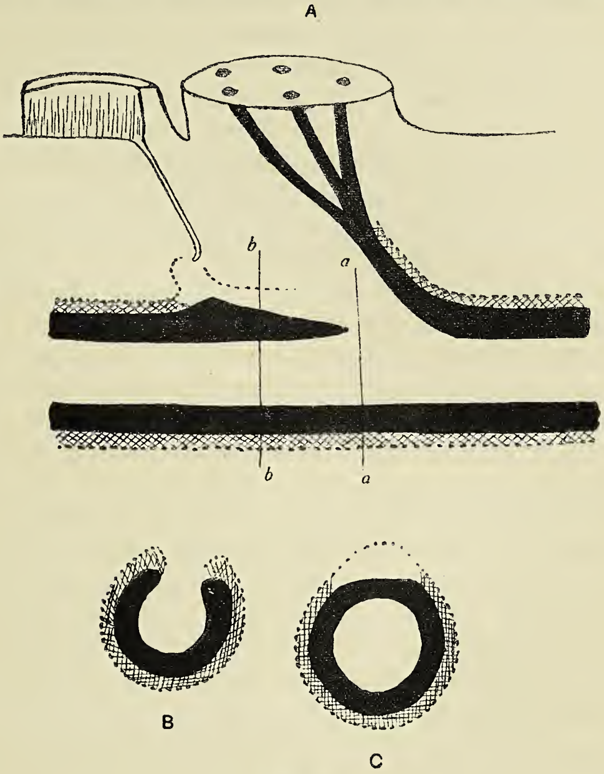

Fig. 19.

This ridge of parenchyma runs forward for some distance, finally ending in a small obliquely truncate conical projection inclined somewhat towards the apex. The endodermis forms a complete sheath around the projection except at its apex. The parenchymatous strand therefore communicates with both pith and cortex at the leaf-gap, and with the latter again at its forward termination.

The xylem ring, having closed up again after the leaf-gap, becomes especially thick opposite the projection, so that it forms a small outward protrusion underneath it. Immediately in front of this point the phloem ring becomes complete once more. The endodermis sheathing the projection usually bulges out in a saccate manner on the side nearest the apex, so that the open surface of the cone faces obliquely backwards. It is immediately above this aperture that the internal termination of the canal is situated. The canal runs from the surface of the stem obliquely backwards towards the tip of the projection, but just before its blind end it usually bends slightly forwards towards the apex.

In transverse sections of the stem the canal appears as a very narrow slit at different depths in the cortex according to the level of the section; the cortical cells in contact with it are arranged more or less radially around it. The termination of the canal occurs at the point where the trace of the leaf next above is about to depart from the opposite side of the stele.

These structures are of constant occurrence in all plants I have examined, and they acquire additional interest when it is stated that they are also present in the young plantlet. Some preparations made by Dr. Lang from young plants attached to prothalli, which he was kind enough to let me examine, show this to be the case, and that a canal is found in relation to the earliest leaves, even to the very first, which (allowance being made for the fact that the young plant at this stage is in the protostelic condition) is essentially similar to that described above.

Although suggestions are possible it is not easy to find an entirely satisfactory explanation for these curious structures. In the first place it is possible that they represent the last indications of vestigial axillary buds. Although at the present day *Helminthostachys* does not normally branch at all, Farmer[1] finds that branches frequently

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[1] Farmer, On the structure and affinities of *Helminthostachys Zeylanica*. Annals of Botany, Vol. xiii. No. LI, 1899.

arise from adventitious buds upon old parts of the rhizome. Possibly *Helminthostachys* or its ancestors branched more copiously, and Farmer's adventitious buds are due to the fact that this latent capability may still be stimulated into action under certain conditions. The fact that these buds are most frequently found upon almost decorticated fragments of rhizome appears to give colour to this suggestion.

It may also be suggested that they represent glandular organs of some kind; but, at the present day, the cells surrounding them give no particular evidence of a glandular nature.

D. T. GWYNNE-VAUGHAN.

GLASGOW.

ON SECONDARY THICKENING IN ANGIOPTERIS EVECTA.—For some time past Professor Farmer and the writer have been engaged upon an investigation into the structure of certain Marattiaceae. Various interesting features have come to light, amongst which is secondary thickening in *Angiopteris evecta.*

As is well known the steles of this plant are concentric in structure, the xylem being surrounded by the phloem. Both these tissues are arranged in an irregular manner, and between them there may often be seen elements exhibiting a marked radial arrangement, exactly presenting the appearance usually associated with that of a cambium. This cambium does not by any means surround the xylem, but is of local occurrence. There can be no doubt that the tissue in question owes its presence to post-embryonic merismatic activity, in fact to the existence of a cambium, though restricted to localized areas.

Additional evidence is afforded by the fact that on the inner side of this tissue semi-lignified elements with protoplasmic contents are often formed.

The only other view that could be held regarding this formative tissue is that its occurrence is due to the retention of the arrangement of primary meristem. It is, however, extremely doubtful if such a tissue would retain its characteristics for so long a time, for the best cases of secondary tracheides, accompanied by a cambium, were seen in the lower and older regions of the plants.

Secondarily formed tracheides have also been seen in the petioles, but not in the roots.

It may also be mentioned that outside the stele there is evidence of a tentative cambial activity. The latter is again irregular in its distribution, but of more frequent occurrence than the intrastelar secondary thickening described above. In appearance it may be compared to the secondary activity seen in the cortex of *Isoëtes*.

These points, with other matter not mentioned here, will be fully dealt with in a joint paper to be published shortly.

T. G. HILL.

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NOTE ON SOME GRAFTING EXPERIMENTS.—The following results are the outcome of a series of experiments to test the possibility of obtaining improved varieties of cultivated plants by employing the process of grafting.

The experiments of Daniel seem to show conclusively that the stock and scion mutually affect one another, and that, in some cases at all events, the changes so induced become hereditary[1]. So far my experiments have not been carried on for a sufficient time to reach this stage, but as they confirm several other points brought out by Daniel, and introduce new ones, they are of interest.

The most successful grafts were obtained by using seedling plants with from three to six leaves both for stock and scion. In the majority of cases tongue-grafting was used, and the scion fixed in position with a strip of thin gutta-percha wound round twice, and fastened with a ring of lead wire. Such a bandage is readily thrown off by the plant as the root or stem grows. If the operation is carried out in sunny weather, shading for three or four days is almost essential, and the leaf surface should be reduced to check transpiration.

One of the easiest plants to experiment with is the Beet (*Beta vulgaris*), as one can rely on almost every graft being successful.

The varieties used have been Sutton's Mammoth Long Red, Sutton's Yellow Globe, Sutton's Tankard, the Kleinwanzlebener sugar-beet, and the crimson beet. These are readily distinguished by their leaves, petioles, colour, and shape of the roots. In every case (42 plants) the boundary line between stock and scion was sharply marked; the white of the sugar-beet, for instance, did not gradually pass over into the crimson of the Mammoth Red—so affording a striking demonstration of the indiffusibility of the coloured cell-sap.

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[1] Daniel, Ann. d. Sci. Nat., 1898, p. 1.

In no case could the slightest difference be detected between the control plants of either the stock or scion except in size, the grafted plants being slightly dwarfed.

Scions taken from year-old plants and grafted on stocks of the same age have flowered and produced seed which appears to be fertile.

In the case of *Tropaeolum majus* grafted on *T. canariense* and *vice versa*, the results were much the same, both stock and scion retaining their original characters unaltered. The plants were, however, very dwarfed, the *T. canariense* only growing to the height of three feet in the sturdiest specimen. Their flowering period was also retarded for 6 or 8 weeks, and so far the only plants to produce seed have been those grafted on the roots which have been able to acquire a small root-system of their own. The grafted plants, moreover, were peculiarly liable to the attacks of slugs and caterpillars, while the control plants were rarely attacked.

Not only the callus but all parts of the plants were liable to attacks of this kind, probably owing to an accumulation of reserve materials in the scion through an interruption in the process of translocation at the junction with the stock.

The dwarfing effect of grafting was also noticeable in experiments with radishes, *Raphanus raphanistrum*, and the plants were so late in flowering, that an early frost spoiled all prospects of a crop of seed.

The other Cruciferae used were Kale grafted on Drumhead Cabbage, Broccoli on Cabbage, Brussel Sprout on Cabbage, Kohl-rabi on Kale, and *vice versa* in each case. The operation was generally successful, but all the plants (96) were killed, apparently by the nematode *Tylenchus devastatrix*.

Various grafts were also made among the Leguminosae. *Trifolium repens* was grafted on *T. pratense* and *T. hybridum*, *T. pratense* on *T. repens* and *hybridum*, and *T. hybridum* on *T. repens* and *T. pratense*.

The stock has flowered in one or two cases this season, but so far the scions have made relatively little growth.

Medicago sativa has also been successfully grafted on to *T. pratense* and *T. pratense* on *Anthyllis vulneraria*. In this case the scion and stock belong to strikingly different genera.

This series of experiments then confirms Daniel's results that the effect of grafting is often to dwarf the plants, retard their flowering season, and in some cases render them far more liable to the attacks of animal pests. None of them though show any visible signs of the scion and stock affecting one another [1]. This, however, is well shown in a series of potato grafts [2]. The operation was performed by paring off a thick piece of skin containing an eye, or a shoot an inch or two long, from one potato and binding it tightly over a similarly shaped pared patch on another tuber; all the other eyes were then destroyed, leaving only the scion to develop. One set of potatoes (*A*) had thin, smooth-green skins, and numerous deeply sunken eyes, while the other (*B*) was readily distinguished by its thick, rough, brown skin and its few shallow eyes. *A* was grafted on *B* and *B* on *A*. The resulting crop of tubers was the same in each case. From one and the same plant, tubers of type *A* and *B* were obtained (often with their characteristics much exaggerated, e. g. the russet skin cracked so as to resemble a truffle or the eyes exceedingly deep, &c.), and tubers one end of which resembled *A*, the other *B*. In many cases there was a sharp constriction between the *A* and *B* ends, but in some the yellowish-green skin gradually passed over into the rough corky skin, and the tubers were regular in shape. In every instance the 'rose-end' (distal end) of the tuber was of the *A* type, and the heel (proximal end) of the *B* type. Tubers in which the two types were blended never occurred.

Such tubers showing characteristics belonging to both scion and stock have long been recognized as typical 'graft-hybrids,' and they afforded Darwin no small amount of evidence for the theory of pangenesis. In describing them as hybrid, however, stress must be laid on the facts that if halved transversely each portion is indistinguishable from one of its parents, and that the tuber itself shows all the characteristics of its parent and not only certain dominant ones [3]. The graft hybrid then is not comparable with the sexually produced hybrid in this respect, and in the present state of our knowledge it seems impossible to give any adequate explanation of these phenomena.

R. H. BIFFEN.

CAMBRIDGE.

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[1] Cf. Lindemuth, Gard. Chron., 1902, vol. xxxi, p. 61.

[2] For literature see Darwin's Variation of Animals and Plants under Domestication, p. 420.

[3] Cf. Mendel, Journ. Roy. Hort. Soc., 1901, vol. xxvi, p. 1.

THE AFFINITIES AND ANATOMICAL CHARACTERS OF PLAGIOPTERON FRAGRANS, Griff.—In the year 1844 Griffith[1] published an account of a new genus of flowering plants, to which he gave the name *Plagiopteron*, this genus only including a single species, *Pl. fragrans* (= *suaveolens*). Griffith did not attempt to assign any definite systematic position to this curious plant, although he considered it to be related to Malpighiaceae and Sapindaceae. Walpers[2] describes it amongst the Sapindaceae, whilst in a foot-note he states his belief that it would be better placed amongst Malpighiaceae[3]. The first to place it amongst Tiliaceae were Bentham and Hooker[4], who include it in the tribe Prockieae. Their example is followed to some extent by Warburg[5], who however refers it to the order Elaeocarpaceae[6] of Schumann. The plant, that Griffith described, was growing in the gardens at Calcutta, but has since disappeared. The Kew Herbarium contains several specimens, collected by Griffith in Mergui, probably at some time after the date of the above-mentioned publication[1].

The resemblance in habit between *Plagiopteron* and certain species of *Hiptage* at the time of fruiting is certainly very striking, but the arrangement of the ovules in the former genus is not at all like that of Malpighiaceae. The Sapindaceae can scarcely come into consideration, for not alone have we the absence of any correspondence in number between the stamens and the floral envelopes, but most representatives of this order are characterized by the presence of short multicellular glands on the leaves, whereas *Plagiopteron* has no glandular hairs of any kind.

In my opinion *Plagiopteron* is certainly a Tiliaceous plant, and inasmuch as all parts are covered with stellate hairs, it should certainly be included in one of the tribes of the holopetalous Tiliaceae, which alone possess these hairs. Almost all the heteropetalous Tiliaceae (including the tribes Prockieae, Sloaneae and Elaeocarpeae)

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[1] Calcutta Journal of Natural History, vol. iv, p. 244, Plate XIII.

[2] Repertorium Botanices Systematicae, v, p. 370.

[3] Cf. Kurz, Forest Fl. Brit. Burm. i, p. 172.

[4] Genera Plantarum, vol. i, p. 238.

[5] Engler-Prantl, Natürl. Pflanzenfamilien, iii. 6a, pp. 53, 55.

[6] Including the tribes Elaeocarpeae and Sloaneae of Bentham and Hooker; the Prockieae were added later.

have simple hairs[1], and I agree with Schumann[2] in placing them together in a separate order, the Elaeocarpaceae, characterized chiefly anatomically[3] by the absence of mucilage-receptacles (which occur abundantly in almost all holopetalous Tiliaceae) and of stellate hairs.

The ovary of *Plagiopteron* is trilocular and contains two basal collateral ovules. This arrangement of the ovules is to be found in *Brownlowia*, a member of Bentham and Hooker's first tribe, Brownlowieae, in which the ovules are always limited in number. Further the resemblance between the buds of *Plagiopteron* and Brownlowieae is most striking, especially with regard to those of *Berrya* and *Brownlowia*. All have a valvate, slightly gamosepalous calyx, which is small in comparison with the valvate corolla, differing in these points considerably from the buds of Elaeocarpaceae. The stamens of *Plagiopteron* are curious in that they open by four apical pores, and it is partly owing to this mode of dehiscence of the anthers that Warburg (loc. cit.) refers *Plagiopteron* to the Elaeocarpaceae. It seems to me, however, that we can hardly compare the short, globular anthers of our genus with the greatly elongated ones of Elaeocarpaceae. On the contrary, I think that we could more readily compare them with the anthers of Brownlowieae, although I do not attach very much importance to this point at all. The anthers in the latter tribe dehisce by two lateral valves, which are frequently confluent at the apex. If we imagine these lateral valves to become gradually more apical, we should finally arrive at a dehiscence by two broad apical pores, as is sometimes found in *Plagiopteron*.

On the whole, I think that *Plagiopteron* would be best placed amongst the Brownlowieae. It has already been mentioned that practically all holopetalous Tiliaceae are provided with mucilage-receptacles (Schleimbehälter) in mesophyll and cortex. One genus (*Pityranthe*) of the Brownlowieae makes an exception to this rule, so that the fact that they are also wanting in *Plagiopteron* need not disconcert us. Finally, with regard to the opposite leaves of this genus it may be pointed out that they often show a marked tendency to

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[1] Stellate hairs are said to occur in certain species of Sloanea, although I have not come across them as yet.

[2] Cf. Engler-Prantl, Natürl. Pflanzenfamilien; Nachträge zu iii. 6, 1897, p. 230.

[3] The writer is occupied with an investigation of the anatomy of this order, of which one or two general results have just been mentioned.

become alternate. In some points *Plagiopteron* seems to form a connecting link between Elaeocarpaceae and holopetalous Tiliaceae, but in others it appears to stand quite alone.

One of these, which is at the same time the most interesting feature of the plant, is the occurrence of caoutchouc-cells throughout its tissues. If any part of a dried specimen be broken into two halves and these carefully drawn apart from one another, large numbers of elastic threads of a whitish colour are seen to stretch between the two pieces, breaking off when they have been separated to a certain extent. Griffith mentions this phenomenon, saying (loc. cit. p. 246) that the plant 'abounds with spiral vessels.' The true nature of these threads was first determined by Radlkofer[1], who mentions their occurrence in *Plagiopteron,* whilst describing *Wimmeria cyclocarpa,* which is provided with similar caoutchouc-cells. They also closely resemble the caoutchouc-containing elements of certain Hippocrateaceae[2]. In view of the fact that the caoutchouc-cells of *Plagiopteron,* together with those of Hippocrateaceae, &c., will form the subject of a paper 'On Caoutchouc-containing Plants' in a subsequent number of the Annals, I can limit my remarks here to a few general statements.

These cells occur abundantly at the periphery of the pith around the groups of primary xylem and not so commonly in the secondary phloem. They are particularly abundant in the phloem of the petiole, in fact more so than in any other part of the plant. In the leaves they are chiefly found round about the vascular bundles, replacing part of the accompanying sclerenchyma; but they also send slender branches into the mesophyll, which are best seen in surface view. The caoutchouc-cells are further abundant in all parts of the flower[3] and fruit, but, since *Plagiopteron* has never formed seeds in any of the herbarium materials at my disposal, I was unable to determine whether they are also present in the embryo, which I however think very probable. Finally, it is worthy of note that the cells of the mesophyll contain large numbers of small irregular lumps of caout-

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[1] Botanical Gazette, vol. xviii, 1893, p. 199; cf. also Solereder, Systemat. Anat. d. Dicotyl., pp. 176, 178.

[2] See Fritsch, Untersuchungen über das Vorkommen von Kautschuk bei den Hippocrateaceen. Bot. Centralbl. 1902, Beihefte, Band XI, Heft v, p. 292.

[3] I found them abundant in petals and sepals and in the walls of the ovary. Several run along to the tip of the style; only a few are to be found in the filaments of the stamens, and these terminate at the point where the anthers commence.

chouc, which in their physical and chemical properties absolutely resemble the contents of the caoutchouc-cells (and are similar to the caoutchouc of Hippocrateaceae).

F. E. FRITSCH.

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ON LIGNIFICATION IN THE PHLOEM OF HELIANTHUS ANNUUS.—An examination of the structure of two plants of the common sunflower grown at Kew last year has yielded one or two results, which do not appear to have been previously recorded, viz. the occurrence in this plant of: (1) sieve-tubes and companion-cells, whose walls ultimately become lignified; and (2) sieve-tubes and companion-cells, whose *contents* give reactions resembling those of lignin.

One of the plants was cut down and put into spirit in August, when it was already forming fruit; the other plant was allowed to grow until early in October. In the thicker parts of the stem of the first plant, patches of the medullary-ray-cells in the phloem were lignified. A few sieve-tubes with slightly lignified walls were found. In the second plant the stem had attained a diameter of an inch and a half near the base and for some distance upwards. In parts of this thick region, lignification of the walls had taken place in the whole of the pericycle, in the larger and many of the smaller medullary rays in the phloem, as well as in several of the small strands of sieve-tubes and companion-cells occurring in the outer region of the secondary phloem between the primary bundles, and in a fairly large block of sieve-tube-containing phloem on the inner side of each primary sclerenchyma-strand. The small strands were examined in transverse, radial, and tangential sections, and it was found that fairly frequently some, and occasionally all the sieve-tubes and companion-cells composing them possessed lignified vertical walls. In some cases the sieve-plates were covered with callus, and not lignified; in others they were destitute of callus, and lignified. Lignification of the walls was frequently seen in the single or paired sieve-tubes with companion-cells, which run horizontally or obliquely through the medullary rays, and form tangential connexions between the vertical strands of sieve-tubes, as in *Vitis vinifera*, &c. Lignification of elements (sieve-tubes, companion-cells, and parenchyma) bordering the large, still unlignified phloem-masses, corresponding to the primary bundles, suggested a further progressive lignification of the phloem, especially as the lignin-reaction was often slight, or restricted to one side of an element or graduated in adjacent elements. It may be mentioned here that cambial activity had entirely ceased in this region of the stem. Where unlignified phloem was present, there was no meristematic layer between it and the xylem, but sieve-tubes and companion-cells were in contact with lignified xylem-elements.

In the sieve-tubes and other tissue-elements referred to, the lignification was determined by the use of phloroglucin, aniline sulphate, Molisch's[1] thymol-solution, and the chlorine and sodium-sulphite treatment. The staining of the elements with these different reagents corresponded with that of the xylem-elements of the same plant.

The slight thickening and the lignification of the parenchymatous parts of the pericycle and of the medullary rays unite the primary (pericyclic) sclerenchyma-strands into a more definite mechanical system, attached to the strong xylem ring by the medullary rays. This must give greater rigidity, which no doubt is required by the heavy, fruiting capitula borne by the plant.

Lignification of sieve-tubes is probably of rather rare occurrence among the Dicotyledons. Schumann[2] mentions that sclerosis of sieve-tubes and companion-cells takes place in some few Compositae, and gives *Scorzonera hispanica* and *Aster thyrsiflorus* as examples. He states that especially the sieve-plates are lignified, but with regard to reactions only mentions that they are stained yellow by iodine.

Sclerification of sieve-tubes with frequent obliteration of the cavities is described by Vesque[3] in *Betula alba*, and by Boubier[4] in the same plant and in *Alnus*. *Betula alba* was consequently examined for comparison with *Helianthus*. In this plant numerous masses of sclerotic cells are present in the older secondary phloem, but in the specimen examined no obliteration of the cavities of sieve-tubes, nor lignification of their walls, was to be seen. Only a few sieve-plates were slightly lignified. The lignified elements of the phloem consist

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[1] Molisch, Ein neues Coniferinreagens. Berichte der deutsch. bot. Ges., IV, 1886, p. 303.

[2] Schumann, Beitr. z. Anat. d. Compositenstengels. Botan. Centralblatt, XLI (1890, I), p. 195.

[3] Vesque, Anatomie comparée de l'écorce. Annales des Sci. Nat., Bot., 6e sér., tom. ii, 1875, p. 178.

[4] Boubier, Anatomie systématique des Bétulacées-Corylacées. Univ. de Genève, Laborat. de Botan., 3e sér., fasc. vi, 1896, p. 58.

of masses of usually short sclerotic cells, evidently derived from the parenchyma as stated by Moeller[1].

On treating sections of the old stem of the sunflower with phloroglucin and hydrochloric acid, it was evident that in certain not very numerous cases the *contents* of companion-cells and sieve-tubes were stained in the same way as lignified walls. This was chiefly seen where lignification was just beginning in the walls of the elements to which the contents belonged. In the stem of the younger plant it was well seen in numbers of sieve-tubes and companion-cells in the parts of the phloem, which subsequently become lignified. In the main root of the older plant, at about 2 inches below the base of the stem (where the root was about $\frac{3}{4}$ of an inch thick), none of the walls of the phloem-elements were lignified, but the contents of a large proportion of the companion-cells and sieve-tubes gave the phloroglucin-reaction. The contents were much as one would expect to find in these elements (though apparently often showing signs of disintegration): in the companion-cells fairly dense and often showing a nucleus clearly, in the sieve-tubes taking the form of a parietal layer often massed into a 'Schleimkopf' on the sieve-plate, and giving the xanthoproteic reaction in both elements. The contents of these elements also gave reactions with aniline sulphate and with thymol, identical with those of the lignified walls of the same plant; they further gave the coloration with chlorine and sodium-sulphite described by Cross and Bevan (p. 115) as characteristic of lignocellulose. The fact that the colour produced by the thymol-reaction is here, as in the lignified walls, blue-green would be taken, according to Molisch's researches[2], as probably indicating the presence of coniferin. Without going into such questions as the identity of lignin with coniferin, or with a mixture of coniferin and vanillin, or the occurrence of lignin in combination as a lignocellulose, as deduced by Cross and Bevan[3], it may be pointed out that the facts described above, as far as they go, suggest that lignin may here be elaborated and accumulated in the cell-contents (in different manner or degree from what takes place in xylem-elements) before being infiltrated into, or combined with the cellulose composing the walls. From the material examined it cannot be said

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[1] Moeller, Anatomie der Baumrinden, Berlin, 1882, p. 51.

[2] Molisch, loc. cit.

[3] Cross and Bevan, Cellulose, London, 1895, p. 94.

whether the accumulation of the lignin-like substance in the root was preparatory to lignification of the walls, but in the stem this was suggested by its mode of occurrence.

The extent of lignification of the phloem and pericycle might perhaps vary considerably in different specimens, depending on the robustness of the plant, and that again on the cultural treatment. An examination of the structure of other annuals collected late in the year might perhaps yield results bearing on some of the many problems connected with the physiology of plants.

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Two Malayan 'Myrmecophilous' Ferns, Polypodium (Lecanopteris) carnosum (Blume), and Polypodium sinuosum, Wall.

BY

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With Plates X, XI, and XII.

INTRODUCTION.

IN Hooker's 'Species Filicum,'[1] published in 1864, occurs the following passage:—

'Notwithstanding the striking difference between the fronds of this remarkable plant (*Polypodium lomarioides*, Kze.) and those of *Polypodium sinuosum*, Wall., I am disposed to think, from the nature of the caudex and the venation, that these two may prove not specifically different. On mentioning to Mr. J. Smith my views regarding the unity of these two very distinct-looking Ferns, he not only was disposed to agree with me, but suggested that another Fern, viz. *Lecanopteris carnosa*, Blume, universally looked upon as a distinct genus, was equally an abnormal form of our present *Polypodium*, and

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[1] Hooker ('64), p. 79.

[Annals of Botany, Vol. XVI. No. LXII. June, 1902.]

he is perfectly correct. The caudex (perhaps in itself abnormal, but the same in all three) and the fertile segments are abnormal, inasmuch as there is a suppression of the substance of the frond between the sori ; the consequence is that these segments form marginal lobes, which in a dry state are turned back on the upper side of the frond (as the fructifications of *Nephroma resupinata* among the Lichens). The venation is the same in all three ; and if we can believe that *Lecanopteris carnosa* is a state of *P. sinuosum*, Wall., there will be no difficulty in referring Blume's *L. pumila* to *L. carnosa*.'

It is with the anatomy, biology, and systematic position of *Lecanopteris carnosa*, Bl., and *Polypodium sinuosum*, Wall. (two of the Ferns referred to above) that this paper proposes to deal.

The systematic position of these two Ferns will be discussed later, as well as the question of the identity of *L. carnosa*, Bl., and *L. pumila*, Bl. ; but in the meantime it is interesting to note, in view of the passage quoted above, that although *Lecanopteris carnosa* and *Polypodium sinuosum* are beyond doubt specifically distinct, and differ widely in external appearance, yet an examination of their internal structure reveals the fact that, after all, their resemblances are more remarkable than their differences, and that instead of being placed in separate genera, they must be recognized as closely allied species.

That being so, *Lecanopteris carnosa*, Blume, will be in future referred to in this paper as *Polypodium* (*Lecanopteris*) *carnosum*, (Blume), or, to avoid needless repetition, as *Polypodium carnosum*.

Both of these Ferns belong to the so-called myrmecophilous plants. Their thick, fleshy rhizomes are tunnelled by a system of galleries, which are invariably inhabited by colonies of ants. They are both epiphytes of the Malay region.

Polypodium carnosum grows only on the higher branches of trees, and usually, at all events, on fairly high mountains. It forms thick encrusting masses, often several feet in length, completely encircling the branches of its host, and is fully exposed both to the rains and the scorching sun of its tropical environment.

Blume's type specimens were collected in the Moluccas, but the plant is also known from the Philippines, Celebes, Borneo, Java, Singapore (Mr. Ridley informs me that it grows on Bukit[1] Timah, at a height of about 600 ft. above sea-level), and the following localities in Perak (one of the western states of the Malay Peninsula):—Birch's Hill; Gunong[2] Bubu, 5,000 ft.; Larut, 3,000–5,000 ft.; while the material used in the preparation of this paper was collected by myself[3] on Gunong Inas (4–5,300 ft.), a mountain on the northern borders of Perak.

Polypodium sinuosum, on the other hand, is often found almost at sea-level. Its creeping rhizomes (which do not form such compact and massive growths as those of *Polypodium carnosum*) are frequently to be seen quite near the ground, and usually on the trunk itself or on the main branches of its host. It may thus be shaded to some extent from the rays of the sun by the foliage of the tree on which it grows[4].

Its distribution is more extended than that of *P. carnosum*. It has been recorded from Malacca and other parts of the Malay Peninsula as far north as Mergui; Amboyna, Isle of Jobi, &c.; while eastwards it extends to the New Hebrides and the Solomon Islands. The spirit-material I have examined is from the Botanic Gardens at Singapore. I am greatly indebted to Mr. H. N. Ridley for his kindness in preserving and forwarding this material to me.

Some idea of the general habit of these remarkable Ferns may be obtained from the photographs forming Figs. 1 and 2.

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[1] *Bukit* in Malay means a hill.

[2] *Gunong* is a Malay word for mountain, not necessarily a larger peak than *bukit*, but usually more precipitous and rugged.

[3] During the Cambridge expedition of 1899–1900 to the Siamese-Malay states, under the leadership of Mr. W. W. Skeat.

[4] Karsten ('95, p. 182), however, states that in Amboyna he has found it growing in very sunny exposed situations.

That of *P. carnosum* (Fig. 1) was taken near the summit of Gunong Inas in Perak, at a height of 5,300 ft. At that elevation the jungle is dwarfed sufficiently to allow a photograph of the Fern as it appears in nature to be taken without much difficulty.

The photograph of *P. sinuosum* (Fig. 2) was taken on Pulau[1] Redang, the largest of a small group of islands in the China Sea, a little to the N.E. of Trĕngganu, one of the eastern states of the Malay Peninsula. The tree on which it grew was only a few feet above sea-level, at the edge of the jungle which covers these islands, as indeed it does almost all the available land in this region.

Although these Ferns are referred to in the works of numerous authors, yet comparatively little is known of their anatomy, their external features alone having attracted attention in most cases. So far as I am aware, the only papers dealing with their internal structure are those by Goebel[2] and Karsten[3]. These authors limit their descriptions to a few of the most striking points, and in either case very little mention is made of *Polypodium carnosum.* The descriptions are, moreover, supported by but few figures.

I. POLYPODIUM CARNOSUM (Blume).

External Morphology.

(*a*) *Stem.* The rhizome is thick and fleshy, glabrous but for the presence of minute multicellular hairs, which are often branched (Fig. 13), and are scattered over the surface of the young parts of the stem, especially on the flanks, but generally completely disappear from the older parts. It is furnished with a thin covering of wax, which is doubtless of importance in the reduction of transpiration, serving a purpose similar to that of the dense covering of peltate scales found in *Polypodium sinuosum* and other allied Ferns.

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[1] *Pulau* is Malay for an island.

[2] Goebel ('88), pp. 16 et seq.; see also Goebel ('89), pp. 204 et seq.

[3] Karsten, loc. cit., pp. 178 et seq.

The stem has a dorsiventral structure, being roughly semicircular in cross-section, except near the apex, where it is more nearly circular. The lower surface, however, is often by no means flat, as it has to adapt itself to irregularities of the substratum.

The numerous dark-brown roots are confined to the lower surface, and appear to be developed irregularly.

The leaves arise in regular acropetal succession[1] on the upper surface of the rhizome, and have a distichous arrangement, the members of one longitudinal series alternating with those of the other. The petioles are articulated upon large, more or less conical processes of the rhizome, which are usually directed forwards, i. e. towards the apex of the stem (Fig. 23). These conical projections or leaf-cushions are, especially on the main stem, often flattened antero-posteriorly. They are closely set together (two consecutive leaves of one longitudinal series being rarely more than 1·7 cm. apart, and usually less), and are separated from each other by transverse furrows on the stem. The surface of the rhizome thus presents a very rough and irregular appearance, broken up as it is and bristling with these conical leaf-cushions, which persist after the fall of the leaf (Figs. 3 and 19).

The branching of the rhizome is, as in all Polypodiaceae[2], monopodial. Lateral branches are given off from both sides of the main stem with great regularity (Fig. 6), each branch arising opposite to one of the leaf-cushions of its own side. The branches originating in this way are closely set together, and as they themselves give rise to secondary or tertiary branches in a similar manner, whenever space and other conditions allow of this, and these branches frequently creep over the older parts of the rhizome which come in their way, the final result is a compact, tangled mass of interlacing branches, so tightly packed as to form practically one solid

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[1] At least the leaf-cushions (*vide infra*) are developed regularly, though many of them, especially those on the smaller branches, have apparently never borne leaves.

[2] Campbell ('95), p. 321.

whole, almost every crevice of which is filled up by the growth of some branchlet or other. The mass thus formed may acquire a thickness of 10 or more cm., and as it completely encircles the branch on which it grows, the total diameter may reach, in the case of old plants, and depending of course on the thickness of the supporting branch, upwards of 30 cm., with a length of several times as much.

In the living state the younger portions of the stem are, in the specimens I have seen, of a pale greenish-yellow colour, though in Burck's figure[1] they are represented as being a very decided green. The older parts are black and apparently dead. Thus, as the plant grows, the mass may come to consist of a number of living plants, isolated by the dying-off of the older parts behind, but still connected together by these persistent, apparently dead parts[2]. That the oldest parts of the rhizome in such a mass are really dead, even when few visible signs of decay are present, is, I think, a fact, though the stem, or parts of it, may undoubtedly continue to live for a considerable time after the blackening process has set in. This is proved by the following facts: first, that living and healthy leaves may be present on parts that have become perfectly black, which shows that the vascular bundles at least are still living; and secondly, one occasionally finds small greenish knobs of living tissue isolated amongst completely blackened parts (*a*, *a*, Fig. 6). These occur in the position where lateral branches normally arise, and are, in fact, incipient branches which have either developed unusually late, or have lain dormant during the further growth of the parent branch.

In both the above cases the living parts, whether leaves or incipient branches, are never very remote from the apex, but are only found on parts of the rhizome near the young growing portions.

(β) *Leaf.* The fronds are dimorphic, the fertile ones being

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[1] Burck ('84), Plate VII.

[2] This condition of things is somewhat analogous to that found in a branched colony of corals.

usually confined to the main stem and the largest and most vigorous branches. Both kinds are glabrous, pinnatisect with a terminal lobe, lamina glaucous and sub-coriaceous, petiole, rachis and midribs dark brown.

Sterile fronds 2–9 cm. long (including petiole), 1·5–4·5 cm. wide, with one terminal lobe and 1–3 pairs of lateral segments. Segments shortly-oblong to oblong-ovate, obtuse, somewhat contracted at the base, margin entire or repand. Veins immersed except the midribs, which are more prominent on the upper than the lower surface. The lateral veins branch and anastomose freely, forming on each side of the midrib two or three series of areolae enclosing free veinlets with swollen terminations. The costal series of areolae is the largest (Fig. 45). Petiole short, 2·5 cm. at most, somewhat semicircular in cross-section (the flatter side facing apex of stem), usually slightly winged almost to the base.

Fertile fronds often 30 cm. or more long (including petiole), and 4 or more cm. wide, with one terminal lobe and 15–25 pairs of lateral segments, the lower sterile and similar to those of the sterile fronds, the upper fertile, narrowly oblong, obtuse, bearing 2–12 marginal lobes, each of which bears one deeply sunken sorus. The size of the segments diminishes slightly from base to apex.

The sori are circular, and commence in slight depressions on the lower surface of the marginal lobes of the leaf-segment. During development, the depressions become deeper and deeper until they assume a cup or bucket shape. Meanwhile, the soriferous lobes bend gradually upwards, until they are completely reflexed upon the upper (ventral) surface of the leaf. In order to accommodate the depth of the sorus-cups, the margin of the leaf is also bent upwards. Various stages in this process are shown diagrammatically in Fig. 42, *a*, *b*, *c*, *d*. As is usual in the Polypodiaceae, the sori contain sporangia in all stages of development. When mature, the sporangia are long-stalked, but in a young sorus the stalks do not elongate until the sorus-cup is almost fully formed. At this stage the mouth of the cup is oblong, but as the sporangia mature and fill up the cup, the mouth becomes oval-orbicular in shape. The longer diameter of a mature sorus-cup is about 2·2 mm., and its depth about 2 mm. A drawing of part of a fertile segment with several sori is seen in Fig. 43, while Fig. 4 shows a number of the reflexed sori on part of an adult fertile frond.

In Presl's[1] description of *Lecanopteris* it is said that the receptacle is covered with hairs ('undique capsulis pilisque densissimis obtectum'). Hooker[2], in the description accompanying Bauer's figures of *Lecanopteris*, reproduces the same phrase, though no drawing of the hairs in question is given. I have found no trace of such structures in my material; a few paraphyses are present amongst the sporangia, but these are quite minute, and could not possibly be the hairs referred to. The most probable explanation is that given by Fée[3], i. e. that these hairs are merely sporangia stalks. In every mature sorus numbers of these hair-like stalks may be found (Fig. 39), and it seems highly probable that these form the structures referred to.

The sporangia themselves will be described under the section on the internal structure of the leaf.

The venation of the fertile segments is similar to that of the sterile except as regards the supply to the sorus-cups. The main lateral veins run almost direct to the margin, where they enter the soriferous lobes. The latter are also supplied by one or two smaller veins, usually coming from the margin of the leaf (Fig. 46).

Petiole about 9 cm. long, slightly winged for a short distance below the lamina. In both the sterile and fertile fronds the petioles often undergo a torsion through an angle of about 90° or more.

Nearly all the leaves found, of whatever size, were mature. One or two immature fertile fronds are present, but no unfolding fronds or rudimentary leaves could be found. This may perhaps indicate that growth in this fern is very slow,

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[1] Presl ('36), p. 203.

[2] Hooker and Bauer ('42), Tab. CX, B.

[3] Fée ('50–'52), p. 259.

and that the leaves are long-lived, being formed only at comparatively long intervals. It might perhaps be expected that young leaves would be formed chiefly at certain periods of the year, but it is curious to note that the specimens of *P. carnosum* collected by myself were found in December, towards the close of one of the rainiest periods of the year, while the material of *P. sinuosum* sent me by Mr. Ridley, which appears to be equally devoid of immature leaves, was collected in March, soon after the commencement of rainy weather, which had been preceded by an unusually long spell of drought [1].

The description of the external features of *Polypodium carnosum* as given above is taken from the specimens collected on Gunong Inas; those from other mountains in Perak are precisely similar. The description given by Burck [2] of Javanese specimens differs only in a few unimportant details, but the specimens from other parts of the Malay Archipelago, which include Blume's types, differ somewhat more extensively. These differences will be discussed at greater length in the section devoted to systematic position.

Internal Structure.

A. *Rhizome.* A cross-section through an old stem reveals the presence of an extensive system of hollow spaces in the ground-tissue (Figs. 14 and 15). These are the ant-galleries. If they are followed towards the apex of the stem, they are found to be replaced in the younger parts by a fragile, large-celled, thin-walled tissue, which by breaking down gives rise to the galleries: the latter are therefore of lysigenous origin.

Externally the rhizome is coated with a thin layer of wax, while on the dorsal and lateral surfaces, in the young parts at least, are small scattered epidermal hairs, one of which is

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[1] Although some periods of the year in the Malay Peninsula can usually boast a considerably greater rainfall than others, there are no well-marked wet and dry seasons, the climate being more or less hot and moist all the year round.

[2] Burck ('84), p. 96.

shown in Fig. 13. I have found no mention of these by previous writers.

Immediately below the epidermis is a somewhat ill-defined hypoderma, consisting of several layers of small and comparatively thick-walled cells. Internally the latter pass by degrees into the larger parenchymatous cells of the ordinary cortex. On approaching the galleries the cells of the ground-tissue again diminish in size, and form a zone of small cells, several layers deep, surrounding the galleries. The cells of this zone also form numerous more or less irregular promontories projecting for a short distance into the lumina of the galleries (Fig. 12). The walls of these small cells are considerably thinner than those of the hypoderma. In the partition-wall between two adjacent galleries the ordinary cells of the ground-tissue are usually narrow, and elongated in the direction of length of the partition-wall. They present the appearance of having been crushed.

At a comparatively early period, prior to the disintegration of the large-celled tissue, the walls of the two or three layers of small cells immediately surrounding it become impregnated with a yellowish-brown colouring matter (Figs. 9 and 12), which is probably the same as that found in the sclerenchyma of most Ferns. The same is true of the thick-walled hypoderma. Later, the brown colour gradually extends to the whole of the ordinary ground-tissue, until the latter, when seen in mass, has a deep-brown or almost black appearance. It is this wholesale impregnation of the cell-walls with colouring matter that causes all except the youngest parts of the stem to appear black and dead. According to Walter [1], the brown colouring matter itself is a substance called phlobaphene. As Poirault [2] and Boodle [3] have found in other Ferns, the cell-walls can be decolourized by Eau de Javelle, and will then give the cellulose reaction with Schultze's solution. Poirault [4] also states that membranes impregnated with this brown colouring matter are much more resistant

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[1] Walter ('90), p. 18.

[2] Poirault ('93), p. 127.

[3] Boodle ('01), p. 361.

[4] Poirault, loc. cit.

than are those composed of mere cellulose, even sulphuric acid requiring considerable time to act on them. This I have also found to be the case in the tissues of *Polypodium carnosum.* But whilst increasing the resistance of tissues, the brown substance by no means renders them impervious to water, for even the living and apparently functional root-hairs of this Fern are deeply stained with it.

The cell-walls of the ground-tissue are, when mature, considerably thickened. During the primary thickening of these walls, minute spindle-shaped thin places are left, which give the walls a faintly punctate appearance. Later on, broad thickening bands are laid down, which may join or cross each other so as to form an irregular network (Fig. 30). According to Baranetzki[1], the thickening of parenchymatous cell-walls by threads or bands is very common, but is not always easily seen without the use of special staining methods. He remarks that lignification often makes it more obvious. This is also true of the brown colouring matter referred to above, as the thickening bands stand out with perfect distinctness on the brown walls of the old ground-tissue, while they are much more difficult to see before the tissue is coloured.

A striking feature of the ground-tissue is the almost entire absence of intercellular spaces, both in the young and old parenchyma: at all events, I have been able to recognize only a very few, and these extremely minute ones in the thick-walled hypoderma.

The vascular system. The structure of the steles is of the polypodiaceous type, and their arrangement resembles that found in other species of *Polypodium* with dorsi-ventral rhizomes[2]. The modifications in the course of the bundles are connected chiefly with the arrangement of the ant-galleries.

In a transverse section of the stem, there is seen a single median ventrally-placed gallery, surrounded by a single ring of steles. These steles anastomose to form a network which has the shape of a modified cylinder.

[1] Baranetzki ('86), p. 135.

[2] Cf. Klein ('81), pp. 335 et seq.

Dorsally, along the median line, there runs a single vascular bundle, a little thicker than the rest, in a slightly sinuous course. On either side of this, in two alternating longitudinal rows, are the large foliar gaps. These are oblong in shape, and about 11–12 mm. long, by 5–6 mm. wide (*d.* Fig. 35).

On either side of each foliar gap, two vertical steles are given off, one from the hinder corner and the other about half-way along the gap. These branch and anastomose with each other and with the steles from the other side of the gap to form a network extending up into the leaf-cushion and arching over the gap, completely roofing it in except in front. A horizontal section through a leaf-cushion thus shows a horseshoe-shaped arrangement of bundles (with the open part pointing forwards) passing up towards the petiole (Fig. 18). Each foliar bundle given off from the central dorsal stele usually branches into two. One branch forms the anterior bundle (on the inner side) of one leaf-trace, and the other the posterior bundle of the next leaf-trace on the other side of the middle line (*a.* Fig. 35). Sometimes, however, these two bundles may arise separately from the dorsal stele. The consecutive foliar gaps of one longitudinal series are separated by a single transverse row of small meshes (*b.* Fig. 35).

Laterally the vascular cylinder is composed of small polygonal meshes, about 4–5 mm. long, and not quite so broad. Its continuity is interrupted opposite each foliar gap of the same side by a large gap corresponding to the origin of a lateral branch (*c.* Fig. 35). The meshes bounding this gap are continuous with those forming the cylinder of the branch.

Ventrally the meshes are similar to the lateral ones. At irregular intervals, either from the side of a mesh or from a point of anastomosis, a stele is given off which passes obliquely downwards and forwards to a root.

The connexion between the vascular system and the galleries will be described later.

The individual stele is of the bicollateral type, and need not be described in great detail. It is of small size, and is elliptical in cross-section. The xylem, as in many Polypodiaceae[1], consists entirely of tracheides, and is somewhat scanty in amount. Between the phloem and the endodermis (which has the usual thickened radial walls) is the pericycle. This is composed of one or two layers of relatively large cells, which are superposed upon those of the endodermis (*vide* Fig. 33). This probably indicates that we are here dealing with a so-called 'double endodermis' and not a true pericycle[2].

The bundle is surrounded by a dark-brown sheath composed of a single layer of cortical cells, with very much thickened inner walls (*s.* Fig. 33). These walls are traversed by numerous large radial pits.

Origin of the galleries. The growing point of the stem is fleshy and presents a blunt, somewhat rounded appearance. There is nothing to indicate the exact position of the actual apex. Several attempts were made, by means of serial sections, both freehand and microtome, to determine whether a single apical cell is present or not, but without success.

Immediately behind the growing point a transverse section of the stem is very uniform in appearance, consisting, with the exception of the epidermis and the procambial strands, of very thin-walled parenchymatous cells, more or less equal in size. About 1 or 2 mm. from the apex, however, the cells in certain definite areas may be seen to increase in size at a greater rate than do the surrounding cells. This differentiation becomes more marked the greater the distance from the growing point, for not only do these cells themselves increase enormously in size, without undergoing much, if any, division, but the cells surrounding them begin to divide by radial[3] and also to some extent by tangential walls. An early stage in the differentiation is shown in Fig. 8 and a much later one in Fig. 9. The large-celled tissue thus formed is surrounded when mature by a belt, several layers deep, of

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[1] De Bary ('84), p. 344.

[2] Cf. Van Tieghem ('88), p. 404.

[3] Radial as regards these large-celled areas.

relatively small, brown cells. The development of these smaller cells is most marked at those angles which form the meeting-point of several of the outermost large cells. The result of this is that projections (occasionally of considerable length) of the small-celled tissue are found extending between the large cells. Thus the peripheral cells of the large-celled tissue come at length to occupy pocket-like depressions in the small-celled zone. This arrangement can perhaps be rendered more intelligible by the aid of figures. The inward projections of the small cells are seen in longitudinal section in Figs. 9 and 12. Fig. 10 represents a section taken parallel to the surface of the small-celled tissue, and passing transversely through the free ends of a number of these processes. A section in the same direction, but nearer the periphery of the large-celled tissue, is seen in Fig. 11; this shows several of the pocket-like depressions in the zone of small cells, occupied by some of the outermost large cells.

During life the cells of the large-celled tissue are filled chiefly with water, their thin walls being merely lined by a film of protoplasm. The tissue thus probably functions as a water reservoir[1]. In appearance it strikingly resembles the special water-storing tissue of some desert plants[2].

Finally the large-celled tissue breaks down, and is rapidly disintegrated, its place being taken by the ant-galleries. In my material the aqueous tissue was rarely intact at a distance of 2 cm. from the apex of the stem, and was often entirely broken down before that point. Fig. 12 is a microphotograph of a section taken through some partially broken-down aqueous tissue.

Arrangement of the galleries. The system of galleries thus formed by the breaking down of the large-celled tissue,

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[1] The translucency of the tissue, the thinness of its cell-walls, and the absence of intercellular spaces, all point to its being a true aqueous tissue. Cf. Warming ('96), p. 199.

[2] Cf. Volkens ('87), p. 59. Figs. 2, 3 and 4 on Taf. XII show a very similar tissue in the stems of several flowering plants. The resemblance is increased in these cases by the similar ingrowths of a small-celled tissue between the large cells.

though somewhat complicated, is arranged on a perfectly definite plan, following the same course through the stem as that taken by the aqueous tissue just described. As will be seen, the system appears to bear special relation to the large conical leaf-cushions which form such a prominent feature of the exterior of the stem.

There is, as mentioned above, a single median, ventrally-placed gallery, which runs, in a slightly sinuous course, through the whole length of the stem (Figs. 16, 22, &c.). This gallery is usually about two or three times as broad as it is deep, its floor being convex and its roof concave. At regular intervals the central gallery gives off a lateral gallery to each branch of the stem, and a vertical one to each leaf-cushion. As both the leaves and the lateral branches of the main stem are arranged in two longitudinal series, it follows that (unless this regularity is interrupted, as it may be, e.g. if some of the branches do not develop) there are two series of lateral galleries and two series of dorsal ones leaving the main gallery.

One of these lateral galleries originates beneath each leaf-cushion, and passes out immediately below a foliar gap, through the large gap in the vascular cylinder where the branch cylinder (which thus encircles the lateral gallery) leaves the main one. It curves slightly as it does so, first backwards and downwards and then forwards, finally entering a lateral branch, where it behaves like the corresponding gallery of the main stem. A second gallery leaves the central one close to the point of origin of the side-gallery (*a*, Fig. 20). This travels almost vertically upwards through the large foliar gap, and ends blindly in the leaf-cushion, under the base of the petiole (Fig. 15). Before entering the leaf-cushion, however, it sends out a forward diverticulum (Fig. 23) which passes outside the vascular system altogether, by means of the gap in the horseshoe-shaped network of the leaf-trace. This diverticulum immediately branches into two. One branch (*b*. Fig. 21) passes outwards, backwards, downwards and finally upwards, ending blindly in the same leaf-cushion as the parent gallery. The other branch runs forwards and slightly inwards, and ends blindly in the leaf-cushion next in front, on the other side of the stem.

Thus each leaf-cushion contains a transversely arranged series of three blind galleries, of which the middle and outer ones communicate with the ventral gallery at a point immediately below the cushion itself, while the third, or inner one, does so at a point below the leaf-cushion next in order behind. These three galleries are seen in Fig. 18, which shows a horizontal section through a leaf-cushion, some distance below the articulation of the leaf; while Fig. 15 shows the same in vertical section. There are, at least in the case of the larger leaf-cushions, external indications of these three diverticula in the form of slight bulgings of the cushions. These are shown on several of the leaf-cushions in Fig. 19.

The whole system then consists of a central median ventral gallery which gives off, alternately on either side, lateral galleries to the branches, and a dorsal series of chambers, each branched into three. The branches of these chambers are arranged roughly in the form of an h, each limb of which finally turns upwards, the two lower ending blindly in one leaf-cushion, and the upper in the leaf-cushion next in front on the opposite side of the stem. These dorsal chambers communicate with the main gallery close to the points of origin of the side-galleries. Fig. 20 represents diagrammatically a plan of the main gallery and its lateral branches, and Fig. 21 a plan of the dorsal chambers.

The arrangement of galleries in the branches is essentially the same as that of the main stem, except that in those cases where the lateral branchlets of the branches themselves are suppressed, the side galleries are of course not fully developed. Fig. 22 represents a nearly median vertical longitudinal section through the rhizome; it shows the main ventral gallery, and also cuts through the two series of forwardly directed branches of the dorsal chambers. Fig. 23 is a similar section passing through the apices of one of the two longitudinal rows of leaf-cushions (across *cc* in Fig. 20). The slightly sinuous course of the ventral gallery is shown by its interruption at various points. Three of the vertical galleries with their forward diverticula are also shown.

The galleries communicate with the exterior by means of little passages tunnelled by the ants through the outer tissues of the stem. Fig. 5 is a photograph of a transverse section through one of these excavations. It will be noticed that the internal edges are irregular, and show signs of having been gnawed by the ants, while the long processes so characteristic of the naturally formed galleries are quite absent. The external openings of these tunnels are usually situated on the ventral surface of the rhizome, a little below the apices of small branches (*a.* Fig. 15). Shallow pits may also occasionally be found in similar positions. These pits are evidently of the nature of wounds, as the epidermis which should cover them is missing, while the adjacent tissues are usually coloured brown, and are often contracted as if evaporation of water had taken place from the wounded surface. It seems probable that the pits are really the beginnings of tunnels to connect the galleries with the exterior. If this is so, it would appear to be usual for subsequent boring operations, as well as the original ones, to be conducted from the outside. The apical regions of the stem are probably selected by the ants because the tissues there are more easily excavated than are those of the older and tougher parts.

B. *Root.* Adventitious roots are given off at fairly frequent intervals from the ventral meshes of the vascular cylinder of the stem. They commence just below the growing point and develop by means of a single, three-sided apical cell[1]. The developing root passes obliquely forwards through the cortex, and emerges from the stem some little distance in front of its point of origin. Van Tieghem and Douliot[2] have pointed out that this cortical part of the 'root-stele' possesses in reality the structure of a stem-stele and not that of a root. This is the case also in *P. carnosum*, the general arrangement

[1] Cf. Bower ('89), p 309.

[2] Van Tieghem and Douliot ('88), p. 533.

of the stelar tissues as well as the sclerenchymatous sheath conforming to the usual structure of a stem-stele in this Fern. As the young root emerges from the cortex, it is at first covered by a cap formed of the epidermis of the stem. This cap finally ruptures, and is left behind as a collar encircling the root close to where it emerges from the stem[1]. Fig. 37 shows a layer of these collar-cells (*c*) external to the piliferous layer of the root.

The mature root has a diameter of about 1 mm. It possesses a diarch xylem plate, containing only a few tracheides. The one or two central elements of the metaxylem[2] remain unlignified until quite a late stage (Fig. 34). The stele is enclosed in a sclerenchymatous sheath, which, like those in the stem, is of a dark-brown colour. It is composed for the most part of two or three layers of cortical cells with very thick walls and extremely small lumina, while outside there is a layer whose inner walls only are thickened. Opposite to the two protoxylem groups, however, the sheath is very much thinner, and consists merely of the thick inner wall of one large passage-cell (sometimes there are two such cells placed side by side). This thick wall of the passage-cell is traversed radially by very large pits.

The outer cortex consists of about six or seven layers of cells, and is bounded by a piliferous layer. The whole, including the root-hairs, is stained a yellowish-brown with phlobaphene. The cell-walls of the outer cortex are thickened in a similar manner to that described for the stem parenchyma, but in the root the thickening bars are much thinner, and form a more definite and regular network (Fig. 31). In the peripheral part of the cortex the network is comparatively coarse, but on travelling radially inwards the network becomes finer, and many of the thickening rods still thinner, until in the region of the passage cells the walls are covered by a very

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[1] Van Tieghem and Douliot, loc. cit., p. 533, describe similar cases in other Ferns.

[2] *Metaxylem* is used here in the same sense as that employed by Boodle ('00), p. 458, i. e. to include all xylem other than protoxylem.

fine, delicate reticulum with minute, irregular meshes. The appearance of these thickened cell-walls, especially those of the outer cortical cells, reminds one forcibly of the tracheidal cells in the velamen of an epiphytic orchid[1]. Possibly they function in a somewhat similar way, though it must be remembered that these cortical cells are living, while the velamen tracheides are dead. At all events, the numerous and comparatively large thin places between the thickening rods would probably greatly facilitate the transport of water, which would be of service to the plant, as, being an epiphyte with large water-storing capacity, rapid absorption of water during rains would be advantageous. The cortical cells themselves also might very well store the water temporarily, until the somewhat limited vascular tissue of the root could carry off the surplus.

Apparently neither the piliferous layer nor the very persistent root-hairs ever possess this thickening network.

Lateral secondary roots are of frequent occurrence, and are developed in two ranks, emerging from the sclerenchymatous sheath at the thin places opposite to the two protoxylem groups.

C. *Leaf.—Petiole.* In transverse section the petiole is seen to be slightly winged, and more or less semicircular in shape with the flatter side directed towards the apex of the stem (Fig. 38). Beneath the epidermis, which has a rather thick cuticle, is the usual well-marked hypodermal tissue of thick-walled fibrous cells, with pointed ends and no intercellular spaces. The outer layers of the hypoderma are coloured brown, the inner are colourless and pass over into the larger cells of the ordinary petiole parenchyma. At two points, i. e. just behind the two wings, the fibrous hypodermal zone is interrupted by a thinner-walled spongy tissue (*a.* Fig. 38). Communication is thus established between the stomata, which only occur above the spongy tissue, and the intercellular spaces of the internal parenchyma. This tissue, as is often the case in Ferns[2], extends in two narrow, continuous

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[1] Cf. Haberlandt ('96), p. 201, Fig. 77.

[2] Gwynne-Vaughan ('01), p. 83.

bands along practically the whole length of the petiole. Viewed from the exterior, these bands are lighter in colour than the rest of the petiole, owing to the absence of the dark-brown fibrous cells. Gwynne-Vaughan[1] suggests that this spongy tissue represents modified traces of a mesophyll decurrent along the sides of the petiole, and remarks upon its significance with reference to Bower's view that the leaf of the Ferns is a rachis or phyllopodium, fundamentally winged along its whole length[2].

Fig. 32 is a photograph of a longitudinal section through part of the apex of one of the conical leaf-cushions, showing the articulation between petiole and stem. The parenchyma of the leaf-cushion is seen to be deeply coloured with phlobaphene, while the tissues above, with the exception of the stelar sheath, are free from it. At the junction of petiole and leaf-cushion, there is a slight swelling, visible in the photograph as an outward bulging of the tissues. At this point a zone of rather small, isodiametric cells, several layers deep, stretches right across the leaf-base. Leaf-fall occurs by disarticulation along this zone of cells.

As previously mentioned, a horizontal section through a leaf-cushion shows a horseshoe-shaped arrangement of bundles, passing upwards to the leaf, and partially surrounding the central gallery of the cushion. The concavity of the horseshoe is adaxial, its free ends being formed by two bundles which are rather larger than the others. These two bundles, together with several smaller ones (often making a total of six), enter the petiole. Gradually the free ends of the horseshoe[3] converge, and finally the two large bundles fuse with each other, though this does not occur in some cases until the summit of the petiole is nearly reached. The fate of the smaller bundles is not always the same. In the smaller leaves the rule is for the petiole, except at its base, to be

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[1] Gwynne-Vaughan, loc. cit.

[2] Bower ('84), p. 606.

[3] Gwynne-Vaughan, loc. cit., p. 95, points out that the vascular arrangement in the petioles of Ferns almost invariably takes the form of (in cross-section) a more or less modified horseshoe.

provided with only two steles (Fig. 38). Of these, the larger, which is adaxial in position, is, at least in some cases, formed by the fusion of the two large bundles and two of the smaller ones; the other is composed of the remaining two small bundles. In the larger leaves, however, there is not such complete fusion of the steles. The smaller ones anastomose or separate at intervals, but still retain to some extent their individuality.

Lamina. The mesophyll, as seen in a transverse section of a leaf-segment, is differentiated into two parts. The first consists of a single layer of large cells, lying immediately beneath the upper epidermis (*a.* Fig. 51). At the margin of the leaf this layer may be doubled, its cells at the same time becoming smaller. On the under side it passes into the spongy mesophyll. Viewed in optical section, by means of clearing the lamina with Eau de Javelle and staining, this layer is seen to possess no intercellular spaces. Its cells have more regular outlines than those of the ordinary mesophyll. They contain no chlorophyll when mature, and little or none even in the younger stages. This tissue may perhaps be regarded as a hypodermal water reservoir, similar to that found in the leaves of certain Orchidaceae, Velloziaceae, &c.[1] The bulk of the mesophyll, however, consists of the usual spongy tissue, composed of branched cells with irregular outlines and many, though comparatively small, intercellular spaces.

The epidermis has a fairly thick cuticle. Its cells, except the guard-cells, apparently contain no chlorophyll. Stomata are numerous on the lower surface of the leaf, but are absent on the upper. The guard-cells are on the level of the ordinary epidermal cells and are not sunken, as is so often the case in the leaves of xerophytes. Their development corresponds to that described by De Bary[2] for various other Ferns. Successive stages in the formation of young stomata are shown in Fig. 49, *a, b, c, d,* and a mature stoma in Fig. 50.

The general course of the veins in a leaf-segment has been

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[1] Cf. Warming ('96), p. 201.

[2] De Bary ('84), p. 41.

described above. The midrib projects considerably on the upper surface of the segment, but very little on the lower. It contains a single rather small stele, provided with a brown sclerenchymatous sheath similar to those of the stem and petiole. Between the stele and the epidermis (both upper and lower) are thick-walled mechanical elements, completing what is thus an efficient I-shaped girder. The stelar sheath is continued for a short distance only round the main lateral veins, the smaller bundles possessing neither the thick-walled sheath nor the strengthening mechanical tissue. In optical section it can be seen that the bundles usually contain few tracheides, but their number is often increased by the interpolation of a few short curved ones at points where the veins branch or anastomose. The free vein-endings are swollen, and contain numbers of short scalariform tracheides. In the fertile segments the veins supplying a sorus run down the proximal side of the sorus-cup, and form an irregular plexus under the placenta, containing numerous short tracheides (Fig. 46). At the point where the soriferous lobe is sharply bent back upon the rest of the leaf-segment, the vascular bundles are also bent, even the individual tracheides taking part in this curvature.

The sorus-cup differs somewhat in structure from the rest of the lamina. Its mesophyll has a more uniform appearance, and possesses only small intercellular spaces. Normal stomata occur on the inside of the cup (morphologically the lower surface of the leaf), but they are not very numerous.

A mature sorus (Fig. 39) contains sporangia in all stages of development, numerous sporangium stalks, and lastly, a few short paraphyses with small, somewhat club-shaped heads. The sporangia have long stalks, composed of three rows of cells, most of which are extremely elongated (Fig. 44).

The total length of a mature sporangium and stalk is usually about 1·7 mm. The annulus is vertical and incomplete. The inner and radial walls of the three cells of the annulus immediately above the stomium remain comparatively thin (Fig. 44), though all the walls of these cells are deep brown in colour. The spores are tetrahedrally arranged, are slightly curved with blunt, rather narrow ends, and have smooth outer walls.

II. POLYPODIUM SINUOSUM, Wallich.

External Morphology.

(*a*) *Stem.* The rhizome resembles that of *Polypodium carnosum* in its dorsi-ventral structure, the lower surface (which bears the roots) being flattened, except near the growing point; also in its swollen, fleshy habit, and in the distichous arrangement of its leaves, which are similarly borne on prominent swollen leaf-cushions. It is, however, smaller; my specimens rarely have a greater width than 1·4 cm., though the plant may attain a larger size than this, Christ[1] stating that they are 3 cm. broad.

The surface of the rhizome (including the leaf-cushions) is densely covered near the apex with adpressed, imbricating peltate scales, which arch over and protect the growing point. On the older parts they become somewhat more scattered, owing to the elongation of the stem. They are found, though rather more sparingly, on the lower surface[2] as well as the upper. These scales are nearly orbicular in shape, usually about 2 mm. in diameter, and are composed of numerous, radially arranged cells[3]. The centre is black and slightly raised, and is surrounded by a brown zone, while the margin of the scale is white and scarious.

The leaf-cushions are less swollen in the transverse direction than in *P. carnosum*, and are not placed so close together, two consecutive cushions of the same side being often as much as 4 or 5 cm. apart.

The branching in the two Ferns is similar, but much less frequent in *P. sinuosum*. It is, however, usual to find at

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[1] Christ ('97), p. 112.

[2] Christ, loc. cit., only describes the scales on the upper surface.

[3] See figure in Diels ('99), p. 320.

about the level of each leaf-cushion, on the opposite[1] side of the stem, a slight lateral projection (*a*, Fig. 7). These projections sometimes develop into lateral branches, but more often lie dormant. As a result of this limited branching, the rhizomes never form a compact, solid mass such as is seen in *P. carnosum*, though they may overlap each other to a considerable extent[2].

(β) *Leaf.* The fronds are sub-dimorphic, entire, glabrous and sub-coriaceous. The petiole and the midrib are brown.

Sterile fronds 9–12 cm. long (including petiole), and about 2 cm. wide; elliptical-oblong to oblong, obtuse, margin entire, gradually narrowed at base into the petiole, sometimes cuneate.

Fertile fronds 11–22 cm. long, 1–1·5 cm. broad; linear-oblong, obtuse, margin minute, base as in sterile fronds. Sori about 4–5 mm. long, oval or oblong, often becoming nearly circular towards apex of frond. They are rather deeply sunken (the pits producing oval projections on the upper side of the frond), and are arranged in a single longitudinal row on each side, nearer the margin than the midrib.

The venation is of the same type as that of *P. carnosum*, but the costal areolae are longer and narrower in *P. sinuosum* (Figs. 47 and 48), and in the sterile fronds the larger areolae may contain smaller ones, formed by the anastomosis of the enclosed veinlets.

Petiole 2–3·5 cm. long, approximately circular in cross-section.

Internal Structure.

The structure of *P. sinuosum* closely resembles in many respects that of *P. carnosum*, and need not be described in very great detail. Only those points in which the two Ferns differ markedly from each other will be dealt with at any length.

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[1] In *P. carnosum* the branches arise at about the level of the leaf-cushions of the *same* side.

[2] Cf. Mr. Parish's remarks in Hooker ('64), p. 62.

a. Rhizome. Here and there, in a transverse section of the stem, occur pit-like depressions, the sides of which are lined by the epidermis. From the floors of the pits spring the cylindrical stalks of the peltate scales. These stalks are composed of a number of elongated cells, with very thick brown walls. The cells immediately above the stalk have comparatively large lumina, and these pass in all directions into the shallow, radially arranged cells of the scale. The radial walls of the latter cells are marked with numerous large pits [1].

There is no special thick-walled hypoderma.

The vascular cylinder in this Fern is somewhat flattened dorsi-ventrally. In a transverse section of the stem it appears as an oval ring of steles (Figs. 24, 25). A semi-diagrammatic drawing of a dissection showing the dorsal part of the vascular cylinder is seen in Fig. 36. The meshes of the network are small and elongated. It is difficult to define the actual limits of the foliar gaps, but apparently they are much elongated, with pointed ends. The supposed boundaries of one of them are indicated in Fig. 36, by the slightly thicker steles lying between the points *a* and *b*. From the edges of this gap numbers of steles are given off, which branch and anastomose to form an extensive network (similar in appearance to that of the main cylinder) arching over the foliar gap behind, but rising more abruptly in front to enter the leaf-cushion. Laterally, secondary cylinders are given off to the branches, and from the ventral meshes steles pass downwards to the roots, much in the same manner as in *P. carnosum*. In fact, the whole vascular cylinder of *P. sinuosum* much resembles that of *P. carnosum*, if we can imagine the latter stretched or pulled out in a longitudinal direction [2].

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[1] Karsten ('95), p. 180, describes the structure of these scales in detail. He regards their function as twofold, (1) to protect the stem against excessive transpiration, (2) to collect and temporarily store water during the fall of rain, for the subsequent use of the roots. Water is quickly sucked up by the expanded part of the scale, but from the structure of the stalk Karsten thinks it unlikely that any finds its way directly into the stem.

[2] Boodle ('01, 2nd paper), p. 739, points out that strongly xerophytic conditions are likely to conduce to shortening of internodes and decrease of rate of growth in stems. Probably the shorter internodes (and therefore the apparently contracted

The stele is of the same type as that of *P. carnosum.* The pericycle, in this case also a false one, as it originates from the same layer as the endodermis, is here only one layer thick throughout. The sclerenchymatous sheath is similar, but the radial pit-canals are often much more branched than is the case in *P. carnosum.*

In the material at my disposal the impregnation of the cell-walls by phlobaphene is most marked in the two or three layers of small cells surrounding the galleries, the general ground-tissue never assuming the deep brown colour found in *P. carnosum* : this, however, may be due to the fact that my material did not include any very old pieces of stem. Moreover, the thickening of the cell-walls by bands is largely confined to these small cells. In *P. carnosum*, on the other hand, the small-celled zone seldom, if ever, has the thickening bands developed on its cell-walls to any extent. Probably correlated with the early thickening of the walls of these small cells in *P. sinuosum* is the fact that although the cells do divide in early stages of growth, yet this division is never carried so far as in *P. carnosum.* Thus the curious projections of the small-celled zone between the large cells of the aqueous tissue (which originates in a similar manner in both Ferns) are never found in *P. sinuosum.*

The aqueous tissue finally breaks down and forms galleries similar to those of *P. carnosum.*

The arrangement of the ant-galleries in *P. sinuosum* has been described by Goebel [1], but a few points may be added to his description, and a comparison made with the gallery-system of *P. carnosum.* As in *P. carnosum*, there is a single main ventral gallery, three or four times as wide as deep. It is seen in transverse section in Figs. 24 and 25, in median vertical longitudinal section in Fig. 28, and in horizontal longitudinal section in Fig. 27. Laterally it gives off side-galleries to

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condition of the vascular cylinder) of *P. carnosum* may be correlated with its very exposed situation, which renders it liable to intense insolation. It cannot, however, be assumed, merely on general grounds of this sort, that originally the stems of the two Ferns were precisely similar in this respect.

[1] Goebel ('88), p. 16.

the branches, but in *P. sinuosum* the latter being much less numerous than in *P. carnosum*, the lateral galleries are not developed with such regularity. Sections, however, taken through those lateral projections of the stem which we have seen are to be regarded as undeveloped branches, show pocket-like diverticula of the main gallery extending into them (*d* in Figs. 24 and 27).

Each leaf-cushion contains a single vertical gallery (oblong in cross-section) which ends blindly some distance below the leaf-articulation. Just after leaving the main gallery, it sends out a single diverticulum which does not branch, but travels backwards in a straight line for a distance of about 1 cm., and ends blindly in a blunt point. There is usually an external swelling on the stem corresponding to this diverticulum (Figs. 29 and 36).

The relation of this dorsal chamber to the vascular system differs from the arrangement found in *P. carnosum*. In both Ferns the vertical gallery passes outside the vascular cylinder through a foliar gap, but while in *P. carnosum* the diverticulum given off from this gallery is directed forwards, and passes out through the gap left in the network of foliar bundles, that of *P. sinuosum* is directed backwards, and does not pass to the exterior of the vascular system at all, as the foliar bundles form a vaulted network over it.

The gallery system communicates with the exterior both by the dying-off of the older parts of the stem [1], and also, as in *P. carnosum*, by means of small lateral or ventral openings made by the ants themselves.

b. Root. The root of *P. sinuosum* is an almost exact counterpart of that of *P. carnosum*, but on a smaller scale.

The outer cortex is only about three or four cells thick, including the piliferous layer. The walls of its cells possess the same prominent network of thickening bars as do those of *P. carnosum*, while the cells of the inner cortex form a sclerenchymatous stelar-sheath of precisely the same nature.

c. Leaf. The petiole is generally almost circular in transverse

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[1] Goebel, loc. cit., p. 17.

section throughout the greater part of its length, though towards its summit it is more or less winged, the leaf-lamina being often slightly decurrent. The arrangement of tissues is the same as in *P. carnosum.* There are the same brown hypodermal fibrous cells, interrupted by the two lateral lines of spongy tissue, above which are the stomata, in this case even fewer in number than in the other Fern. The steles are usually two in number, a large elliptical one, adaxial in position, and a smaller circular one.

The leaf-lamina, too, has a similar structure in both Ferns, but in *P. sinuosum* the large cells under the upper epidermis appear to contain a certain number of chloroplasts. This is, no doubt, correlated with the difference in habitat of the two plants, *P. sinuosum* usually growing in somewhat shadier situations than *P. carnosum.*

A diagrammatic drawing of a transverse section through a sorus is seen in Fig. 40. It is not so deeply sunken as the sorus of *P. carnosum*, and consequently the stalks of the sporangia are shorter ; the sporangia themselves, also, are not quite so large. Paraphyses, consisting of simple filaments of four or five cells, the terminal one rounded but not swollen, are fairly numerous. That part of the leaf-lamina which constitutes the bottom of the sorus-pits is thinner than is the case elsewhere. At the edges of the sorus-pits the cells of the epidermis are considerably deeper than is usually the case (*a*. Fig. 40).

BIOLOGICAL CONSIDERATIONS.

Under this heading may be discussed the curious reflexed position of the sori in *Polypodium carnosum*, and the meaning to be attached to the galleries which occupy such extensive tracts in the tissues of the stem in both Ferns. With the latter point is connected the question of the relations existing between the ants and their hosts.

The reflexing of the sori of *P. carnosum* upon the upper surface of the leaf is a phenomenon in all probability nearly unique in Ferns, the only other cases of which I am aware being found[1] within the limits of Blume's genus *Lecanopteris*[2]. The meaning of the flexion is not at first sight obvious. The only explanation that suggests itself to me is that it may possibly be connected with spore distribution. As we have seen, *P. carnosum* grows on mountains, as an epiphyte on the *upper* branches of trees. Often these trees are tall[3], and it is only when the jungle is dwarfed on the highest mountain tops that it approaches at all near to the ground. Now the reflexing of the sori causes most at least of the little sorus-cups to face skywards instead of towards the ground (*vide* Fig. 1). The effect that this position of the sori would have on the ejection of the spores would probably be to cause most of them to be ejected from the sorus only when a considerable wind was blowing. Thus, if the sporangia had previously dehisced, a large proportion of the spores would still remain inside the sorus-cup or even on the concave upper surface of the leaf-segment, until the force of the wind were sufficient to shake the frond and carry them away. Under these conditions, the spores would have a much better chance of reaching their destination, i. e. the topmost branches of trees, than if they fell to the ground first, as would often happen on still days, if the sori occupied the position usual in Ferns[4].

P. sinuosum, being a low-growing epiphyte, would have much less need of an adaptation of this sort.

The reflexed sori, in their new position, would of course be more exposed to the effects of the heavy tropical rains than before. This, however, in all probability would not be a very serious drawback, as their most vulnerable part, i. e. the long thin stalks of the sporangia, would be safely hidden

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[1] In a few Ferns sori may be actually borne upon the upper surface of the frond; e. g. *Deparia Moorei*, Hook., whose sori are usually marginal, frequently bears additional sori scattered over the upper surface of the leaf.

[2] This genus is characterized by having the sori borne on marginal lobes, which are either bent back upon the upper surface of the leaf, or twisted to one side.

[3] Mr. Ridley informs me that on Bukit Timah, in Singapore, *Polypodium carnosum* never grows at less than eighty feet from the ground.

[4] Mr. F. Darwin has suggested to me that this may be compared with the 'Censer' mechanism found in the fruits of the Poppy and other flowering plants.

away behind the walls of the deep sorus-cups[1]; while above, the tightly packed sporangia, protected by their strongly thickened annuli, would probably suffer little, even in the heaviest downpour.

The question as to the function to be ascribed to the galleries in these Ferns is more complicated. Three possibilities present themselves. First, that the galleries are a special adaptation on behalf of the ants, both the plant and its guests deriving benefit from the symbiosis. The second is that they are more or less accidental, simply replacing the effete aqueous tissue of the stem, and themselves serving no special purpose; while a third possible explanation is that they may be connected with the interchange of gases in the stem, as suggested by Treub[2] in the case of the ant-galleries of *Myrmecodia*.

Nothing approaching the extensive and regular system of hollows traversing the stem in these Ferns appears to be known among the other Filices, though a few closely allied Malayan species[3], which are also inhabited by ants, in all probability possess similar structures. At the same time, cavities in the stems of other Ferns are by no means unknown. For instance, *Ceratopteris thalictroides*, Brong., possesses hollow spaces of schizogenous origin in the cortical tissues of both stem and root. Campbell[4] states that—

'In *Onoclea struthiopteris* characteristic air-chambers are formed in the young medulla at an early period. At certain points the cells become longer and their contents more transparent. These cells divide less rapidly than the surrounding tissue, and large intercellular spaces are formed. The loose cells about these form masses of trichomes, either

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[1] Christ ('96), p. 93, points out that many of the species of *Polypodium* found in the rainy mountainous districts of the Malay Archipelago possess these deeply sunken sori. He regards them as a protection against heavy rains, such an adaptation being especially necessary in this genus, as the indusium found in most other Ferns is absent.

[2] Treub ('88), p. 206.

[3] Such are *Polypodium lomarioides*, Kze., *P. sarcopus*, De Vriese et Teysm., and the remaining species of Blume's genus *Lecanopteris*.

[4] Campbell ('95), p. 323.

hairs or scales, which later dry up and leave a large empty space, which may or may not communicate with the exterior through the foliar gaps.'

A plant which may perhaps afford in some respects an interesting parallel to the case of the Ferns under consideration is *Polypodium bifrons*, Hook. The following note is appended to Hooker's description of this Fern[1]:—

'Hab. Ecuador, on a tree by the river side . . . the plants were partially immersed in water, and to the root or caudex were attached hollow succulent tubers, in which the ants had taken refuge.'

Unfortunately nothing appears to be known respecting the origin of the hollows referred to.

The association of ants and Ferns is by no means limited to the cases already mentioned. Beccari[2] and Goebel[3] quote a number of instances in which the relationship varies from cases where the ants actually inhabit cavities in the substance of the plant itself, down to those where the insects merely nest in the humus which collects around the roots and leaf-bases of so many epiphytes, both Ferns and flowering plants. In fact, one of the things which first strikes an observer in the tropics is the fact that ants are almost everywhere present. Any convenient hole or corner, whether above or below the ground, generally affords shelter to a colony of ants. It is not surprising therefore that such eminently suitable nests as are afforded by the ramifying galleries of these Ferns, and the similar ones of *Myrmecodia* and *Hydnophytum*, should be so invariably appropriated by ants[4]. The very ubiquity of the ants, however, combined with their undoubtedly high degree of intelligence, would suggest that they, like bees and other insects, may not have been without their influence on the evolution of plants[5]. Undoubtedly the mere presence of ants does sometimes protect plants from their insect enemies. Ludwig[6] cites several instances in which

[1] Hooker ('64), p. 79.

[2] Beccari ('84–'86), pp. 243 et seq.

[3] Goebel ('88), pp. 16 et seq.

[4] Cf. Treub ('88), p. 207.

[5] Cf. Lubbock ('91), p. 57.

[6] Ludwig ('95), p. 243.

this protection is purposely utilized by man. For instance, the Chinese of Canton, who cultivate orange-trees in large groves, connect the trees together by means of long bamboo staves, so that the tree-dwelling ants may readily travel from tree to tree, and thus prevent the ravages of insect pests.

In many instances the relations between ants and plants are without doubt of a merely casual nature, to which no special biological meaning is to be attached; but these chance alliances may on the other hand, when mutual benefit results, lead on to such cases as those of various species of *Cecropia*, in which, as shown by Schimper, the adaptation would seem to be truly reciprocal[1].

As, in the numerous cases of so-called myrmecophily, different parts of plants, plants of different genera and orders, and ants of different genera are concerned, Professor Bower[2] suggests that the origin of the inhabited hollows and the question of the mutual advantage derived from the symbiosis should be considered independently in each case. It is, moreover, desirable to collect all available data regarding the food and habits of the ants, and the homes inhabited by the different species.

Dr. August Forel has very kindly undertaken the identification of the ants found in the two species of *Polypodium*. The ant inhabiting the material of *P. sinuosum* from Singapore proved to be *Technomyrmex albipes*, Smith, which belongs to the sub-family Dolichoderinae[3]. That found associated with *P. carnosum* is a new species of *Cremastogaster*, *C. Yappi*, Forel[4]. In addition to the ants, an egg-capsule of a species of cockroach[5] was discovered in the galleries of *P. sinuosum*,

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[1] Schimper ('88). Buscalioni and Huber ('00) have recently arrived at rather different conclusions from those of Schimper, i. e. that the ants have taken to live in the Cecropias, not in quest of food, but in order to get a nest above flood level.

[2] Bower ('87), p. 320.

[3] Forel ('94), p. 496, states that most of the species of this group keep no plant-lice, but lick up secretions of plants, or else live on insects.

[4] Forel ('01), p. 374.

[5] Goebel ('89), p. 208, states that cockroaches were found by Guppy in the chambers of a species of *Hydnophytum*; but the galleries of *P. sinuosum* are small,

while a centipede (*Mecistocephalus punctifrons*, Haase) and two small specimens of some lepidopterous larva[1] were found in *P. carnosum.* Moreover, the roots of an epiphytic orchid, growing on the massive stem of this Fern, had in some cases penetrated to the interior of the galleries.

Nothing, so far as I am aware, is known of the special enemies of these two Ferns, or whether indeed they have any, and consequently it is impossible to state anything definite respecting the protection afforded them by the ants. It is true that on attempting to remove a plant of *P. carnosum* from the tree on which it grew, great numbers of its tiny inhabitants sallied forth and attacked the intruder with great pugnacity; but this proves nothing, as the case would be an exceptional one.

Unfortunately I was unable to procure any young plants of either species, and so could not investigate the origin of the first-formed gallery. From analogy with the case of *Myrmecodia*[2], however, it would seem probable that the presence of ants is unnecessary for its formation.

On the whole, although the possibility of the existence of a true adaptation between the ants and these Ferns cannot be denied, yet such evidence as is available seems to point to Goebel's[3] view being the correct one, i. e. that the ants are merely 'Raumparasiten' or dwellers in cavities formed without reference to their future inhabitants; and this more particularly so, as no attractions in the form of food appear to be offered to the ants.

It seems to me most probable that the large-celled tissue

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and it seems scarcely likely that cockroaches would live in them. This solitary egg-capsule may very well have been carried in by the ants.

[1] Dr. Sharp concludes, from the absence of colour and other markings, and the presence of only simple hairs on the bodies of these larvae, that the dark recesses of the stem of this Fern form their natural habitat. Larvae, such as *Zeuzera* or *Hipialus*, which live in dark confined places, usually have these characteristics. Meyrick ('95), p. 782, instances the case of a moth (*Myrmecozela ochraceella*, Tgst., one of the Tineidae) whose larva lives in ants' nests (*Formica rufa*), both in England and on the Continent, though he states that this appears to be unique amongst known Lepidoptera.

[2] Treub ('83), p. 154.

[3] Goebel ('88), p. 21.

of the stem is developed in the first instance as a special water reservoir[1]. The character of the tissue; its remarkable similarity to the aqueous tissue of certain other xerophytes; its position with regard to the leaf-cushions, which is such as would ensure an abundant supply of water to the young developing leaves; the fact that during life it does undoubtedly contain large quantities of water; and finally, the statement made by Goebel[2] that a leaf attached to part of the stem remained fresh for a number of days in a warm dry room, afford, I think, sufficient evidence of this.

At the same time, we have to explain the somewhat remarkable fact that this elaborate tissue has an extremely short life. In *P. carnosum* I have rarely found the aqueous tissue intact at a distance of 2 cm. from the growing point; though in *P. sinuosum* Goebel[3] states that the living aqueous tissue is found at distances varying from 2 or 3 to 7 or more cm. from the apex of the stem. Karsten[4], however, says that this is exceptional, the stem being usually hollow at a point 1–2 cm. behind the apex.

Now although the oldest parts of the rhizome in both Ferns are usually quite dead, the ordinary tissues of the stem have a much longer life than the aqueous tissue, so that the galleries do undoubtedly penetrate living parts of the plant. The question is whether these galleries, as such, fulfil any useful purpose, or whether they merely take the place of the aqueous tissue, when this tissue has fulfilled its function, and is now no longer required. It is possible that the latter may be the true explanation, but in view of the short life of the water tissue, it would seem to be hardly sufficient.

There remains yet the third possibility, i. e. that these cavities may act as air-shafts, a function suggested by

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[1] Goebel, loc. cit., p. 16, regards it as a true aqueous tissue, but Karsten ('95), p. 182, appears to think that the function of water storage is equally well fulfilled by the other tissues of the stem. He lays stress on the absence of the tissue in other Ferns, and its early degradation in cases where it exists.

[2] Goebel, loc. cit., p. 18. Of course the external cortical parenchyma might have contributed some at least of this supply of water to the leaf.

[3] Goebel, loc. cit., p. 18.

[4] Karsten ('95), p. 182.

Treub[1] for the galleries of *Myrmecodia*. He supposed that aeration of the fleshy tissues of the swollen stem is affected by means of these moist chambers, without an undue loss of water. Haberlandt[2] adopts this view, but Goebel[3] remarks that while there is much to be said for it, yet the need for this elaborate mechanism for the interchange of gases is, in the case of *Myrmecodia*, by no means proved, especially as the tuber is not green, and therefore cannot assimilate. Karsten[4] is of the opinion that the galleries of *P. sinuosum* serve for the purpose of aeration.

Now in spite of the fact that the younger parts of the rhizomes of these Ferns contain chlorophyll[5], there appear to be no stomata on the stem. Moreover, the system of intercellular spaces usual in massive tissues[6] is here almost entirely absent[7]. To whatever cause this latter fact is to be ascribed[8], it would seem possible that in a tissue which is practically devoid of the usual adaptations for gaseous inter-

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[1] Treub ('88), p. 206.

[2] Haberlandt ('96), p. 350.

[3] Goebel ('89), p. 212.

[4] Karsten, loc. cit.

[5] This is certainly true for *P. carnosum*, and I believe for *P. sinuosum* also.

[6] Devaux ('91), p. 311.

[7] The rhizomes of several other Ferns (i. e. *Polypodium conjugatum*, *P. aureum*, *P. quercifolium* and *Davallia Fijiensis*) were examined. The intercellular spaces varied considerably in size in different species, in some being very minute, but in each case they were better developed than in the two species under consideration.

[8] External conditions, resulting in the marked xerophytism of these Ferns, may perhaps be sufficient to account for this [cf. Stahl ('83), p. 17, on the relative sizes of intercellular spaces in sun and shade leaves]. It is also conceivable that the absence of intercellular spaces may be a more or less mechanical effect, due to the formation of the aqueous tissue itself. This tissue, when alive, usually contains large quantities of water. Now even a thin-walled cell, when perfectly turgid, can exert an enormous outward pressure [cf. Pfeffer ('00), p. 139]. Such hydrostatic pressure (aided perhaps by the growth and division of the cells immediately surrounding the aqueous tissue) exerted at a time when the remaining tissues of the stem were soft and plastic, might possibly inhibit to some extent the formation of intercellular spaces. The crushed appearance of many of the ground-tissue cells, seen more especially in the partitions between adjacent galleries, as also the fact that in *P. sinuosum* the walls of the small cells surrounding the galleries have their stoutest thickening bands more or less radial in position [cf. Baranetzki ('86), p. 199, on the mechanical principle involved], would seem to point to some such force having acted radially outwards from the region occupied by the aqueous tissue.

change, and which yet assimilates, there may exist a tendency to a state of partial asphyxiation, such as that stated by Devaux[1] to exist, even at normal temperatures, in the deeply seated tissues of many woody stems. This state of affairs, if it exists, would be relieved by the early breaking down of the aqueous tissue, resulting in the formation of extensive compensating air-passages. In any case, it seems probable that, whatever its original significance, this system of galleries, which penetrates to almost all parts of the rhizome, and is in communication with the outer air, does, to some extent at least, assist in the interchange of gases in the stem. Moreover, Karsten[2] states that water applied to the layers of small pitted cells surrounding the galleries of *P. sinuosum* is at once sucked up by these cells. He thinks that water-vapour given off into the galleries when the stem is heated by the sun, would condense again on their walls and be reabsorbed. Further, during heavy rain, it is possible that a certain amount of water may find its way into the galleries, and probably this would be similarly absorbed by the plant. Thus the galleries, in addition to allowing gaseous interchange to take place without undue loss of water, may be perhaps, so far as water is concerned, an actual source of gain[3].

Fresh observations, if possible by direct experiment on the living plants, are needed to further elucidate the true function of the galleries. The result of one such experiment is recorded by Goebel[4]. He states that a plant of *P. sinuosum* in the Buitenzorg Gardens, Java, developed side-shoots when its galleries were stopped with paraffin. The precise bearing of this on the matter in question is not quite obvious.

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[1] Devaux ('99), p. 94, but cf. also ('99, 2nd paper), p. 129.

[2] Karsten, loc. cit., pp. 180 et seq.

[3] Goebel ('89), p. 208, and Forbes ('85), p. 79, record cases in which the galleries of certain species of *Myrmecodia* and *Hydnophytum* actually contained fluid water. Probably this would rarely happen in the two *Polypodia*, as the external openings are more or less ventral in position.

[4] Goebel ('88), p. 18.

SYSTEMATIC POSITION.

While very little doubt as to the fact of *Polypodium sinuosum* being a true *Polypodium* appears to have ever existed, the position occupied by *P. carnosum* has been a debatable one.

Reinwardt[1] originally placed it in the genus *Onychium*, but a few years later it was described as the type of a new genus, *Lecanopteris*, by Blume[2], who shortly afterwards in the Flora Javae (Filices)[3] published figures of two species, *L. carnosa* and *L. pumila*. The latter species never appears to have been described. Several closely allied species, however, have since been discovered, which Baker[4] has placed in the same genus. *Polypodium patelliferum*, Burck[5], is probably identical with *L. carnosa*, though Beccari[6] regarded the name as a synonym of *L. deparioides* (Cezati).

The majority of writers[7] have maintained *Lecanopteris*, Blume, as a genus, though, as we have seen, both Hooker and Smith[8] recognized its close affinity to *Polypodium lomarioides* and *P. sinuosum*. Christ[9] includes *Lecanopteris* as a sub-genus, in *Polypodium*; another sub-genus, to which he gives the name *Myrmecophila*, comprises *P. sinuosum*, *P. lomarioides*, and one or two closely allied forms which are similarly inhabited by ants. Diels[10] maintains *Lecanopteris* as a distinct genus, at the same time admitting to generic rank *Drynaria*, *Niphobolus*, and other groups often regarded merely as sub-genera. In 1892 Baker[11] wrote, 'I now think that *Lecanopteris* will have to stand as a distinct genus, in the neighbourhood of *Dicksonia*, from which it differs in having an indusium

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[1] Reinwardt ('25), p. 48.

[2] Blume ('27), p. 120.

[3] Blume ('29), tab. 94.

[4] Baker ('92), p. 19; also ('94), p. 123, and Cezati ('76), p. 13.

[5] Burck ('84), p. 97.

[6] Beccari ('84–'86), p. 244.

[7] Amongst others, Presl ('36), p. 202; Fée ('50–'52), p. 259; and Moore ('57–'63), p. 80.

[8] Smith ('75), p. 106, retains the genus *Lecanopteris*, regarding the names *P. lomarioides* and *P. sinuosum* merely as synonyms of *Lecanopteris carnosa*.

[9] Christ ('97), p. 116.

[10] Diels ('99), p. 326.

[11] Baker ('92), p. 19.

formed of only a single valve, and in the curious rootstock.' The indusium, says Mr. Baker, consists of 'a cup, formed from the edge of the frond, holding a small globose sorus.' Christ[1], however, has pointed out that there is really no true indusium. Blume[2] and Mettenius[3] also distinctly refer to the sori as being non-indusiate. What has been regarded as an indusium is in reality part of the ordinary leaf-lamina, which here, as in many other species of *Polypodium*, forms a deep pit, at the bottom of which lies the placenta (compare Figs. 39, 40 and 41). Moreover, the inner wall of the sorus-cup possesses normal stomata, though these are comparatively few in number. This again would suggest that we are simply dealing with part of the leaf-lamina. The extraordinary rhizome of this Fern being already paralleled in the genus *Polypodium* by those of *P. sinuosum* and other forms, the only reason that remains for retaining *Lecanopteris* as a distinct genus is the curious reflexed position of the sori[4]. In all other respects these plants would fall naturally into the section *Phymatodes*[5] of the genus *Polypodium*. The wisdom of maintaining such huge, unwieldy genera as *Polypodium* may perhaps be doubted[6], but so long as distinct groups like *Drynaria*, &c., are retained merely as sub-genera of *Polypodium*, I think that this is at most the highest rank that should be given to *Lecanopteris*.

Further, as has been seen, the internal structure of *P. carnosum* is in many respects very similar to that of *P. sinuosum*. One of the most striking of these resemblances is the possession by both species of a specialized water-storing tissue in the stem, whose mode of origin, distribution and fate, though not in all respects identical, is substantially the same in both. These similarities, coupled with the external resemblances

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[1] Christ ('98), p. 73.

[2] Blume ('27), p. 120.

[3] Mettenius ('56), p. 38.

[4] Some other species of *Polypodium* also have their sori borne on marginal lobes, though these are not reflexed as in *Lecanopteris*, e.g. *P.* (*Phymatodes*) *sorridens*, Hook.; vide Hooker ('64), p. 60, Tab. 283 B.

[5] As defined by Hooker in the Species Filicum, vol. v, p. 55.

[6] Cf. Fée ('50–'52) in the preface to his 7th Mémoire.

recognized by some of the older botanists, seem to indicate that a close relationship exists between the two Ferns. It may be pointed out, moreover, that certain other species, which are also ant-inhabited epiphytes of the Malayan region, are apparently, so far as their external features are concerned, actually intermediate between our two forms; e.g. *P. lomarioides*, Kze., and *P. sarcopus*, De Vriese et Teysm., possess the peltate scales of *P. sinuosum* but have pinnate fronds, whilst the habit of *P. sarcopus* and *P. carnosum* is almost precisely similar[1].

In fact, when the structure of these additional forms is more fully known, it may perhaps be possible to place them all (including *Lecanopteris*) into a single natural group, which might either stand as a section of the genus *Polypodium*, or as a subdivision of the section *Phymatodes*. To this group the name '*Myrmecophila*,' adopted by Christ[2] in a rather more limited sense, might not inappropriately be applied.

Some such arrangement as the following may perhaps be found convenient:—

MYRMECOPHILA. Epiphytic Ferns whose fleshy creeping rhizomes are traversed by a regularly arranged system of galleries, which are inhabited by ants. Leaves borne on prominent, more or less conical leaf-cushions.

α. Rhizome covered with peltate scales. Sori sunken, but not borne on marginal lobes. This sub-group (which forms the *Myrmecophila* of Christ[3]) would contain such forms as *P. sinuosum*, *P. lomarioides* and *P. sarcopus*.

β. Rhizome without peltate scales. Sori sunken, and borne on marginal lobes, which are either reflexed upon the upper surface of the leaf, or twisted to one side, so that the sorus faces the apex of the frond.

This would include *P. carnosum* and the other species of Blume's genus *Lecanopteris*.

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[1] Christ ('98), p. 160, and Pl. XVI, Fig. 25*c*.

[2] Christ ('97), p. 112.

[3] Christ includes *P. imbricatum*, Karsten, in this group: but this differs from the other species in possessing black scale-hairs, and apparently also in the structure of the stem [Karsten ('95), p. 168].

Mention has been made of the fact that Blume figured two species of *Lecanopteris*, though he only described one. The differences between the figures of these two species seem to lie chiefly in the respective shapes of the leaf-segments. Those of *L. carnosa* are represented as comparatively wide, and tapering to the acuminate apex, those of *L. pumila* as narrower, and rounded at the apex.

Lecanopteris pumila is not represented in the Kew Herbarium, while there are seven sheets of specimens identified as *L. carnosa*. Of these four are from Perak, one from the Philippines, and two from the Malay Archipelago. The plants from these several localities differ from each other in the size and shape of the leaf-segments. Those from the Malay Islands correspond to Blume's type figure of *L. carnosa*, that from the Philippines forms a type by itself, while those from Perak bear considerable resemblance to Blume's figure of *L. pumila*. In the absence of more complete material, it is difficult to decide whether *L. pumila* can be maintained as a species or not, but in view of the great variability of the leaf-lamina in many Ferns, it would seem likely that these three forms may be nothing more than local varieties of *L. carnosa*. For the present therefore, it will be best to leave the Perak specimens (including those from Gunong Inas) under the name of *Polypodium* (*Lecanopteris*) *carnosum*; though, if *P.* (*Lecanopteris*) *pumilum* (Blume) should ultimately be found to be a distinct species, they would in all probability belong to it rather than to *P. carnosum*.

SUMMARY.

1. *Polypodium carnosum* and *P. sinuosum* are two Malayan epiphytes, whose thick fleshy rhizomes are tunnelled by a system of galleries, similar to those of *Myrmecodia* and *Hydnophytum*, and, like them, invariably inhabited by ants.

2. In both Ferns a tissue consisting of large cells with thin walls and no intercellular spaces is formed in certain definite areas near the apex of the stem. This tissue breaks down at

an early period, its place being taken by the ant-galleries, which are thus of lysigenous origin.

3. The gallery system consists in both cases of a main ventral gallery which runs longitudinally through the stem, giving off two lateral series of galleries to the branches, and two series of vertical ones leading to the swollen leaf-cushions. Soon after leaving the main gallery the vertical ones branch so as to form two longitudinal series of dorsal chambers. In *P. sinuosum* these are entirely internal to the vascular system, and each consists of two limbs, one of which (the continuation of the vertical gallery itself) ends blindly in the leaf-cushion, while the other passes backwards through the tissues of the stem. In *P. carnosum* each dorsal chamber (the greater part of which is external to the vascular system) consists of three limbs; two of these finally end blindly in one leaf-cushion, whilst the third passes forwards and ends in the leaf-cushion next in front on the opposite side of the stem. Thus each leaf-cushion in *P. carnosum* contains three blind galleries (arranged transversely), those of *P. sinuosum* being only provided with a single one.

4. Communication between the galleries and the external air is effected by means of short passages excavated by the ants themselves in the soft tissues of the younger parts of the stem.

5. The character and topographical position of the large-celled tissue seem to indicate that it was developed in the first instance as a special water-reservoir; but the fact that it is so soon disintegrated may perhaps point to some degree of change of function, i.e. that the galleries which replace it have some important function to fulfil. There is no evidence that the galleries are an adaptation on behalf of the ants, and indeed their meaning is still somewhat obscure. Perhaps they serve as organs for the aeration of the stem, which is in both cases almost devoid of intercellular spaces. It is also possible that they assist to a slight extent in the absorption of water.

6. The sori of *P. carnosum* are borne on marginal lobes,

which are reflexed when mature upon the upper surface of the frond. This is possibly an adaptation to prevent the scattering of the spores unless a considerable wind is blowing. This plant is only found on the topmost branches of trees, and so it is during a wind that the spores would have the best chance of reaching their ultimate destination.

7. Though formerly placed in different genera, both the external features and internal structure of these two Ferns indicate that they must be regarded as closely allied species.

In conclusion, I desire to express my thanks to Mr. A. C. Seward for his valuable advice and suggestions during the progress of this investigation. Also to Professor A. Forel, Dr. Sharp, and Mr. F. G. Sinclair for information concerning the ants and other animals found in the galleries of the Ferns.

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EXPLANATION OF FIGURES IN PLATES X, XI, AND XII.

Illustrating Mr. Yapp's paper on 'Myrmecophilous' Ferns.

Unless otherwise stated, the figures refer to *Polypodium carnosum* (Blume).

The arrows accompanying some of the figures point in each case towards the apex of the stem.

The microphotographs constituting Figs. 5, 12, and 32 were taken by Mr. W. Tams of Cambridge.

PLATE X.

Fig. 1. *Polypodium carnosum*, showing its natural habitat.

Fig. 2. *Polypodium sinuosum*, ditto.

Fig. 3. *P. carnosum*, part of the mass of interlacing rhizomes seen in Fig. 1.

Fig. 4. Upper part of a single fertile frond.

Fig. 5. *P. carnosum*, transverse section through a tunnel leading to the exterior, excavated by the ants.

PLATE XI.

Fig. 6. *P. carnosum*, diagram showing mode of branching of stem. *a. a.* knobs of living tissue (incipient branches).

Fig. 7. *P. sinuosum*, ditto. *a. a.* undeveloped branches.

Fig. 8. *P. carnosum*, transverse section of part of the stem near the apex, showing an early stage in the formation of the large-celled tissue. (× 42.)

Fig. 9. Later stage, showing aqueous tissue fully formed. (× 33.)

Fig, 10. Section through the aqueous tissue taken parallel to the small-celled zone, and cutting transversely several unusually long small-celled projections. (× 33.)

Fig. 11. Ditto, taken close to periphery of aqueous tissue, showing four of the pocket-like pits occupied by one or two large aqueous cells. (× 33.)

Fig. 12. Microphotograph of a section showing the large-celled tissue breaking down to form a gallery.

Fig. 13. A single branched epidermal hair. (× 75.)

Fig. 14. A section through part of a mass of stems, showing the way in which the younger stems overlap the older. The galleries are seen cut in various directions. *b.* twig of host tree. ($\frac{5}{8}$ nat. size.)

Fig. 15. A transverse section through an old piece of stem, showing the galleries. The section also cuts a very short branch longitudinally, at the apex of which is an opening (*a.*) to the exterior made by the ants. ($\frac{3}{4}$ nat. size.)

Figs. 16 and 17. Two transverse sections near apex of rhizome. Aqueous tissue is still present. *v.* position of main ventral gallery. ($\frac{3}{4}$ nat. size.)

Fig. 18. Horizontal section near apex of leaf-cushion, showing the three blind galleries cut across. ($\frac{3}{4}$ nat. size.)

Fig. 19. External view of part of main stem, showing the commencement of two lateral branches. (Nat. size.)

Fig. 20. Plan of main ventral gallery, showing lateral galleries (*l.*), and the position (*a.*) of the vertical galleries with respect to them.

Fig. 21. Plan of the dorsal chambers. *a.* position of vertical gallery; *b.* outermost branch of one of the chambers.

Fig. 22. Median vertical longitudinal section of stem. (¾ nat. size.)

Fig. 23. Vertical longitudinal section of stem, passing through the series of leaf-cushions of one side, i.e. across line *c. c.* in Fig. 20. (¾ nat. size.)

Fig. 24. *P. sinuosum*, transverse section of stem, passing vertically through a leaf-cushion. *d.* a diverticulum of main gallery entering an incipient branch. (¾ nat. size.)

Fig. 25. Ditto, passing through main gallery and also a blind dorsal gallery. (¾ nat. size.)

Fig. 26. *P. sinuosum*, plan of dorsal chambers. *a.* is position of vertical gallery, communicating below with the ventral gallery. *c.* blind dorsal gallery. (¾ nat. size.)

Fig. 27. *P. sinuosum.* Plan of ventral gallery and its lateral branches. *d.* a pocket-like diverticulum entering an incipient branch. *aq.* partly broken down aqueous tissue. (¾ nat. size.)

Fig. 28. *P. sinuosum.* Median vertical longitudinal section of stem. (¾ nat. size.)

Fig. 29. *P. sinuosum.* Vertical longitudinal section passing through two leaf-cushions. *c.* a blind dorsal gallery. (¾ nat. size.)

Fig. 30. *P. carnosum.* Some of the old ground-tissue cells of the stem, to show band-like thickenings. (× 105.)

Fig. 31. *P. carnosum.* Three cortical cells from a longitudinal section of a root. (× 190.)

Fig. 32. *P. carnosum.* Microphotograph of a longitudinal section through base of petiole, showing its articulation with the leaf-cushion.

PLATE XII.

Fig. 33. *P. carnosum.* Transverse section of a stem-stele. *e.* outer endodermis. *p.* false pericycle or inner endodermis. *s.* sclerenchymatous sheath. (× 258.)

Fig. 34. *P. carnosum.* Part of transverse section of root. (× 67·5.)

Fig. 35. *P. carnosum.* Dorsal part of vascular cylinder. *a.* one of the foliar bundles leaving the edge of the foliar gap. *b.* small meshes separating two foliar gaps. *c.* place of origin of a lateral branch cylinder. *d.* a foliar gap. (× about 1½.)

Fig. 36. *P. sinuosum.* Semi-diagrammatic drawing of a dissection showing the dorsal part of the vascular network. *a. b.* supposed limits of a foliar gap. (× about 1½.)

Fig. 37. *P. carnosum.* Part of a longitudinal section of a root, showing the collar (*c.*) formed by the ruptured epidermis of stem. Beneath this is seen the piliferous layer of root. (× 75.)

Fig. 38. *P. carnosum.* Diagrammatic transverse section of petiole. *a.* interruption of thick-walled hypoderma by the thin-walled spongy tissue.

Fig. 39. *P. carnosum.* Diagrammatic section through a sorus-cup.

Fig. 40. *P. sinuosum.* Diagrammatic section through a sorus. *a.* enlarged cells of epidermis at edge of pit.

Fig. 41. *Polypodium nigrescens.* Diagrammatic section through a sunken sorus, to show its similarity to that of *P. carnosum.*

Fig. 42. *P. carnosum.* Diagrammatic sections showing successive stages (*a. b. c. d.*) in the reflexing of the soriferous lobes.

Fig. 43. *P. carnosum.* Part of a fertile leaf-segment, showing reflexed position of mature sori. (× about 3.)

Fig. 44. *P. carnosum.* A sporangium. (× 92.)

Fig. 45. *P. carnosum.* A sterile leaf-segment, bleached by Eau de Javelle, and stained to show venation. (× 3.)

Fig. 46. *P. carnosum.* Part of a fertile leaf-segment treated in the same way. The sorus-cup is diagrammatically represented as if no flexion had occurred. (× 8.)

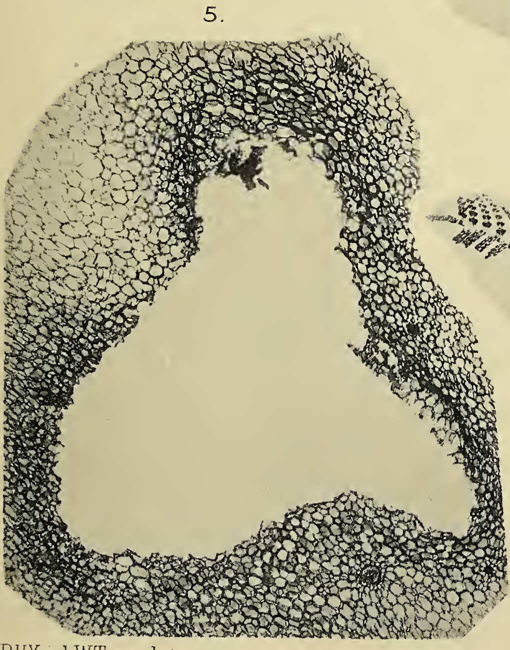
Fig. 47. *P. sinuosum.* Part of a fertile frond, to show venation. *s.* sorus. (× 3.)

Fig. 48. *P. sinuosum.* Part of a sterile frond. (× 3.)

Fig. 49. *P. carnosum.* Developing stomata, taken from an upper leaf-segment of a young frond. *a. b. c. d.* successive stages. (× 197.)

Fig. 50. A mature stoma. (× 197.)

Fig. 51. *P. carnosum.* Part of a transverse section through a leaf-segment. *a.* layer of large colourless cells beneath the upper epidermis. (× 246.)



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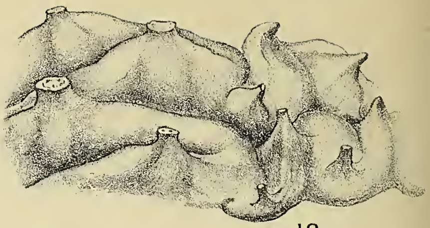

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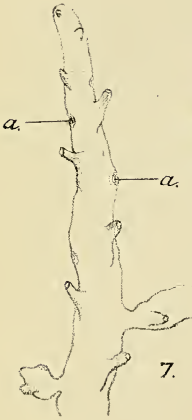

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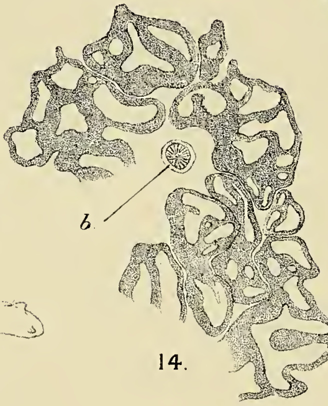

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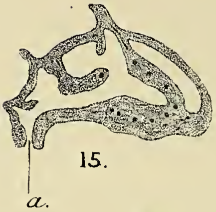

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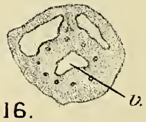

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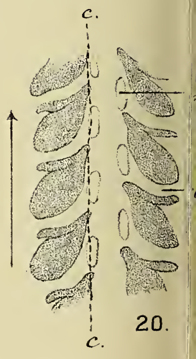

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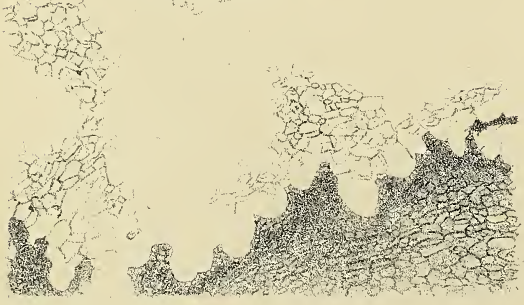

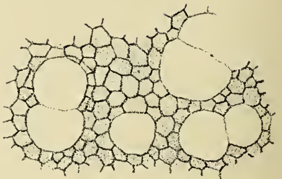

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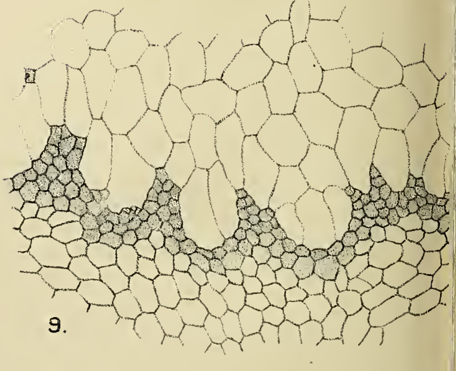

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R.H.Y. del.
W. Tams, photo.

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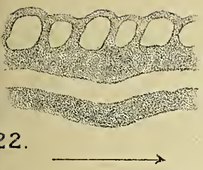

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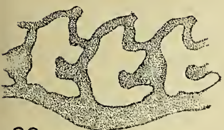

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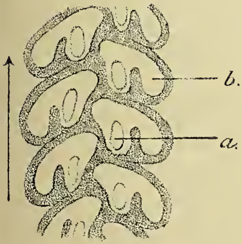

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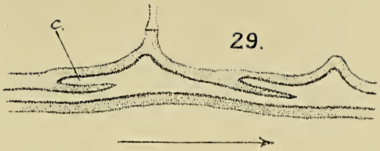

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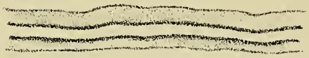

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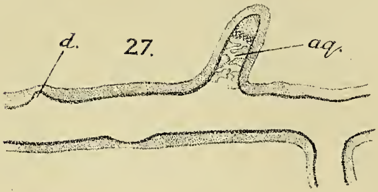

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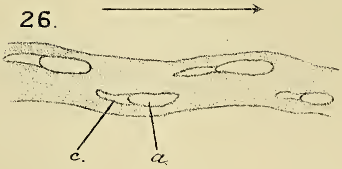

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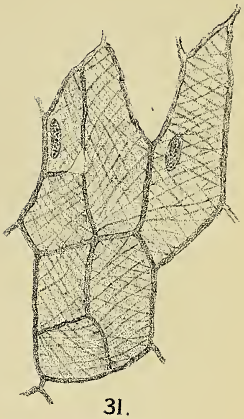

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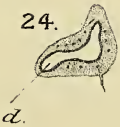

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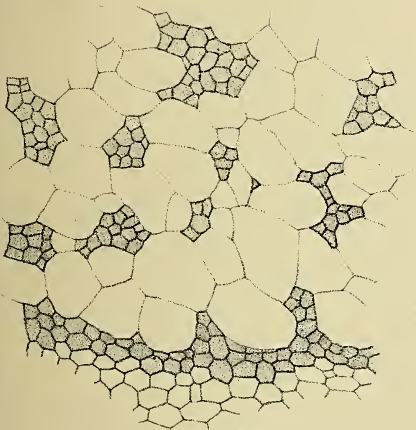

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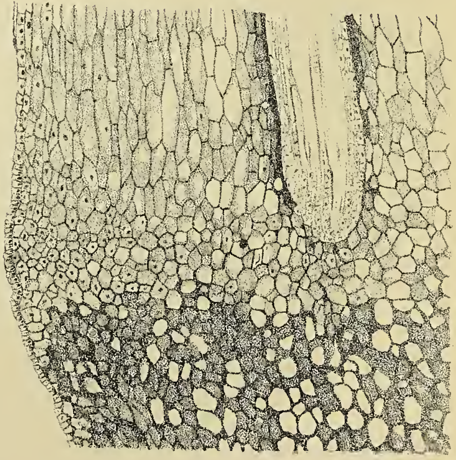

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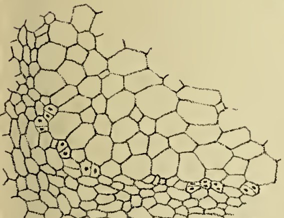

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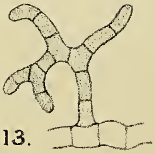

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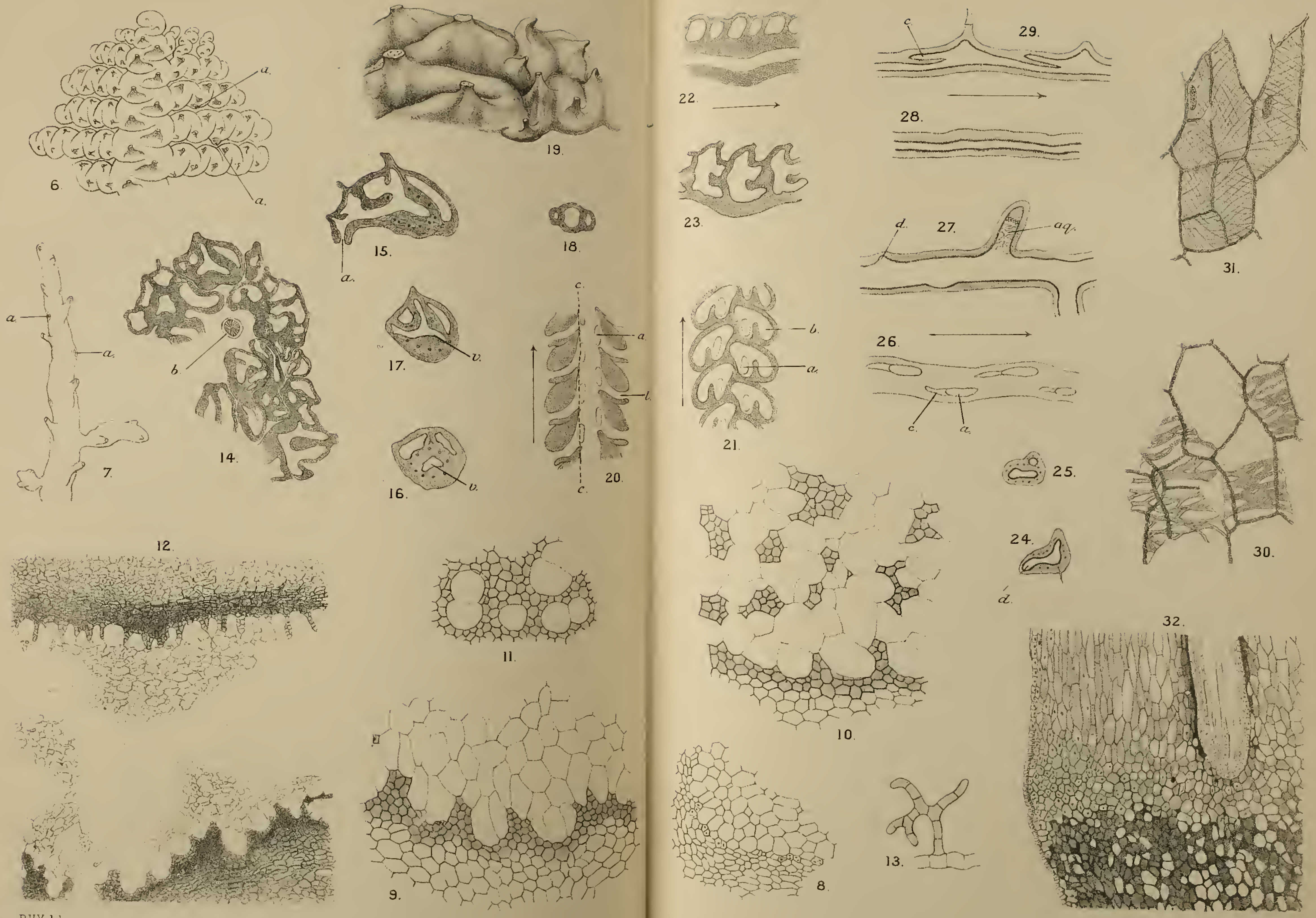

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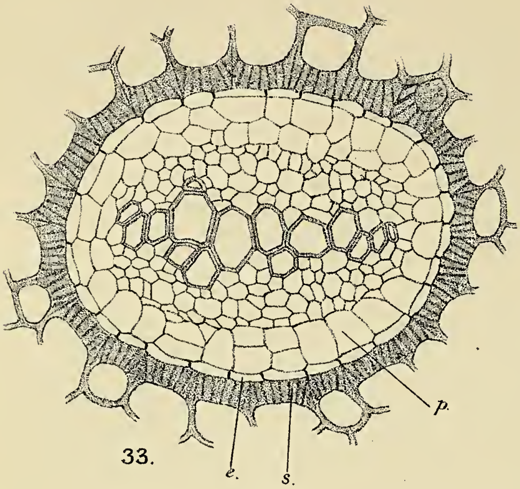
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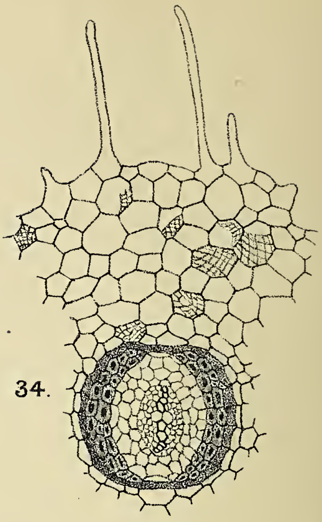
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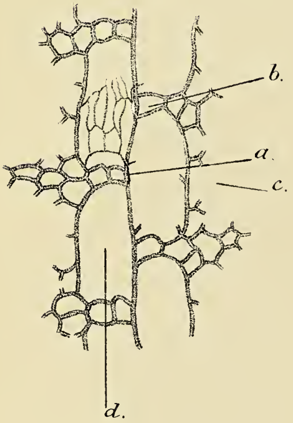

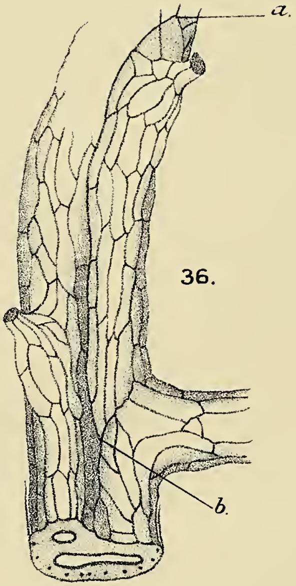
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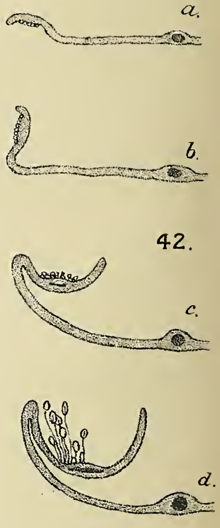
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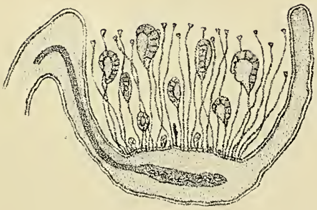

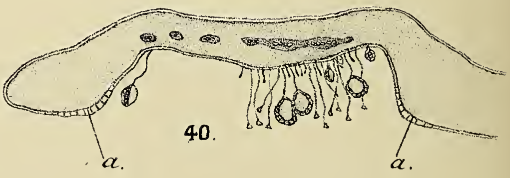
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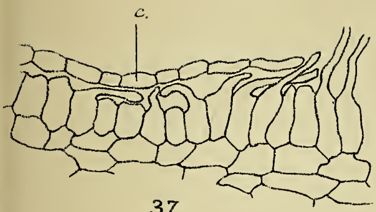

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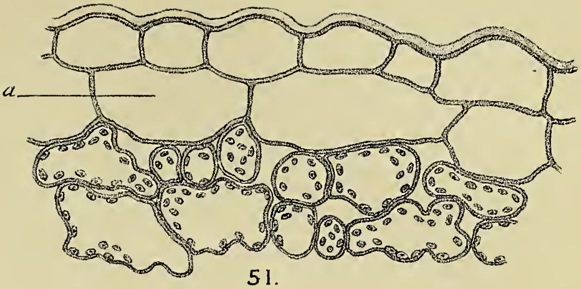

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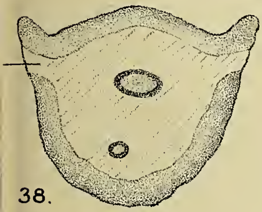

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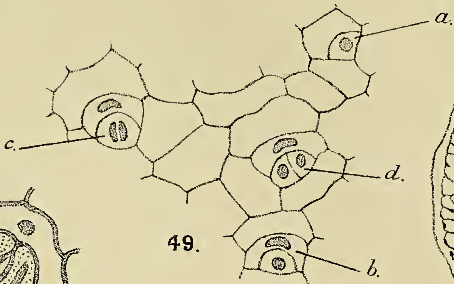

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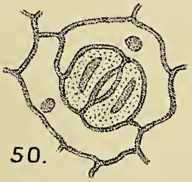

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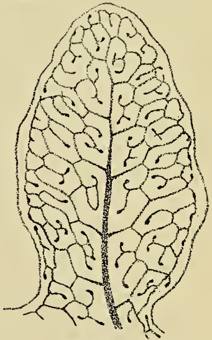

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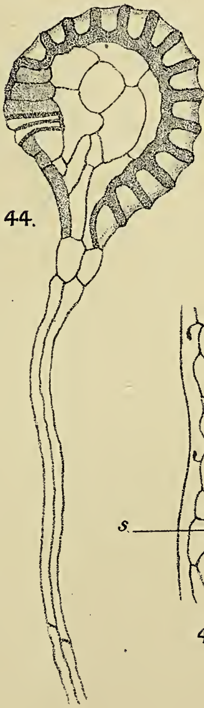

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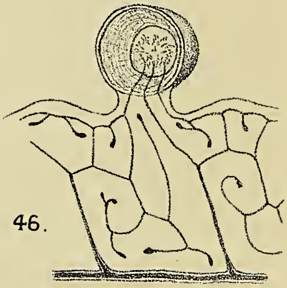

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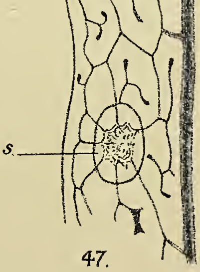

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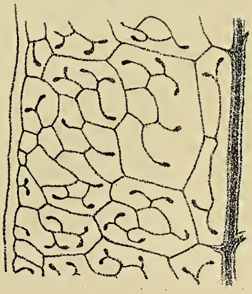

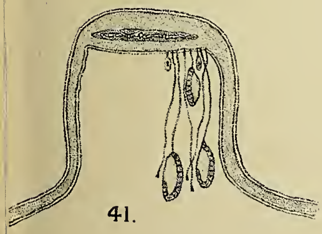

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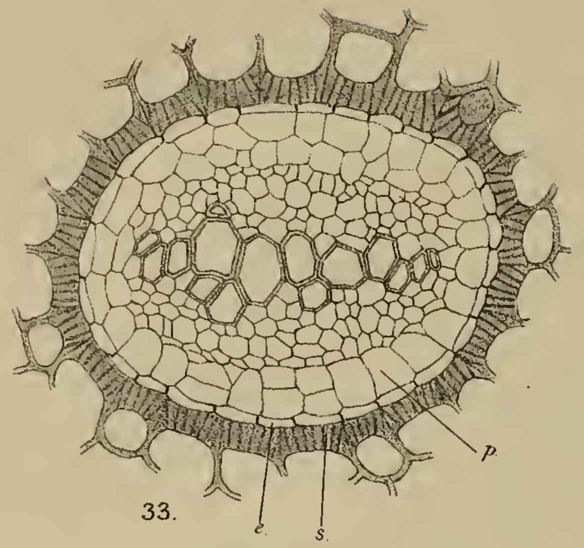

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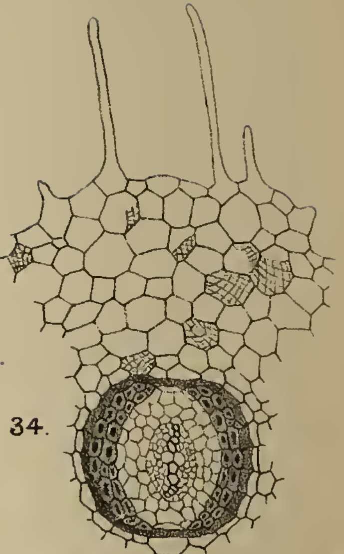

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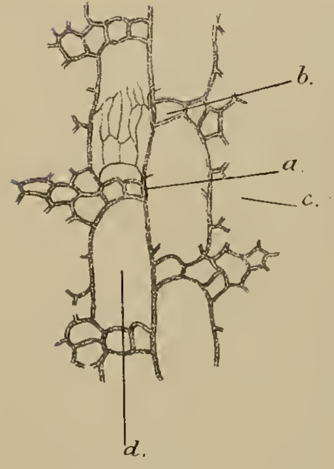

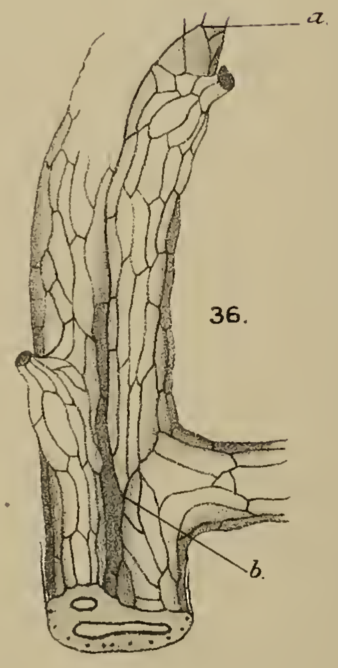

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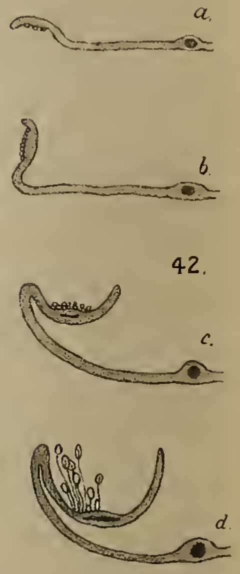

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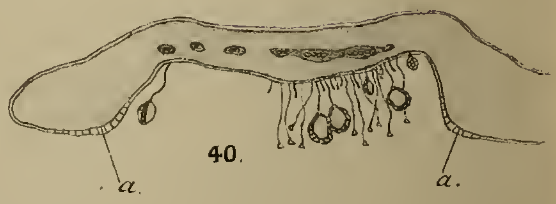

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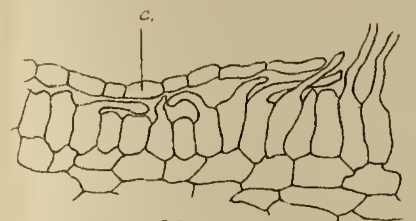

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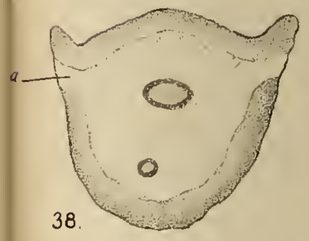

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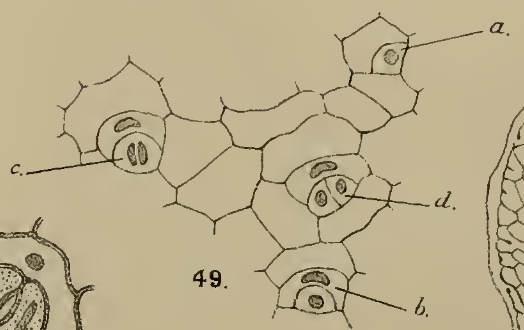

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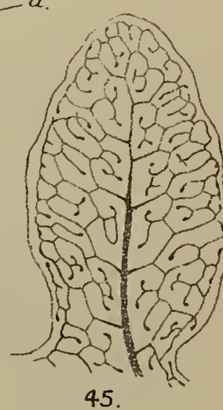

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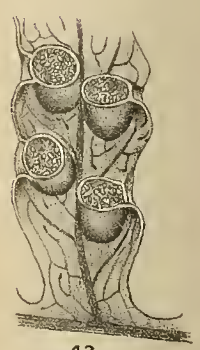

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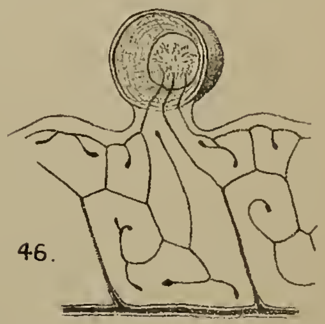

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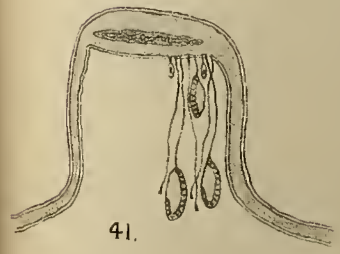

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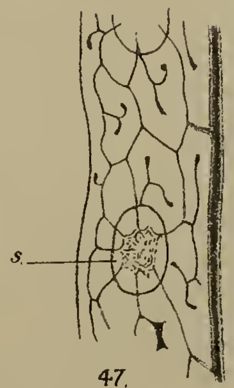

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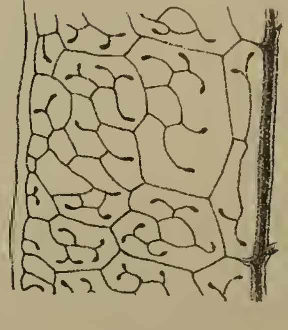

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On the Relations between Host and Parasite in the Bromes and their Brown Rust, Puccinia dispersa (Erikss.)

BY

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1. INTRODUCTORY.

SOME years ago I gave a summary of the factors and questions involved in the study of the relations between host and parasite in certain epidemic diseases of plants [1], and have at various opportunities since then continued investigations into that subject. In particular, I have for some time been occupied with researches planned with the object of ascertaining more concerning the modes of infection and attack of the Uredo-form of certain Rust-fungi.

During the course of this work I had occasion to select a particular genus of grasses, viz. the Bromes—with the view of examining their anatomy and histology in detail, in reference to the behaviour of the fungus in their tissues. In course of time a series of phenomena came to light which led me to go further into the conditions of infection, and to make numerous experiments with the Uredo of the Brown Rust—*Puccinia dispersa*—so common on certain species of this genus. These experiments led to some unexpected results, and the purpose of the present paper is to put together these

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[1] Croonian Lecture, Proc. R. S., vol. 47, 1890, p. 393.

[Annals of Botany, Vol. XVI. No. LXII. June, 1902.]

results, since they appear not only of considerable interest and importance by themselves, but promise to throw additional light on some vexed questions of parasitism and immunity, and on the relations between the host-plant and its invading or attacking fungus.

I shall here confine myself entirely to the genus *Bromus* and the Uredo of the Brown Rust—*Puccinia dispersa*—leaving any questions concerning the Teleutospores and Aecidia for further investigation, except in so far as it may be necessary to make reference to them in the form of notes in the sequel.

The plan of the work, as thus extended, concerns the characters and behaviour of the 'seed' and the seedlings of the species of *Bromus* examined, together with observations on the leaves of young plants, and the systematic relationships of these species: the description of methods of culture by which these grasses can be grown and kept growing absolutely free from danger of accidental infection by rust fungi: the means by which pure cultures of the Uredo in question can be transferred to such pure cultures of the Bromes, and the comparison of infected and non-infected plants compared; and, lastly, the behaviour of the Uredo itself on, and in, the different species.

The facts and experiments soon raised a number of questions in their turn, among which those of specialized parasitism, the persistence of the Uredo-form and the delimitation of species, and Eriksson's 'mycoplasm' theory are important.

In my work on *Hemileia* in 1881–2, the uredine which caused the coffee-leaf disease in Ceylon, I was much impressed by the probability, amounting almost to a certainty, that the species *Hemileia vastatrix* on *Coffea* had originated by the special adaptation of a certain species, *Hemileia Canthii*, wild in the native forests on *Canthium*, to the cultivated coffee. When once this fungus had learned, so to speak, to attack the coffee-plant, it proved a disastrous parasite capable of becoming epidemic on its new host. Complete experimental proof of this was not obtained, but

I was able to show that the *Hemileia* on *Coffea Arabica* will infect *C. Liberica.*

Since then Eriksson has elaborated a theory of adapted parasitism in connexion with the rusts of our cereal grasses, which has assumed a degree of importance so grave, and so full of consequence for the understanding of the epidemic diseases of cereals, that any investigations throwing further light on the matter are welcome. Eriksson found, in fact, that the so-called rust of wheat (*Puccinia graminis*) is a collective species, the morphological characters of which are now very thoroughly known, which behaves differently according to the particular host to which it has adapted itself as a parasite [1]. For instance, if we take the uredospores growing on wheat and sow them on rye, barley, or oats, the results are negative. Nevertheless *P. graminis* occurs on these plants, and forms uredospores on them. If, similarly, the uredospores from rye be sown on oats, the results are negative, whereas if sown on barley they infect it.

In other words *Puccinia graminis*, while it infects all the above-mentioned plants, and preserves its morphological characters on all of them, is so closely adapted to the particular host it happens to be on at the time, that the uredospores from this host can only attack successfully and directly either this particular host or a limited number of its immediate allies. And the same specialized parasitism occurs in the case of other species of rusts, growing on different hosts.

It thus becomes evident that we must modify our ideas considerably as to the danger of infection of wheat by the uredospores of *P. graminis* growing in its neighbourhood on some other grass. Further research showed, for instance, that the uredospores of this fungus on the weed-grass *Agropyrum repens* will infect rye but not wheat, and similarly with that on *Elymus arenarius*. On the other hand, the uredospores—of the same *Puccinia*—growing on *Dactylis* will attack oats but not rye, and similarly in other cases. The

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[1] See Eriksson in Bot. Gaz., 1898, vol. xxv, p. 26, for summary and literature.

next question which arises is: How does this fungus pass successfully through its summer form—the Uredo-stage—if its power of direct infection is thus limited? We know of course, since De Bary's classical proof, that it passes the winter in the teleutospore-stage to infect barberries in the spring by means of the sporidia borne on its pro-mycelium, and so forth. But, as Barclay showed, there are districts where the barberry is either wanting or very rare, and nevertheless the Uredo-form is never wanting on the cereals. To some extent the explanation is afforded by the repeated and continual infection and re-infection of grasses which follow on one after the other as regards the growing season. But Eriksson's researches led him to conclude that there is evidence of there being limits to this, and although the Uredo *may* thus persist on the weed-grasses, it by no means follows that it does so to such an extent as theory has demanded.

Another idea which arose out of these results was that the different specialized forms—which, though not *morphologically* distinct are *physiologically* different one from another—are incipient species; that the particular specialized race adapted to growth on wheat, but not on rye or barley, is in course of becoming a species, and may during the lapse of time actually become a species of *Puccinia*, which will eventually show morphological differences in addition to the physiological ones it already shows. Various names have been proposed for these physiologically, but as yet not morphologically, different varieties of *Puccinia graminis*. Eriksson termed them 'special forms' (*formae speciales*[1]), Rostrup names them 'Biological species' (*biologische Arten*), Schroeter chose the term *Species sorores*, and Magnus calls them 'adapted races' (*Gewohnheitsrassen*). Not much of importance is perhaps to be derived from the terminology, but it is pretty clear that each authority recognizes more or less clearly some aspect of one and the same underlying idea, viz. that each of these specialized forms has received from its host an impress, not perceptible in any visible difference

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[1] Eriksson, l. c., p. 92.

of shape, size, colour or other morphological characters, but differing in some capacity of reaction towards another host. It is, of course, a matter of pure hypothesis as to whether these intangible physiological differences will ever bring about morphological changes of so obvious and relatively permanent a nature that we should then recognize the differences as specific. As will be seen, also, there is danger of some confusion of ideas as regards adaptation and variation on the part of the fungus, and we must not lose sight of possible reactions of the nature of resistance or predisposition on the part of the host.

So impressed was Eriksson with the significance of his share of the foregoing facts, and especially with certain difficulties met with in explaining the sudden and serious epidemic outbreaks of rust which occasionally occur, that he committed himself in 1897 to the remarkable hypothesis that at certain seasons the rust-fungus attacks the grass, e. g. wheat, and passes the protoplasm of its spores into the embryo, or some other part of the plant, where it mingles with the protoplasm of the host, and lives a common life of *symbiosis* with the living cell-contents, to break out suddenly at a favourable opportunity as rust. This supposed symbiotic form merged in the protoplasm of the host he termed *Mycoplasm.* This is not the place to enlarge upon the fact, which all who have followed his splendid investigations into wheat-rust must admit, that anything on this question coming from Eriksson is entitled to respectful consideration; but it does appear pertinent here to say that the question may be raised, whether Eriksson had not done better to retain the first term which gave the title[1] to his communication on this subject; for while there is plenty of evidence that the mycelium can remain dormant at certain times and under certain conditions in leaves unsuitable for its further development, there is little or none so far as I can find to support his hypothesis of this mysterious *Mycoplasm.*

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[1] Vie latente et plasmatique de certaines Urédinées. Compt. Rend., 1897, p. 475.

2. THE RUSTS OF THE BROMES.

In their book on the Rusts of the Cereals, published in 1896[1], Eriksson and Henning gave detailed descriptions of six species of *Puccinia*. Of these four also occur on various species of *Bromus*.

These are (1) *P. graminis*, Pers., or Black Rust, found on *Bromus asper*, *B. brizaeformis*, *B. erectus*, *B. giganteus*, *B. Gussonii*, *B. lanuginosus*, *B. longiflorus*, *B. maximus*, *B. tectorum*, *B. Wolgensis*—all recorded for Sweden—and on *B. mollis* and *B. pitensis* according to other authorities.

The Aecidium-form of this species is the classical *Aecidium berberidis* so well known since De Bary's discovery of heteroecism.

(2) *P. glumarum*, Schm., or Yellow Rust, found on *Bromus adoënsis*, *B. asper*, *B. arvensis*, *B. mollis*, *B. secalinus*, *B. sterilis*, and *B. tectorum* by various authorities who have referred it to *P. rubigo-vera.* D. C. (*P. striaeformis*, Westd., and *P. straminis*, Fuck.) No Aecidium-form of this has yet been discovered.

(3) *P. dispersa*, Erikss. and Henn., or Brown Rust, is found on *B. arduennensis*, *B. arvensis*, *B. patulus*, *B. squarrosus*, and, judging from herbarium specimens, on *B. mollis*, *B. sterilis*, and *B. tectorum*.

The Aecidium-form of this species is said to occur on *Anchusa*.

(4) *P. coronata*, Corda, or Crown Rust, occurs on *B. asper*, *B. inermis*, and *B. mollis* according to various authorities.

The Aecidium-form of this species is found on species of *Rhamnus*.

With the other two species of Eriksson and Henning's book we are not concerned, since they do not occur on Bromes. It may suffice to note that one of them, viz. *P. Phlei-pratensis*, Erikss. and Henn., the Timothy Rust, is a species separated off from the old *P. graminis*, Pers., as peculiar to the grass

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[1] Die Getreideroste. Stockholm, 1896.

whence its name is derived, while the other, *P. simplex*, Kcke., has been separated off from the old *P. rubigo-vera*, D. C., as peculiar to *Hordeum*.

In 1897, in fact, the three hitherto accepted species of grain-rusts had been broken up as follows :—

(1) *P. graminis*, Pers., into *P. graminis* and *P. Phlei-pratensis*.

(2) *P. rubigo-vera*, D. C., into *P. glumarum*, Er. and Henn., *P. dispersa*, Er. and Henn., and the variety *P. simplex*, Kcke.

(3) *P. coronata*, Corda, into *P. coronifera*, Kleb, *P. coronata*, Kleb, and an eighth form on *Calamagrostis* and *Melica* as yet unnamed.

Moreover, each of these species possessed several form-species, or specialized races, morphologically indistinguishable but physiologically confined to certain hosts [1].

Since I am here concerned only with the Uredo-forms of the species given, the following comparison must be supplemented by reference to the authorities quoted for information as to the teleutospores, &c.

I may, however, add the morphological definitions of the species, so far as the Uredo-forms are concerned.

Puccinia graminis, Pers. The Black Rust of cereals.

The Uredo pustules occur as large elongated spots, 2–3 mm. in length and sometimes confluent, especially on the sheaths, and may then be very long, up to 10 mm. or more. They are yellow-brown—brown-ochre, or sienna—in colour, and bear uredospores which are of a dirty yellow hue, and echinulate, and measure about $17–40 \times 14–22\ \mu$.

Puccinia glumarum, Er. and Henn. The Yellow Rust of wheat.

The Uredo pustules, or sori, are 0·1–1 mm. long and 0·3–0·4 mm. broad. In linear series confluent in long streaks at the leaf-apex, and may be there grouped into disease-flecks as much as 70 mm. long. They are apt to be more

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[1] See Eriksson, Ber. d. D. Bot. Ges., 1897, Bd. xv, p. 183, and Bot. Gaz., 1898, vol. xxv, p. 28, for details.

scattered on the inside of the glumes and paleae. The colour is citron-yellow or pale-cadmium. The spores are globoid, or shortly ellipsoid, echinulate and yellow, measuring 25–30 μ in diameter.

Puccinia dispersa, Er. The Brown Rust of cereals.

The spots or sori of uredospores are 1–1·5 mm. long by hardly 1 mm. broad, and are scattered without definite order over the whole leaf-surface, instead of forming defined confluent soral flecks. The colour is brown, i. e. brown-ochre or sienna. The uredospores are globoid or shortly ellipsoid, and echinulate. Yellow and from 19–29 μ diameter.

Puccinia coronata, Corda. The Crown Rust of cereals.

The uredo-spots or sori are sometimes long, up to 9 mm. or so, and somewhat confluent, but they may be only 0·3–0·2 mm. diameter. On the lamina they occur mostly above, rarely on the sheath, haulms, glumes, or paleae, and are red-yellow in colour. The uredospores are globoid or shortly ellipsoid, and echinulate, of a bright yellow hue, and measure 20–32 μ diameter or 28–32 x 20–24 μ.

In 1900, Eriksson[1] passed on to a further subdivision of the Brown Rust of the cereals (*Puccinia dispersa*). Having found that the forms on *Secale*, on *Triticum,* on *Bromus*, and on *Agropyrum* are mutually exclusive as to their host-genera, he proposes to regard each as a species, under the names *Puccinia dispersa* (on *Secale*), *P. triticina*, *P. bromina*, and *P. agropyrina*. To these he adds *P. holcina* and *P. Triseti.* We are here concerned only with the form named by him *P. bromina*, the Uredo of which may be described as follows[2]: sori 1–10 mm. long x 1 mm. broad, ferruginous, throughout the lamina, at first above, aggregated. At length occupying the sheath and even the inflorescence. Spores globose-ellipsoid, echinulate, 20·8–24 μ diameter. Easily germinating.

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[1] Nouvelles études sur la rouille brune des céréales. Ann. des Sc. Nat., 7e sér., T. ix, p. 241. Eriksson here accepts thirteen species in all.

[2] The aecidium-form has since been discovered, according to Müller, Beitr. z. Bot. Cent., Bd. x, 1901, p. 182, and is found on *Pulmonaria* and *Symphytum*, not on *Anchusa*.

I have found the fungus thus described on the following plants:—*B. mollis*, common and very strongly developed both in the open fields and in the garden; *B. sterilis*, equally common, though the pustules on the wild plants in the hedgerows and fields were never so strongly developed or so large as on the wild *B. mollis*. In the gardens, on well-grown plants, they were sometimes equally good however. On *B. secalinus*, in the garden only, where the pustules were finer than any others. *B. brizaeformis*, only in the Botanic Garden, and strongly developed. On *B. arvensis*, *B. macrostachys*, *B. brevirostratus*, *B. longiflorus*, and *B. purpureus*, all growing in the gardens in tufts close to those already mentioned, the pustules were fewer and, as a rule, less well-developed.

I have failed to observe this fungus on *B. inermis*, *B. echinaceus*, *B. madritensis*, or *B. maximus*, even on tufts growing close to and intermingled with those mentioned.

On a species marked *B. asper*, in the gardens, but which turned out to be *B. arvensis* when critically examined in flower, a second Uredo was equally common with that of the Brown Rust, *Puccinia dispersa*, viz. *P. glumarum*, the Yellow Rust, a point of some importance in connexion with certain experiments.

This confusion of names also brings prominently forward the necessity of having perfectly accurately named 'seed' of the varieties and species to be experimented with, and I had to go into this question very carefully in preparation for what follows.

3. ON THE SPECIES OF BROMUS USED IN THE EXPERIMENTS.

Hackel, following to some extent Bentham and Hooker[1], divides the genus Bromus into five subgenera as follows:—

(1) *Festucoides*. Perennial, mostly tall and with loose panicles. The first glume 1-nerved, the second 3-nerved.

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[1] See Genera Plantarum, vol. iii, p. 1200, and Hackel, Die natürl. Pflanzenfamilien, 11. Th., 2. Abt., p. 75. See also Ascherson, Syn. d. mittel-europ. Fl., 1901, p. 574, for a critical review and differences in detail.

Outer palea shortly awned, the upper very finely ciliate on the ridges:—e. g. *B. erectus*, Huds., *B. inermis*, Leyss., *B. asper*, Murr., *B. ciliatus*, L.

(2) *Stenobromus.* Low annuals, with narrow spikelets broadening upwards. Glumes as in (1). Lower palea keeled, long-awned; the upper stiffly ciliated. Weeds, e. g. *B. tectorum*, L., *B. sterilis*, L., *B. madritensis*, L., *B. maximus*, Desf., *B. giganteus*, L.

(3) *Zeobroma* (*Serrafalcus*). Annuals with ovoid or lanceolate spikelets narrowing upwards. Outer glume 3–5-, inner 5–7-nerved. Lower palea 7–9-nerved, and keelless; awn often spreading, rarely obsolete. Upper palea stiffly ciliate, e.g. *B. brizaeformis*, Fisch. and Mey., *B. macrostachys*, Desf., *B. secalinus*, L., *B. arvensis*, L., *B. mollis*, L., *B. racemosus*, L.

(4) *Libertia.* As Zeobromus, but the outer palea with two lateral projections. *B. arduennensis,* Kunth.

(5) *Ceratochloa.* Spikelets lanceolate, compressed. Glumes and paleae many nerved, keeled; ovary evidently 3-humped, e. g. *B. unioloides*, Kunth.

Of these I have made a more or less thorough examination of the following representatives. In the following notes on the 'seeds' and seedlings the British forms are marked with an asterisk. It should be borne in mind that these notes are only intended to indicate the plants I have been using; materials are being accumulated for a more comprehensive treatment of the whole genus on which I am engaged[1].

(1) *Festucoides.*

**B. erectus*, Huds. *B. inermis*, Leyss.
**B. asper*, Murr. *B. ciliatus*, L.

B. erectus, Huds.

A native of Europe and Asia Minor and N. Africa, is essentially a dry meadow species, and is scattered but not uncommon throughout the chalk districts of Cambridge. It

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[1] I am glad to take this opportunity of thanking Mr. Lynch, the Curator of the Botanic Garden, for the trouble he has taken in germinating and growing in pots for me many species of Bromes.

is regarded as a valuable fodder-grass in some regions, and Chatin[1] mentions it as having been one of the best of all grasses in withstanding the hot dry summer of 1892.

B. erectus is allied to *B. asper*, as is evident in the form and constitution of the spikelets, but its contracted stiffer panicle, narrower leaves, and differences in sheaths, habitat, &c., distinguish it. It is, however, an extremely variable species, and numerous races and varieties are described[2].

The 'seed'[3] of *B. erectus* is narrow and long, about 10–14 × 1 mm. or, with the awn, 14–20 mm. Rachilla oblique above, 2–4 mm. long, and beset with rough short hairs. Lower palea papery at edges, nearly flat, fimbriated above; the upper palea almost fully exposed, very thin. Caryopsis navicular, dark-brown, with a broad shallow ventral groove. Hilum a narrow black line. There is a faint dorsal keel. Apex tufted with remains of style. Colour in the mass grey, the darker caryopsis shining through the pale-yellowish paleae.

The 'seed' germinated very badly, and only very few plants were as a rule obtained. In a second consignment, in fact, none germinated in a sample of thirty-four sown (No. 745).

B. asper, Murr.

Is a species of Europe, except the extreme north, and the Orient extending into India and N. Asia, and has been introduced into N. America. All authorities agree that it comes near *B. erectus*, and we may therefore put it here. In the London Catalogue it is indexed as *B. ramosus*, Huds., with two varieties. The dispute as to the name and varieties is dealt with by Trimen and others[4], and need not concern us here; but I can lay no stress on the characters of ramification of the panicle, and it seems difficult to keep the varieties apart.

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[1] Compt. Rend., cxv, 1892, p. 397.

[2] See Ascherson, Syn. d. mittel-europ. Fl., 1901, p. 577.

[3] 'Seed' here signifies the true fruit (caryopsis) enclosed in its paleae.

[4] Trimen, Journal of Botany, viii, 1870, p. 376. See also Ascherson, Syn. d. mittel-europ. Fl., p. 575.

The 'seed' of *B. asper* resembles that of *B. erectus* in general shape and size, but is heavier and more plump. It is somewhat cylindroid, measuring about 10 × 1·5 mm., and with short awn (4–5 mm.), palea finely nerved and upper end ciliate. Rachilla somewhat long.

The four-day seedlings of *B. asper* showed very slow germination, the radicle having only just appeared, the plumule not yet evident from between the pale thin yellow paleae. Awn short and fine. Outer palea flatter and thinner than in the *B. sterilis* type, and approaching the 'boat type'[1] of the *Serrafalcus* group.

B. inermis, Leyss.

Occurs in Europe, the Caucasus, and N. Asia. It is regarded as an important grass for very dry climates, its perennial creeping rhizomes enabling it to withstand the aridity of the Steppes and dry prairies. *B. inermis* is closely allied to the widely spread North American *B. ciliatus*, L., which may be regarded as its New World representative; but although *B. inermis* is not a native of America, it grows well there—e. g. on the Pacific Coast—and has been widely introduced elsewhere, as the Hungarian or Awnless Brome.

The 'seed' of *B. inermis* is much flattened; and awnless or with a mere trace of awn. Size 10–12 × 2 mm. Lower palea flat, distinctly nerved above, margins curved in slightly below. Apex somewhat torn. Upper palea closely adherent to caryopsis. Rachilla short, about 2·5 mm., stiffly hairy, hardly projecting. Caryopsis 6–10 mm. long, very flat, slightly sinuous, acute at both ends, hairy above. Median ventral furrow very shallow; hilum a mere ridge or keel owing to the adherent palea. 'Seed' in the mass yellowish-grey.

The 'seed' germinates fairly well, but slowly. Of 41 'seeds' sown, only 13 germinated in five days, and on the sixth day the seedling was somewhat characteristic owing to the bluntly rounded, somewhat torn palea.

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[1] See Marshall Ward, 'Grasses,' pp. 127–128.

B. ciliatus, L.

Is a N. American species occurring all over from Newfoundland to New York, westward to Minnesota, Iowa, and northwards into Canada, and south to Texas. It is placed by Britton and Brown next *B. erectus* and *B. asper*, and grows in woods and thickets. It has wider leaves, stouter culms, and more diffuse and drooping branches to the panicle than *B. erectus*, and the sheaths are devoid of the long retrorse hairs so characteristic of *B. asper*. Several varieties have been described[1], of which *B. purgans* (*B. pubescens*, Muhl.) is well marked by its more pubescent paleae hairy all over, and *B. laeviglumis*, Scribner, which has nearly glabrous paleae with at most a very slight pubescence on the margins near the base. The latter occurs in Maine to N. Carolina and extends into Canada.

I have not as yet had the opportunity of growing and experimenting with the true *B. ciliatus*, L. Under the name *B. ciliaris*, Torr., I have received what is a totally different plant, as the seeds and seedlings show.

B. canadensis is somewhat like *B. asper* in general appearance, but rather flatter, 13–14 × 2 mm. and with fimbriated membranous palea above; awn 8 mm. Nerves indistinct, glabrous. Colour yellow-grey.

B. canadensis, Michx., is the same as *B. ciliatus*, L., according to the 'Index Kewensis,' cf. Michx. Flor. Bor. Ann. i. 65 and Linn. Sp. Plant. 76.

B. canadensis was found to germinate very poorly. In five days only two, and on the sixth day only five had moved out of a batch of nineteen sown.

(2) *Stenobromus*.

B. tectorum, L. **B. sterilis*, L.
**B. madritensis*, L. *B. maximus*, Desf.

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[1] *B. ciliatus* (Huds.) is the very different *B. madritensis* (L.); and *B. ciliatus* (Muhl.) is *B. Kahlmii* (A. Gray). *B. ciliatus* (Lam.) is *Brachypodium distachycum* (Beauv.).

B. sterilis, L.

Is common in Europe, the Orient, and North Asia. It is an abundant and well-known weed, and one of the earliest of our grasses, extremely common in Cambridge, and one of our most characteristic hedge species. It is now extensively naturalized in Ohio and other parts of America, in Jamaica, in Australia, and elsewhere in our Colonies.

B. sterilis 'seed' is so like that of *B. maximus* that one can only distinguish them by the size. 'Seed' 15 × 1·5 mm. exclusive of paleal teeth (3–4) and awn (24 mm.) The purple colour is perhaps more pronounced however, and the steely-blue colour which diffuses out on germination seems characteristic, since no such stain comes from *B. maximus*, though it does from *B. tectorum* and, to a less extent, *B. madritensis*.

Seedlings four days old show a spear 8–10 mm. long, and a beautiful steel-blue colour diffuses around into the filter paper.

In a week pot-plants were 5–10 mm. high. The first sheath pink, and the spear very narrow. In five days the spears in the intermediate pit were 5–10 mm. up.

Seedlings in the open with 3–4 leaves had the lamina 8–8·5 cm. × 3·5 mm. There is a distinct keel, running down on to the sheath, and about six light lines on either side of the midrib. Ridges above, low and rounded, and about three show on each side of the sheath-keel. Spreading hairs, especially on the upper surface, keel and edges of the blade, but mostly on the keel of the sheath. The sheath is split at its apex, but complete elsewhere. The right edge rolls over the right, and the broad leaves are soon reflexed, and tend to twist.

B. tectorum, L.

Is native in Europe, North Africa, the Orient, and North Asia. It is, like *B. sterilis*, a weed of poor soil, &c. I found it abundant at Stalden, and in some other parts of the Saas Valley. It occurs occasionally in England, but only as an introduced alien. The 'seed' sent me as *B. ciliaris*, Torr., is very similar (see below, p. 256). The spikelets do not readily break up, the cylindroid narrow 'seeds' are grey with a purple or rosy cast, 9·5–10 × 1 mm, with an awn longer than itself, 15 mm., springing from between two teeth of the papery palea. These teeth are colourless and 1·5–2 mm. long, transparent. Nerves about five and fairly clear.

B. tectorum germinated readily, sixteen out of twenty-five 'seeds' sown having germinated on the fourth day (No. 745). The seedling was scarcely distinguishable from that of *B. sterilis*, and the same steel-blue stain diffused out during the first two days.

B. madritensis, L.

Is a species of Europe, North Africa, and the Orient. It occurs in Jersey, and has become established here and there on the Channel coasts of England and Ireland. *B. diandrus*, Curt., is a form with two stamens, a condition not confined to this Brome. *B. madritensis* is almost indistinguishable from *B. sterilis.* It is about 16 × 2 mm. Awn 25 mm. Teeth and long rachilla similar. All authorities put it near *B. sterilis.*

The four-day seedlings, as well as those in pots a week old, were quite like those of *B. sterilis*, but slower in growth, the sheaths of the spears, 5–10 mm. high, being green without any bronze. In five days in the intermediate pit, the spears were 5 mm. high, but two of them had leaves opening and 2 cm. long.

B. maximus, Desf.

Is a native of the Mediterranean and Caucasus, occurring also in Jersey, and comes close to *B. sterilis* and *B. tectorum*, but is larger. Boissier puts it near *B. madritensis*[1]. It is reported also from South Africa.

B. maximus. The 'seed' is long and narrow, the much-

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[1] According to the Index Kewensis, *B. maximus* (Desf.) is the same as *B. rigidus* (Roth.) Cf. Desf. Flor. Atl., i, 95, t. 26, and Roth in Roem. and Ust. Mag. Bot., iv (1790), 21. Ascherson, Syn. d. mittel-europ. Fl., p. 594, adopts the name *B. villosus*, Forsk.

inrolled palea terminating in two long slender papery teeth from between which the long slender awn arises. From base of 'seed' to apex of teeth 23–25 mm., the teeth themselves 5–6 mm. Awn about 40 mm. Breadth of 'seed' about 2 m. Colour dark-grey—mouse colour—with a purple cast. Rachilla long. The whole 'seed' and awn covered with minute forward asperities. Seedlings when four days old a spear about 2 mm. long, and much like the smaller and more quickly growing *B. sterilis*.

In a week the pot-seedlings had a leaf projecting 2 cm. above the ground, the apex unfolding and the whole of a beautiful bronze-green. It showed five veins, and had stiff short hairs on the back, and was 2 mm. broad. The direction of rolling seemed to vary, but was usually such that the right edge comes over the left.

In five days, forced plants in the intermediate pit had strong spears 5–10 mm. high.

(3) *Zeobromus*, Serrafalcus.

**B. secalinus*, **B. velutinus*, **B. mollis*, **B. interruptus*, **B. racemosus*, *B. commutatus*, *B. arvensis*, *B. brizaeformis*, *B. macrostachys*.

On comparing the 'seeds' of *B. mollis*, L., *B. interruptus*, Hack., *B. arvensis*, L., *B. racemosus*, L., *B. commutatus*, Schrad., *B. secalinus*, L., *B. velutinus*, it is clear that we have a series of very closely allied forms, bearing out Bentham's contention that they should all be put as varieties or subspecies of one—*B. arvensis*. It is now usually conceded that *B. arvensis*, L., is not native in this country, and that *B. secalinus* with its variety *B. velutinus*, *B. mollis* with its variety *B. interruptus*, and *B. racemosus* with its variety *B. commutatus*, may be claimed as species[1]. In any case they are undoubtedly closely allied, and form the typical nucleus of the group or sub-genus *Serrafalcus*, formerly indeed separated as a genus from *Bromus*.

On comparing a series of the germinated seedlings of these

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[1] See Ascherson, Syn. d. mittel-europ. Fl., for a critical survey of these relationships.

species, all sown at the same time on moist filter-paper in glass dishes, and kept side by side, also very little difference can be seen between them except in minute points, as is evident on comparing the ripe 'seed' and the seedlings on the fourth day.

Seedlings in pots, also treated exactly alike, gave the following points, which, as before, I append to notes on the species as here understood.

B. arvensis, L.

Is common in Europe, the Orient, and North Asia, and has spread to the Cape and elsewhere. It often gives the impression of being a diminutive or starved form on arid lands, and frequently occurs on sea-coasts. It is, however, not often found wild in this country and is probably not native—the view taken by the London Catalogue, 9th ed., 1895, p. 44. There is room for suspicion that *B. arvensis* is sometimes confused with other species. The 'seed' of *B. arvensis* is the smallest of all I have experimented with, except perhaps the one called *B. pratensis*, and averages 7 mm. by 1 mm., the awn being about as long, viz. 7 mm. The papery margin of the palea is much infolded and the nerves not very distinct. In the mass the 'seed' is grey-yellow with touches of purple.

B. arvensis, a week old, had a leaf 1·5 cm. long by about 1 mm. broad, bronzed, and rolled, with stiff spreading hairs. Forced in the intermediate pit, the spears averaged 1 cm. high. Seedlings a fortnight old showed a single blade 6·5 cm. long by 1 mm., with two ridges each side the midrib, and ciliated as were also the margins. Sheath almost devoid of hairs. 'Seed' small.

It is smaller than *B. racemosus* but similarly flat, with thin membranous edges to the outer palea. The plumule is also perhaps a trifle longer and pinkish above. The whole outline narrower and the awn longer.

In seedlings grown in the open ground and having three or four green leaves, the lamina of the first developed leaf averaged 4–5 cm. long by 1 mm. broad. It had a few spreading hairs, but showed very few positive characters. The sheath was completely closed to near the apex, the ligule short and slightly fringed, and the lamina showed about three whitish lines on each side of the midrib. The first developed leaf is hardly acute: the succeeding taper to a long point and measure 10–12 cm. by 2 mm. The keel is hardly noticeable. These seedlings were the narrowest of all as regards leaves.

B. mollis, L.[1]

The 'seed' of *B. mollis* comes next in size, being 9 × 1·5–2 mm. and the awn 8–9 mm. The five nerves on the palea are quite clear at the top, where the palea is also flattened, giving the greater width and tendency to a 'coracle-shape' to the whole. In the mass the seed is pale greyish-yellow.

The palea of the germinating seed (four days old) was broader and more flattened than in the preceding three forms. In seedlings a week old the one leaf stands up 2 cm. and is 1·25 mm. broad, with three veins and a few hairs especially on the upper surface. The sheath bronzed and veined, but soon becoming bright green. In the intermediate pit the spears were 1 cm. high in five days. In three-leafed seedlings the first leaf is 6–7 cm. by 1·25 mm. and acute, the third about 9 cm. by 2 mm. with three pale lines and four ridges each side the midrib. Keel hardly observable. Habit somewhat stiff. Hairiness not pronounced. Sheaths slightly tinged with red.

On the whole it is most like *B. racemosus*, but even more expanded and more distinctly nerved in the outer palea: plumule green.

B. mollis comes from Europe, Africa, and North Asia, and is one of our commonest road-side and farm-weeds. It is not confined to dry places, however, and I find it common in the wet meadows near Lingay Fen, and elsewhere in Cambridge. There are at least three ordinary varieties, according

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[1] *B. hordeaceus*, L. See Ascherson, Syn. d. mittel-europ. Fl.

to the London Catalogue. Like so many other Bromes, and perhaps more than most, it has been extensively introduced as a weed of cultivation into the Colonies and elsewhere abroad: e. g., Canada, Australia, the United States, India, &c.

B. interruptus, Hack.

Approaches *B. mollis* and *B. racemosus* in many characters, measuring 9 x 2 mm. and awn 9–10 mm. It is slightly downy. In the mass the colour, &c., are the same. It differs in the marked tendency of the florets to remain in the spikelet. Its chief characteristic, however, is the split inner palea, which is cut to the base in the median line.

B. interruptus seemed sharply distinct by the non-separation of the 'seeds' in the spikelet, and consequently germinates in tufts of about 5–7. It was not up in a week, but quickly rose about the eighth or ninth day. In other respects it resembles *B. arvensis*, *B. mollis*, and *B. racemosus*. In the intermediate pit the spears were 1 cm. high in five days. The third leaf is 10–12 cm. by 2 mm. and resembles the species named.

The four-day seedlings are also exactly like parallel cultures of *B. mollis*, except that the spikelets do not so readily break up, and the germination is slower. The plumule is green and not bronzed.

B. interruptus, Hack., is regarded by the editors of the London Catalogue, 9th ed., 1895, as a variety of *B. mollis*, L., a view supported by my examination of the seedlings. It was discovered by Druce in 1895[1] in England, and is sharply marked by the deeply split inner palea.

B. racemosus, L.

Has a larger 'seed' than *B. mollis*—e. g., 10 x 2–2·5 mm. with awn 9–10 mm.—though otherwise they are similar in shape (the palea lying open) and colour. Perhaps the ciliation and nervation are less evident in *B. racemosus*. In the mass

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[1] See Journ. Bot., 1895, p. 344, and 1897, p. 18. Also Journ. Linn. Soc., 1896, vol. xxxii, p. 426.

it is difficult to detect any difference beyond size. The four-day seedlings are like those of the last species. In a week the first leaf-spear is 1–2 mm. above ground, and in a pot five days in the intermediate pit only two spears showed, about 5 mm. high. *B. racemosus*, L., is a common European plant, and regarded by Bentham as merely a smoother variety of *B. arvensis*. But we must bear in mind the extensive definition of the latter species given by Bentham. The more usual view is to regard it as a good species[1].

B. commutatus.

Is quite like *B. racemosus*, of which it is often regarded as a variety. The 'seed' measures 10 x 2 mm. with an awn the same length. The colour may be a trifle paler in the mass, but there are no marked points of difference to be seized.

The seedlings of *B. commutatus* are also very like those of *B. racemosus*. In a week the spears were 2–3 mm. high, and in the intermediate pit the tips only just showed in five days.

In a fortnight the total height was about 8 cm. The leaf averaged 6 cm. x 2 mm. and had seven ribs; the cilia, hairs, ridges, &c., were like *B. arvensis*, and the sheath almost smooth.

B. commutatus resembles also *B. mollis* in four-day seedlings, but is far behind it in rapidity of germination.

B. commutatus, Schrad., is synonymous with *B. racemosus* according to the *Index Kewensis*, cf. Fl. Germ., i. 353. In the London Catalogue, 9th ed., 1895, p. 44, it is accorded specific rank[2], however, with two varieties.

B. secalinus, L.

Next in point and size comes *B. secalinus*, which is rounded and fatter and more bulky and corn-shaped than any of the foregoing. Length 7 mm., breadth 2 mm., and thickness about the same. Awn 5–6 mm. In the mass the 'seed' is distinctly heavier: in colour it is grey-yellow like *B. mollis*.

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[1] Lond. Cat., ninth ed., 1895, p. 44.

[2] See also Ascherson, l. c., p. 613.

B. secalinus. On the fourth day no differences were observable beyond the shorter spear and the characters of the paleae.

In a week the spear was less than a centimetre high, the membranous sheath being smooth and brown-pink. Slightly forced in the intermediate pit, the spears were not above ground on the fifth day. Three-leafed seedlings are more robust and taller than those of *B. arvensis*, the third leaf being 12–15 cm. long by 2·5–3 mm. wide, with 3–4 pale lines each side the midrib. The first leaf—about 6 cm. by 2·3 mm. —is soon reflexed, as is also the case in *B. arvensis.* Beyond the broader leaves and more robust habit—very noticeable in pots of several—however, it was not easy to distinguish them.

The four-day seedlings of *B. secalinus* bring out well the character of plumpness of the 'seed' as compared with *B. racemosus.* The spear is also stout and pink-sheathed, not green as in that form. The awn is also shorter and the nervature of the inner palea less evident: this palea is ciliate, the outer one slightly hairy. *B. secalinus*, L., is a native of Europe, the Mediterranean, and N. Asia. It is regarded by Bentham as a tall cornfield variety of *B. arvensis*, but we must remember that he gives a very wide definition to the latter[1]. It has spread widely to the United States, Canada, and elsewhere.

B. velutinus seems indistinguishable from *B. secalinus* in size, shape, and colour. It is a trifle more hairy, however, though that is only seen on close examination. In the mass the colour and weight are similar. *B. velutinus* is very like *B. secalinus* in four-day seedlings. The seed is fat, a trifle hairy and ciliate, and the short plumule slightly pink above.

B. velutinus was indistinguishable from *B. secalinus* by any positive characters. The awn of the 'seed' appeared a trifle longer, and the length of the third leaves somewhat shorter, but in all essential respects they appear to be the same species.

B. velutinus, Schrad., is given as a synonym of *B. secalinus*

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[1] See Ascherson, l. c., p. 602.

in *Index Kewensis*, cf. Flor. Germ., i. 349, t. 6, f. 3. It is generally regarded as a distinct variety of that species—see Lond. Cat., 1895, 9th ed., p. 44.

In all these species—or varieties—the leaf seems to be so rolled that the right edge comes over the left as the observer looks on the upper surface of the lamina [1].

Another phenomenon common to all is the reflexion of the first leaf soon after the second leaf has unfolded. The mechanism of this reflexion has not, I believe, been explained.

It seems clear from the foregoing that no facts of sufficient morphological importance are forthcoming to enable us to separate the forms as good species, further than has been done on the other botanical characters. Indeed the 'seeds' and seedlings support very strongly the view adopted by Bentham that these species and varieties all graduate one into the other.

B. brizaeformis, Fisch and Mey.

Is a Caucasian and Persian species. It is put in the Serrafalcus section by Boissier, a view completely supported by examination of the 'seeds.'

B. brizaeformis is a remarkable form. Its widely spread palea and flattened form give it the resemblance to *Briza*, whence the name. Length about 9, breadth 5 mm. There is no awn, the membranous, 7–9 veined smooth palea cut into lobes at the apex. Colour pale-yellowish, with the large flat brown ovate caryopsis shining distinctly. Rachilla short.

My specimens of *B. brizaeformis* germinated well, twenty-one out of twenty-five having come up on the sixth day.

B. macrostachys, Desf.

Occurs in the Mediterranean region, and is placed by Bossier near *B. brizaeformis*, from which it differs in several respects in addition to being awned.

B. macrostachys is a well-marked form with a silky-woolly tomentum all over the 'seed,' and the awn (15–18 mm.) arising sub-terminally from the base of two teeth (4–5 mm.

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[1] See p. 308 for explanation.

long) of the palea. Total length of 'seed' without awn 13–14 mm.: breadth about 3 mm. The awn ascends with a curved base, and the woolly 'seeds,' remaining adherent in the spikelet, stick together. Rachilla stout and woolly. I found *B. macrostachys* germinate very slowly and badly. Only five out of twenty-four had germinated in six days.

(4) *Libertia.*

B. arduennensis. I have as yet had no opportunity of experimenting with this species, which stands alone as the only member of its group, and so am compelled to leave out of account all reference to this group in the sequel.

(5) *Ceratochloa.*

B. unioloides. B. Schraderi.

B. unioloides, H. B. and K.

Is a species from the hotter parts of America. It is an ornamental plant, and, though valuable as fodder in warm lands, easily freezes in the north. It is common from British Columbia to Patagonia and Juan Fernandez, and is widely cultivated[1]. It has also been extensively introduced into South Africa, Australia, and Tasmania[2]. I have not as yet had sufficient material for a thorough examination of the species in detail, but the following appears to be, as it is accepted as being, the same species with, possibly, slight varietal differences.

B. Schraderi, Kunth.

B. Schraderi, Kunth, is the same as *B. unioloides*, H. B. and K., according to *Index Kewensis*—Cf. Kunth, Enum. Pl. i. 416, and H. B. and K., Nov. Gen. et Sp. i. 151.

The seed is laterally compressed, the palea being closed like a mussel-shell, and smooth and much veined. 15–16 × 2·5–3 μ the awn a mere point 1 mm. long. In the mass pale

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[1] Hemsley in *Challenger* Report.

[2] See an excellent short account by Maiden in Agr. Gaz. of N. S. Wales, Dec. 1898.

yellow-grey. The shape of the 'seed' makes it lie on the side, and not as in so many on the flattened back.

My samples germinated slowly, and not very well. Of twenty-two 'seeds' sown, only eleven had put forth root-hairs in five days, though on the sixth day twenty were showing signs of germination: of these, however, only five had put out a spear.

In addition to these I have examined, less thoroughly as yet, the following.

B. giganteus is of the *B. sterilis* or *B. madritensis* type but with the five nerves of the palea well marked. It is 12–13 mm. long, excluding the two fine papery teeth 2–3 mm. and awn 14–15 mm. and about 1 mm. broad. Duller grey-yellow than any of the above. *B. giganteus*, L., is a native of Europe and Siberia. It is frequently regarded as—or, possibly, confounded with—a Fescue—*Festuca gigantea* (Vill.).

It is being cultivated for further examination.

'*B. pratensis*.'

Is a form very like a depauperate variety of *B. arvensis*, 6–6·5 × 1·75–2 mm. with a fine awn about 4 mm. long, but flatter, broader, and of paler colour, and with no purple hue in the mass. It is much smaller than *B. racemosus* and quite different from *B. erectus*, but as there was another form mixed with it, I defer judgement until later.

B. pratensis according to the *Index Kewensis* is a synonym for *B. racemosus* or *B. erectus*, both of which differ in my samples from the 'seeds' received under this name.

'*B. ciliaris*,' Torr.

Was received under this name, but as yet I have been unable to trace it satisfactorily, and am cultivating it for further determination[1].

B. ciliaris, Torr., resembles *B. tectorum*, 10 × 1 mm., awn

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[1] It seems probable that this is wrongly named, and was sent over by a collector who made some error: I have been unable to trace the name in the literature (see p. 246).

16–17 mm., the purplish 'seeds' remaining adherent in the spikelet, &c., as before. Perhaps the 'seed' is a trifle more pubescent, but I can detect no essential difference.

B. ciliaris germinated freely, seventeen out of nineteen sown having come up well in five days.

4. THE GERMINATION OF THE BROMES.

It was necessary, at a certain stage in the experiments, to obtain some information as to the germinating capacity—in the sense in which this term is used by nurserymen and experts—of the 'seeds.'

To do this I employed ordinary Petri-dishes, with a filter-paper above and below, and sowed the 'seeds' on the lower paper. When the first root-hairs[1] form, the seed becomes firmly adherent to the paper, and many advantages can be taken of this fact. For instance, it is easy to lift the germinating seedling up with forceps, by tearing the wet paper, and so transfer the whole bodily to a tube, &c.; and since the radicle rapidly pierces the paper in many cases, this procedure often obviates any rupture of the delicate roots and root-hairs.

Such seedlings in dishes are extremely geotropic and heliotropic, and it is easy to take advantage of this fact when infecting the first leaf of the plumule. If the Petri-dish is left flat, the green leaf curves up and soon presses against the lid, and if spores are sown on the leaf the film of water between leaf and lid is of advantage in the germination of the spores. In obtaining infected leaves for hardening and subsequent section-cutting it is useful to have the seedlings quite straight. This is easily done by laying the 'seeds' with their axes parallel and apices all turned one way. As soon as the radicle begins to emerge, and the first root-hairs have fixed the seedling, the whole dish can be placed vertically on its edges, and so illuminated that root and shoot grow out in one straight line—the axis of the 'seed.' The plumule can

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[1] These first hairs would be more properly described as anchoring-hairs; they are developed not from the root but from the coleorhiza surrounding it.

also be thus compelled to grow on in contact with the damp filter-paper and not lift itself off from the spores shed on the leaves, by geotropic or other curving.

The annexed tables I and II will give an idea of the germination capacity of the principal species used.

TABLE I.

Exp. No. 710. Germination of 'seeds' sown on damp filter-paper in Petri-dishes, sterilized by steaming. Incubated at 17·5° C, rising to 20° C.

No.	*Date.*	*Seed sown.*	*Treatment.*	*Date of germination.*	*Degree of germination.*
710*a*	June 12	B. mollis	Filter-paper at 17–20° in incubator	15	Good
,, *b*	,,	B. velutinus	,,	16	,,
,, *c*	,,	B. maximus	,,	16	,,
,, *d*	,,	B. sterilis	,,	15	,,
,, *e*	,,	B. madritensis	,,	15	,,
,, *f*	,,	B. asper	,,	0*	0
,, *g*	,,	B. commutatus	,,	0*	0
,, *h*	,,	B. arvensis	,,	15	Good
,, *i*	,,	B. secalinus	,,	16	,,
,, *k*	,,	B. interruptus	,,	16	,,
,, *l*	,,	B. racemosus	,,	15	,,

* Did not germinate.

TABLE II.

Exp. Nos. 745 and 746. Germination of 'seeds' on damp filter-paper in Petri-dishes, at 20°–23° C.

No.	*Date.*	*Seed sown.*	*Treatment.*	*No. sown.*	*No. germinated.*	*Approx. %*	*Date of germination.*	*Height on 6th day.*
745	July 3	B. Schraderi	on damp filter-paper Normal t. = 23° C.	22	20	91	July 6	
,,	,,	B. tectorum	,,	25	16	64	July 5	10 mm.
,,	,,	B. ciliaris	,,	19	17	90	,,	20–30 mm.
,,	,,	B. macrostachys	,,	24	5	21	July 8	
,,	,,	B. brizaeformis	,,	25	21	84	July 6	5 mm.
,,	,,	B. erectus	,,	34	0	0	0	0
,,	,,	B. canadensis	,,	19	5	26	July 6	
,,	,,	B. asper	,,	32	0	0	0	0
,,	,,	B. inermis	,,	41	13	31	July 6	1–2 mm.
,,	July 5	B. sterilis	,,	6	6	100	July 7	20 mm.
,,	,,	B. maximus	,,	6	6	100	,,	
,,	,,	B. madritensis	,,	6	6	100	,,	
746	,,	B. pratensis	,,	56	12	21	July 8	
,,	,,	B. giganteus	,,	24	0	0	0	

In devising some way of killing any possible Uredo-spores attached to the paleae or caryopsis, a few obstacles occurred owing to the difficulty of wetting the dry 'seeds' and the small size of the latter. Perhaps now that we know the maximum temperature for the spores (see p. 269), the best of all antiseptic measures will turn out to be careful heating in the dry state: this point needs further examination. As matter of fact I got good results by heating the seeds to 65–70° C in water: they will not stand 80–85° C. The temperature of 65–70° C appears to be quite fatal to all Uredo-spores.

I attempted to get over the difficulty of penetration of the micropyle, &c., by putting the 'seeds' in various liquids—chloroform, carbolic acid, mercuric chloride, &c.—and placing in a quickly acting air-pump and exhausting rapidly. As Table III shows, some success results, but great care is necessary to avoid damaging the radicle. Possibly more success will yet be met with in a longer series of trials, but I got very good results with chloroform. On the whole, however, heating to 70° C seemed most satisfactory.

5. EXPERIMENTS ON TEMPERATURE.

It seems surprising that we know practically nothing about the temperature of a leaf in the sunshine, yet such appears to be the case. A few observations have been made by placing thermometers with their bulbs stuck in the tissues of fleshy plants, such as Cacti, &c.[1], but these hardly bear on the question concerning leaves, though they give us an insight into the subject of the high temperatures plant-tissues generally may withstand.

Again, Keeble's experiments[2] only bear indirectly on what we are here interested in: moreover they refer to tropical trees.

Darwin, in his admirable memoir on Stomata[3], has one or two records of leaf temperatures in *Tropaeolum*, but he gives no observations showing what temperatures are reached by

[1] Ascherson, Bot. Zeit.

[2] Ann. Bot., vol. ix, 1895, p. 59.

[3] Phil. Trans., 1898, vol. 190, p. 531.

TABLE III.

Exp. Nos. 740, 743. Germination of 'seeds,' sterilized in various ways (col. 4). All started in incubator at 20–22° C.

Exp. No.	*Date.*	*Seed sown.*	*Treatment.*	*Time.*	*No. sown.*	*No. which germinated.*	*Approx. %*
740	June 29	B. sterilis (1)	5% Carbolic	5 min.	17	13	80
,,	,,	,, (2)	17 $HgCl_2$	,,	23	17	74
,,	,,	,, (3)	Boiled up	Just boiled	24	0	0
,,	,,	,, (4)	Scalded	Rapidly cooled	21	0	0
,,	,,	,, (5)	None	[Control]	24	23	96
743	July 2	B. mollis (6)	Sat^{d}. $HgCl_2$ sol.	5 min.	51	15	30
,,	,,	,, (7)	,,	10 min. including exhaustion	35	0	0
,,	,,	,, (8)	,,	30 min. ditto	25	0	0
,,	,,	,, (9)	5% Carbolic	5 min.	50	0	0
,,	,,	,, (10)	,,	10 min. including exhaustion	31	0	0
,,	,,	,, (11)	Pure chloroform	ditto	41	17	41
,,	,,	,, (12)	Scalded	Rapidly cooled	49	0	0
,,	,,	,, (13)	Raised to 85° C	,,	58	0	0
,,	,,	,, (14)	,, 75° C	,,	53	3	6
,,	,,	,, (15)	,, 65° C	,,	52	50	96
,,	,,	,, (16)	None	[Control]	35	35	100

(1, 2) Simply steeped and shook up.
(3) Brought rapidly to the boil and quickly cooled.
(4) Plunged into boiling water and rapidly cooled. (5) Control.
(6) Steeped and shook up.
(7) Put under pump and forced in and washed quickly.
(8) Put under pump, &c., and left steeping. (9) Steeped and shook up.
(10, 11) Put under pump and forced in and washed.
(12) Poured boiling water on and at once cooled.
(13–15) Raised to temp. given and quickly cooled. (16) Control.

leaves of plants, such as grasses, &c., in direct sunshine in the summer.

In order to see if I could obtain any information on this obscure question I started a number of observations with thermometers. One was placed with its bulb resting among the leaves of a tuft of *B. maximus*, so arranged that it was clear of the soil, and well in the shade of the numerous leaves as the sun shone on to the tuft.

By the side of the tuft another thermometer was laid across supports which held it at about the same distance from the soil, the bulb as free as possible in the air.

A third thermometer was hung vertically in the air, well away from the thin glass rod which supported it by a thread, and which was stuck in a pot of soil.

A fourth thermometer with blackened bulb was similarly suspended from another thin glass rod.

And, finally, a similarly suspended thermometer with a long but narrow thin bulb—one of those which I use for inserting into glass cells in which hanging drops are cultivated—was so arranged that the bulb was wrapped in the broad leaves of *B. maximus*, and thus protected from the direct rays of the sun by the thickness of a single leaf.

Various readings were taken on different days, of which the following may be given (Tables IV, V, and VI). It is not claimed that this method gives perfectly accurate results, but it shows quite clearly the kind of temperatures which may be expected in the closed glass vessels in which the spores are put to germinate on the leaves; and even if it is contended that it will not give the exact temperature of the leaf-surface on which the spores are sown, we may fairly assume that it does show an approach to it, and at any rate demonstrates that such leaves may be heated up to temperatures far above the maximum for spore-germination or that which the germ-tubes can withstand, without themselves being damaged.

I am of opinion that more accurate records with a thermopyle will show that the leaves in direct sunshine are heated up to temperatures far higher than is usually assumed.

6. THE GERMINATION OF THE UREDOSPORES.

The germination of the spores—Uredo-spores—is as a rule easily brought about in water, distilled or tap water, but many observers have remarked the curious uncertainty sometimes met with in their behaviour. I have paid some attention to this matter, with a view to discover if possible what are the conditions which dominate the capacity for germination.

In a good batch of spores, signs of germination in water

TABLE IV. Readings of thermometers to show approximate temperature in leaves exposed to direct sunshine in greenhouse with lights open. Facing west.

Date.	*Hour.*	*Conditions.*	*Temp. by black bulb.*	*Temp. by ordinary therm.*	*Temp. by therm. wrapped in leaf.*
July 24	12.30 p.m.	Raining: sun off		17° C	17·2° C
,,	1.30 ,,	Cloudy: ,,		16·4	16·5
,,	5.30 ,,	Clear: ,,		18	18
,, 25	9.50 a.m.	,, ,,		18	18
,,	9.51 ,,	Bright sun on			
,,	10.0 ,,	,, ,,		22	24
,,	12.25 ,,	Clouds: sun off		18	18
,, 26	10.25 ,,	Clear: ,,		18	18
,,	11.0 ,,	Slight sun		19	19·5
,, 27	11.30 ,,	Cloudy: sun off		18·8	19
,,	12.5 noon	Sun on		21·5	21·2
,,	12.6 ,,	,,		22	21·8
,,	12.7 ,,	,,		22·5	22·2
,,	12.8 ,,	Clouded over			
,,	12.22 ,,	Sun out			
,,	12.27 ,,	,,		23	25·5
,,	12.29 ,,	,,		23·7	26
,,	12.30 ,,	Clouded over			
,,	12.38 ,,	Sun out			28·5
,,	12.43 ,,	,,		26	28
,,	12.58 ,,	Hazy		25	28
,,	1.6 p.m.	Sun out		26·5	26·8
,,	1.15 ,,	,,		26·5	27·2
,,	1.16 ,,	,,		27	28
,,	1.20 ,,	,,	29·5	27·2	26·6
,,	1.22 ,,	,,	28	25·5	
,,	1.24 ,,	Drawn blind			24
,,	2.10 ,,	,,	24·2	24	27
,,	2.11 ,,	Blind up	28	25·8	26·8
,,	2.22 ,,	After cloud	27·4	25·6	26·5
,,	2.24 ,,	,,	26·5	25·5	
,,	2.25 ,,	Blind down			21
,,	3.20 ,,	Blind up	21	21·2	22
,,	3.21 ,,	Full sun	22	21·8	25
,,	3.24 ,,	,,	27	23·5	
,,	3.24½ ,,	Cloud			
,,	3.25 ,,	Sun out			25·2
,,	3.26 ,,	Full sun	28	24·5	
,,	3.27 ,,	Cloud			22·8
,,	3.29 ,,	,,	24	22·5	19·5
July 28	9.45 a.m.	Clear: sun off	19·5	19·5	20
,,	11.2 ,,	,, ,,	20	20	
,,	11.3 ,,	Blind up: cloudy			
,,	11.4 ,,	,, ,,	20·2	20·2	20·2
,,	11.6 ,,	,, ,,	20·2	20·2	20·2
,,	11.7 ,,	Cloud passing			
,,	11.8 ,,	,,	23·5	21·5	23
,,	11.9 ,,	Clouding			
,,	11.10 ,,	Cloud off: sun	25·5	22·5	23·5
,,	11.12 ,,	Full sun	28	23·8	25
,,	11.14 ,,	,,	29	24·5	25·5
,,	11.16 ,,	,,	29·5	25	25·6
,,	11.18 ,,	,,	30	25·6	25·7
,,	11.20 ,,	,,	30	25·6	26·5
,,	11.24 ,,	Slight cloud	29	25	27
,,	11.26 ,,	Cloud off	27·5	23·5	26
,,	11.28 ,,	,,	28·5	24·8	27
,,	11.30 ,,	,,	29·5	25·3	27·2
,,	11.32 ,,	Full sun	29·8	25·3	27·2
,,	11.34 ,,	,,	31	25·8	28
,,	11.36 ,,	,,	31	26	28

TABLE V.

Exp. No. 785. Readings of thermometers outside, and compared with ordinary readings on grass and in air.

Date.	*Hour.*	*Conditions.*	*Black bulb thermometer.*	*Ordinary suspended thermometer.*	*Thermometer wrapped in grass-leaf.*	*Thermometer lying in grass-tuft.*	*Thermometer suspended horizontally above ground.*
July 28	11.40 a.m.	Clouded over	21·2° C	21·2° C	21° C	20·6° C	21·1° C
,,	11.45 ,,	Sun out	24·5	22·5	23	21	24
,,	11.50 ,,	Clouding	22·5	21·6	21·8	21·2	22
,,	11.53 ,,	,,	21	21	20·9	20·5	21·5
,,	11.55 ,,	,,	20·6	20·8	20·5	20·4	21·5
,,	12 noon	,,	20·6	20·6	20·6	20·2	21
,,	12.15 ,,	,,	20·5	20·6	20·5	19·8	20·8
		Too cloudy to continue					
July 29	10.45 a.m.	Full sun	25·5	23	24·5	24	23
,,	10.55 ,,	,,	25·8	22·9	24	22*	24·3
,,	11.15 ,,	,,	26·1	23·5	23·5	19·5*	19·9*
,,	11.40 ,,	,,	27	24·1	24	23·5	24·3
,,	12.10 noon	,,	27·4	24·6	25·5	24·5	25
,,	12.20 ,,	,,	29	25·5	26·2	24·9	26·6
,,	12.30 ,,	,,	28·2	25·4	25·8	26	27·8
,,	12.45 ,,	,,	28·2	25	25·9	26	27·5
,,	1 p.m.	,,	29·1	26	26·4	25·6	28
,,	1.15 ,,	,,	28	25·9	26	25·2	27

* Shadow of a distant chimney.

may be visible in half an hour or less, and the germ-pores may begin to swell even earlier. The spores float on the water-drop and are not easily wetted: they usually aggregate in films, in which it is observable that the spores are not in contact, but remain separated by what looks like a clear interval equal to about the diameter of the spore.

The germ-tubes grow very rapidly, attaining lengths equal to from twice to five times the diameter of the spore, in a couple of hours at 20° C.

The germ-tube usually branches when it has reached a length equal to about five times the diameter of the spore, and quickly-growing tubes put out a large number of very short branches along the sides, giving them a curious knotted appearance, a peculiarity already remarked as being characteristic for this species, and figured by Eriksson (loc. cit., plate X, Fig. 115).

It is astonishing how little seems to have been done in

TABLE VI.

Exp. No. 785 continued. Comparative thermometer readings inside and outside of greenhouse.

Date.	*Hour.*	*Conditions.*	*Black bulb in greenhouse.*	*Ordinary in greenhouse.*	*Thermometer wrapped in leaf in greenhouse.*	*On grass outside.*	*Suspended horizontally outside.*
July 29	2.15 p.m.	Clear blue sky and hot sun. Lights open	27·9° C	27·1° C	26·9° C	24° C	27·8° C
,,	2.18 ,,	,, ,, ,, ,,	30·8	28·8	28	24·5	28·9
,,	2.20 ,,	,, ,, ,, ,,	29·2	29·2	29·2	25	29·3
,,	2.22 ,,	,, ,, ,, ,,	31	29·8	30·2	25·8	28·8
,,	2.25 ,,	,, ,, ,, ,,	32·6	30	30·5	26	29·3
,,	2.28 ,,	,, ,, ,, ,,	32·4	29·4	30	26	28·8
,,	2.30 ,,	,, ,, ,, ,,	32·5	29·5	29·5	25·9	28·2
,,	2.31 ,,	,, ,, ,, Closed all lights and doors					
,,	2.32 ,,	,, ,, ,, ,, ,,	33	31	30·8		
,,	2.34 ,,	,, ,, ,, ,, ,,	33·5	32·8	32·1		
,,	2.36 ,,	,, ,, ,, ,, ,,	34	34·5	33·5		
,,	2.38 ,,	,, ,, ,, ,, ,,	35	35·2	34		
,,	2.40 ,,	,, ,, ,, ,, ,,	36·8	35·8	34·9		
,,	2.42 ,,	,, ,, ,, ,, ,,	39·7	36·5	35·6		
,,	2.43 ,,	,, ,, ,, Suddenly flooded floor with water					
,,	2.45 ,,	,, ,, ,, ,, ,,	39·5	37·6	36		
,,	2.47 ,,	,, ,, ,, ,, ,,	39·8	37·8	36·1		
,,	2.49 ,,	,, ,, ,, ,, ,,	38·9	37·5	36		
,,	2.50 ,,	,, ,, ,, ,, ,,	39	37·3	36		
,,	2.51 ,,	,, ,, ,, Opened lights					
,,	4.13 ,,	,, ,, ,, Sun off some time	25·9	26·1	25·5	21·3	22·3

ascertaining the conditions of germination of the Uredospores. De Bary, Plowright, Eriksson, Duggar and a few other observers have given some facts of a general nature, but it seems probable that the subject would repay much closer investigation.

I have, during the course of the experiments, tested various factors which seemed to be influencing the germination of the spores, but it should be borne in mind that the investigation of the temperature effects was not part of the original plan, and it was not until my attention was directed to them by the failure of infection under circumstances (see p. 291) which left little room for doubt that high temperatures were interfering with the process, that I went further into these points.

From the ease with which infection occurs at all ordinary temperatures, it seems to have been generally taken for granted that Uredospores will germinate at almost any ordinary temperature in Summer. As matter of fact this is not the case, and new light is thrown, I think, on some of Eriksson's results by the recognition of the cardinal points here brought forward.

I found that the spores germinate readily in ordinary light or in darkness, in red but not so readily in blue light, in ordinary water or in decoction of the leaves of *Bromus*, in water containing green Algae, fibres of paper-pulp, or even germinating spores of other fungi, provided the temperature did not rise beyond 25° C or thereabouts, and that the spores themselves were properly ripened and fresh.

The best results were obtained with spores gathered early in the morning, before the dew is off, from leaves still green and fairly young. This is undoubtedly because later in the day the ripest spores have been shed, and because exhaustion has set in on older leaves.

The following Table (VII) seems to bring out these conclusions very clearly, though the temperature of germination is somewhat high for the species.

In reply to the criticism that the non-germination of Uredo-

TABLE VII.

Exp. No. 737. Results showing the comparative germination of spores of different ages.

No.	*Date sown.*	*Origin of spores.*	*Age of leaf.*	*State of leaves.*	*State of spores sown.*	*Temp.*
737 *a*	June 27	B. mollis (1)	Young	Fresh	Naturally shed	24°–25° C
,, *a'*	,,	,, (2)	,,	,,	Scraped off after the shedding	,,
,, *b*	,,	,, (3)	Old	Kept 24 hours in moist box	Naturally shed	,,
,, *b'*	,,	,, (4)	Young	,,	,,	,,
,, *b''*	,,	,, (5)	Old	,,	Scraped after shedding	,,
,, *b'''*	,,	,, (6)	Young	,,	,,	,,
,, *c*	,,	B. sterilis (7)	,,	Fresh	Naturally shed	,,
,, *c'*	,,	,, (8)	,,	,,	Scraped after shedding	,,
,, *c''*	,,	,, (9)	Old	,,	,,	,,

(1) Germinated vigorously in 3 hours.
(2) None germinated even in 24 hours.
(3) Only one or two germinated. Several other fungus spores were present.
(4) Germinated vigorously in 3 hours.
(5) None germinated, even in 24 hours. Many spores of other fungi present.
(6) None germinated, though the spores appeared clean.
(7) Vigorous germination in 3 hours.
(8) Also germinated fairly well. (9) None germinated.

spores in certain cases might be due to the presence of the spores of other fungi, e.g., moulds, *Dematium*, &c., while something may no doubt be put down to their agency in robbing the hanging drops of oxygen, and interfering in other ways with the well-being of the Uredospores; I obtained plenty of evidence showing that this is but a minor event in cases where the latter spores are capable of rapid germination: they can hold their own very well in the race for some hours at least, and on green leaves in the open are not likely to be injured by competing saprophytes.

The following Table (VIII) shows the result of a few experiments typical of several others made to test the action of light. Though the number of trials is as yet too few to base any very wide generalization on, the positive results are useful, and clearly point to the conclusion that no ordinary light affects the germination very seriously; and even in the

TABLE VIII.

Nos. 753, 694, 695, 698, 699. Experiments to test the effects of light on the germination of the Uredospores.

No.	*Date.*	*Origin of spores.*	*Nature of light used.*	*Direction of incidence.*	*Temperature.*
753 *a*	July 7	B. mollis (1)	Ordinary	From below	19–20° C
,, *b*	,,	,, (2)	,,	From above	,,
,, *c*	,,	,, (3)	,,	All round	,,
,, *d*	,,	,, (4)	,,	From one side	,,
694 *a*	May 24	B. sterilis (5)	,,	All round	20 C
,, *b*	,,	,, (6)	,,	Light excluded entirely	,,
695 *a*	,,	B. mollis (7)	,,	,,	,,
,, *b*	,,	,, (8)	,,	From all sides	,,
698 *a*	May 25	B. sterilis (9)	Under blue glass	From above	about 16 C[1]
,, *a'*	,,	,, (10)	,,	,,	,,
,, *b*	,,	,, (11)	Under red glass	,,	,,
,, *b'*	,,	,, (12)	,,	,,	,,
699 *a*	,,	,, (13)	Ordinary light	From all sides	18·5 C
,, *b*	,,	,, (14)	,,	Light excluded	,,

[1] The variations of temperature seemed slight, but were not recorded continuously.

(1–4) Germinated well in an hour, and tubes turned chiefly downwards. Numerous foreign fungus-spores present. In 3 hours vigorous.

(5) In 3 hours the germ-tubes were 2–5 times the spore-diameter in length.

(6) Germination not quite so vigorous but still very good.

(7, 8) Similar results.

(9) In 24 hours only 1 spore germinated of 58 in the drop.

(10) In 24 hours none germinated of 114 spores.

(11) In 4 hours tubes 5–8 times the spore-diameter in length. In 24 hours about 150 spores of some 200 have germinated.

(12) Germination begun in 4 hours. In 24 hours about 20 out of 120 had germinated: drop drying up.

(13) Several spores have tubes twice the spore-diameter in length in 4 hours.

(14) At least one spore germinated equally well.

case of the light through blue glass I am inclined to suspect that carefully extended observations may show that the effects are but slight—that the orange-yellow cell contents protect the protoplasm from the action of the blue rays. Nevertheless, there seems to be some slight inhibiting action worth further examination. The chief difficulty will be to get comparative results at similar temperatures.

My reasons for varying the direction of incidence of the light in certain cases were based on some results (as yet inconclusive) that the germ-tubes exhibit heliotropic curvatures: this question demands closer inquiry.

It will also be seen from the Table that the spores germinate in the dark as well as in the light, a fact already known for such fungi in general.

Another set of experiments was made with the intention of seeing if any suggestive results were obtainable when some chlorophyll-bearing organism was present among the germinating spores. The positive results (Table IX) have a certain value, but I think that with the experience now obtained, it might be possible to design experiments more conclusive in nature. The Alga employed was found in a flask of Knop's solution in my laboratory, and was apparently the palmella form of a *Chlamydomonas* not determined.

TABLE IX.

Exp. No. 701. Results of cultures in presence of a chlorophyll-bearing Alga compared with the same in absence of the Alga.

No.	*Date.*	*Origin of Spores.*	*Alga.*	*Nature of illumination.*	*Temperature.*
701	May 26	B. mollis (1)	Absent	Ordinary light	17·5° C
,, *a*	,,	,, (2)	Present	Under red glass	23 C
,, *a'*	,,	,, (3)	,,	,,	,,
,, *b*	,,	,, (4)	,,	Under blue glass	,,
,, *b'*	,,	,, (5)	,,	,,	,,
,, *c*	,,	,, (6)	,,	Ordinary light	17·5–18·5
,, *d*	,,	,, (7)	,,	Darkness	17–18·5

(1) Germinated well in 4 hours.

(2–5) None germinated in 4 hours, but in 24 several spores had put out tubes: (4) and (5) less vigorous.

(6) In 4 hours about 10% had tubes 4–6 times spore-diameter in length.

(7) In 4 hours about 50% had tubes 8–10 times the spore-diameter in length.

The net result is to show that the presence of such an Alga is not an important determining factor, for even under blue glass the spores sometimes germinated during the night. It should be noted that at the time these experiments were made I was not yet in possession of the facts concerning the critical temperatures, nor fully alive to the necessity of choosing recently ripened spores, and possibly other factors of importance were overlooked. Nevertheless it seems worth while noting the positive results.

The effects of different temperatures seem to be much more definite and important.

As regards methods there is little to remark beyond what is told in Table X. The simplest results are those in watch-glasses of water, on the surface of which the spores were sown and the laboratory temperatures noted. In those cases where a definite temperature is given, however, the watch-glass was placed in the incubator.

More accurate results are of course attainable in the cells; i. e. the spores were in hanging drops in culture-cells in the heated microscope culture-box, and in these cases the temperatures, regulated with thermostat, &c., are those of the drop itself and its surrounding atmosphere.

In those cases where the word 'heated' is added, it is to be understood that the temperature of the culture-box was slowly raised accurately to the range given.

It is evident from the experiments (see Table X) that the spores, Uredospores, of this fungus germinate best at or near 20° C, while the maximum is not far from 26–27·5° C, and the minimum about 10–12° C.

It is somewhat surprising that such apparently delicate spores will withstand 10 minutes' freezing, but there can be no doubt of the fact. The watch-glass, with spores in water, was placed in an iced chamber, in a glass vessel surrounded by a freezing mixture, and the temperature, recorded by a small and delicate thermometer, went to $-5°$ C, the mass freezing to a solid block of ice. A piece of this was chipped off and placed in a clean watch-glass at 20° C, with the result given in the Table. The spores germinated in less than $7\frac{1}{2}$ hours. The rest of the frozen spores, kept frozen for 4–5 hours, could not be resuscitated. None of the spores heated to temperatures above 30° C could be resuscitated, and even 27·5° C was found to be a trying temperature in many cases.

It seemed desirable in view of certain eventualities referred to in section 16 to test the possibility of the leaf containing some

TABLE X.

Showing the effects of temperatures, maximum, minimum, and optimum, on the germination of spores.

No.	*Date.*	*Origin of spores.*		*Condition of spores.*	*Further treatment, &c.*	*Temp.*
700 *a*	May 25	B. mollis	(1)	Fresh (wild)	In watch-glasses	17° C
" *b*	"	"	(2)	"	"	"
" *c*	"	"	(3)	"	"	"
" *d*	"	"	(4)	"	"	"
" *e*	"	"	(5)	"	"	"
" *f*	"	"	(6)	"	"	"
711	June 20	"	(7)	"	"	19–20
713	"	"	(8)	"	"	"
714	"	"	(9)	"	"	"
716	June 22	"	(10)	Kept 5 days (wild)	"	25
720	"	"	(11)	" 5 "	In cells	"
"	"	"	(12)	" 5 "	" (heated)	27·5
723	"	"	(13)	" 6 "	"	22
"	"	"	(14)	" 6 "	" (heated)	25–27·5
726	June 23	B. sterilis	(15)	Fresh (from experiment 707 *d′*)	In cells	22
"	"	"	(16)	"	"	25–27·5
728	June 25	"	(17)	Fresh (garden)	"	20
729	"	"	(18)	"	"	"
"	"	B. mollis	(19)	Kept 1 day (wild)	"	"
734	June 26	B. asper	(20)	Fresh (garden)	"	"
"	"	"	(21)	" "	"	"
735	June 27	B. sterilis	(22)	" (wild)	"	25
736	"	B. mollis	(23)	Kept 1 day (wild)	"	"
741	June 30	B. secalinus	(24)	Fresh (garden)	"	"
"	"	"	(25)	"	In watch-glass	"
744	July 2	"	(26)	Kept 2 days (garden)	In cells	20–22
747	July 6	B. mollis	(27)	Kept 1 day (wild)	"	"
748	"	B. secalinus	(28)	Fresh (exp. 713)	"	"
"	"	B. velutinus	(29)	"	"	"
749	July 7	B. interruptus	(30)	"	"	"
"	"	B. mollis	(31)	Kept 1 day (wild)	"	"
751	"	"	(32)	" "	"	"
754	July 8	B. sterilis	(33)	" "	"	20–2
755	July 9	B. secalinus	(34)	" (garden)	"	20–2
759	July 14	B. mollis	(35)	" (wild)	"	20–2

(1) Germinating well in 4 hours.
(2) Traces of germination in 4 hours.
(3) Germinating well in 4 hours.
(4) Traces of germination in 4 hours.
(5–6) Germinating well in 4 hours.
(7–9) Vigorous germination.
(10, 11) Germination feeble.
(12) Germination very feeble.
(13, 14) Germination feeble.
(15) Very feeble.
(16) Only one spore germinated.
(17, 18) Vigorous.
(19) None germinated. Many moulds.
(20) Vigorous germination.
(21) None germinated. Much *Dematium.*
(22–26) Very vigorous.
(27) Fairly good in 3 hours.
(28, 29) Several spores germinated in 3 hours.
(30–32) Very vigorous in 5 hours.
(33, 34) Very vigorous in 2 hours.
(35) Fairly vigorous.

TABLE X (*continued*).

No.	*Date.*	*Origin of spores.*	*Condition of spores.*	*Further treatment, &c.*	*Temp.*
[1]760	July 14	B. sterilis (36)	Fresh (garden)	In watch-glasses	20–25°C
,,	,,	,, (37)	,,	,,	,,
,,	,,	,, (38)	,,	,,	,,
761	,,	B. mollis (39)	,,	,,	,,
763	July 15	,, (40)	Kept 1 day (garden)	,,	23–26
764	,,	B. sterilis (41)	,,	,,	,,
766	July 17	B. mollis (42)	Fresh (garden)	,,	24–30
,,	July 18	,, (43)	Same kept 1 day (garden)	,,	24–25
767	July 17	B. sterilis (44)	Fresh (garden)	,,	24–30
,,	July 18	,, (45)	Same kept 1 day (garden)	,,	24–25
768	,,	B. secalinus (46)	Fresh (garden)	In cells	,,
771	,,	,, (47)	,,	,, (heated)	26–30
,,	,,	,, (48)	,,	,,	18·5
,,	July 19	,, (49)	Same kept 1 day (garden)	,, (heated)	26–30
,,	,,	,, (50)	,,	,,	18·5
777	July 23	B. mollis (51)	Kept 2 days (garden)	,,	17–17·6
,,	,,	,, (52)	,,	,,	20
,,	,,	,, (53)	,,	,, (heated)	27·5–32
,,	,,	,, (54)	,,	,, (on ice)	3–4
,,	,,	,, (55)	,,	Watch-glass (on ice)	,,
,,	,,	,, (56)	,,	Cells (near ice)	8–10
,,	,,	,, (57)	,,	,,	9–10
779 *a*	July 24	,, (58)	Kept 3 days (garden)	Cells in light	19
,, *b*	,,	,, (59)	,,	,, dark	,,
,, *c*	,,	,, (60)	,,	Cells (heated)	33–26
,, *d*	,,	,, (61)	,,	,, (frozen hard 10 minutes)	−5
,, *e*	,,	,, (62)	,,	,, (frozen 4–5 hours)	−5
780 *a*	,,	B. secalinus (63)	Fresh (garden)	Cells and watch-glasses	19–21
,,	,,	,, (64)	,,	,, ,, (heated)	26–29
,,	,,	,, (65)	,,	,, ,, (on ice)	6

[1] It was the behaviour of this series which suggested to me to test the germination of the spore according to the age of the leaf, &c.

(36) Vigorous germination. (37) Poor. (38) None germinated in 24 hours.
(39) Fairly vigorous. (40, 41) Poor. (42) None germinated: appeared paralysed.
(43) Fairly vigorous. (44) None germinated: as if paralysed. (45) Poor.
(46) Very vigorous. (47) None germinated: as if paralysed.
(48) Very vigorous. (49) None germinated. (50) Very vigorous.

(51) In $1\frac{1}{4}$ hours vigorous germination and tubes as long as the spore: in 3 hours = 4–5 spore diameters and branching: in 7 hours 12–20 diameters and much branched.

(52) Very vigorous in both light and dark. In $1\frac{1}{2}$ hours tubes = 1–2 spore diameter: in 3 hours = 6–8 diameters and branching. In 7 hours = 12–20 diameters and much branched.

(53) Total inhibition. (54) Total inhibition in two trials. (55) Total inhibition.

(56) In $1\frac{1}{2}$ hours none germinated: in 3 hours several have tubes 1–3 spore-diameters in length. In 7 hours many have tubes 8–10 spore-diameter. Same in watch-glass.

(57) Similar results, both in light and in darkness.

(58, 59) Vigorous germination in 2 hours. (60) None germinated in 2 days.

(61) On thawing at 19° C none had germinated in 2 hours, but after $7\frac{1}{2}$ hours several spores had put out tubes, and next day the germination was fairly good and general.

(62) No recovery even in two days at 13–19° C.

(63) Normal germination. (64, 65) No germination.

body in the cell-sap which inhibits or promotes the growth of the fungus; and I did so by making a cold-water extract of the pounded fresh leaves, rapidly filtering through a stone or other filter, and sowing the spores in the liquid both raw and boiled. In all cases control sowings were made in water, and only those results regarded where the controls showed the spores to be vigorous.

All attempts of this kind were in vain, however, since vigorous spores germinated equally well in extracts of the leaves of their own host-species and of their antagonistic host-species. See Table XI.

TABLE XI.

Expts. Nos. 739, 781, 782. Testing the germination of spores in extracts of the leaves of grasses.

No.	*Date.*	*Origin of spores.*	*State of spores.*	*Extract.*	*Condition of extract.*
739 *a*	June 27	B. mollis (1)	Shed, from fresh leaves 1 day	Young leaves *B. mollis*	Masson filter not boiled
,, *b*	,,	,, (2)	,,	,,	Masson filter boiled
,, *c*	,,	,, (3)	,,	Water only	
781 *a*	July 25	B. mollis (4)	Kept 1 day in moist box	,,	
,, *b*	,,	,, (5)	,,	Filtered extract of *B. sterilis* leaves	Un-boiled
,, *c*	,,	,, (6)	,,	,,	Boiled
782 *a*	,,	B. secalinus (7)	,,	Water only	
,, *b*	,,	,, (8)	,,	Extract of leaves of *B. sterilis*	Un-boiled
,, *c*	,,	,, (9)	,,	,,	Boiled

(1) One or two germinated.
(2) More than 10 % germinated.
(3, 4) Vigorous.
(5, 6) Germinated freely.
(7) Very vigorous.
(8) Vigorous germination.
(9) Equally vigorous.

Of course these experiments teach very little, since it can hardly be supposed that the cell-contents thus extracted are in the normal condition in which they would exist in the living cell. The positive results do show, however, that the failure of spores from *B. mollis* (see below for details) to develop pustules on *B. sterilis*, for instance, is not due to a mere exudation of some antagonistic soluble extract,—that the antagonism must be due to something far more subtle than a mere soluble poison oozing from the cells.

7. METHODS OF INFECTION.

The methods employed for the principal series of comparative infections were as follows.

The carefully selected 'seeds' of the Bromes were sown in new pots of fresh soil, generally a dozen to a score in a pot, and allowed to germinate under hand-glasses till about a week old. The pots were then placed under bell-jars, kept moist by filter-paper, and put in a west window in the laboratory for 24–48 hours, until the first green leaf (morphologically the second leaf) was well developed. During this period the 'spear,' enveloped in the first morphological leaf, which consists of the sheath only, exudes copious drops of water from the clefts corresponding to water-stomata at its apex.

In some cases I infected the seedlings by putting spores on these 'tip-drops': in others I placed the spores on the flat face of the leaf. It remains to be seen how far differences in results depend on these differences in procedure, as also whether anything depends on the different distribution of the stomata on the front and back of the leaf. The investigations of all these points in detail will require some time, but at present the evidence seems to show that it is immaterial, and that the infecting tubes can pass even into the slits representing water-stomata at the extreme tip.

In any case it is certain that the 'spears' are susceptible of infection when only two or three mm. high, and long before the first green leaf is expanded, a point of some importance in discussing the question of the infectivity of seedlings.

In other cases I infected older seedlings at the base, apex, or intermediate parts of the second or third leaf, and one or two curious points arise in this connexion.

Infection may apparently fail at the base of rapidly growing young leaves, either because the stomata are not fully developed there, or because the rapidly elongating tissues pass forwards before the tips of the germ-tubes can gain an entrance.

It is easy to see a tuft of paper-pulp, e. g., scraped filter-paper, with which spores have been swabbed up, and which has been placed in a young leaf-axil, lifted up bodily by the growth of the basal parts; and next day, instead of the germ-tubes having entered the tissues of both young leaves with which the contaminated swab was in contact, the whole mass may have been lifted up on one leaf, or thrown off bodily on to the ground.

If such a 'swab' is placed on the apex of the growing leaf, on the contrary, it is lifted up as the tip rises and infection occurs. This ready infection of the tips, the oldest part of the grass leaf, seems to explain why pustules ordinarily appear first at the apex of the leaves. The latter are most easily infected there because the 'tip-drops,' emerging from the water-stomata under the action of root-pressure, catch spores readily, and promote their germination just on that part of the leaf where the stomata are most mature; and this would apply particularly to wind-blown spores which lodge in or near the leaf-axils in the tufts of grass.

In sowing the Uredospores I have tried various plans. The simplest is to place the dry spores direct from the pustules on the surface of the leaf by means of the tip of the blade of a knife or a flattened platinum wire. Another is to brush them on with a camel-hair pencil. They may also be sown in water, and a drop of the latter then placed on the leaf by a fine pipette or a wire, &c., but some difficulty is usually met with owing to the tendency of such drops to roll off the slightly waxy or hairy leaf-surface. I found it at first by no means easy to attach such drops to the leaf-surface, especially as the latter is usually vertical.

An interesting proof that this is owing to the difficulty of wetting the leaf is afforded by the following observation. If one takes a slender capillary pipette and blows down it so as to direct the fine stream of moisture-laden air on to a spot on the leaf-surface, the latter will readily take the drop at that spot and hold it. I take it this is owing to the fact that moisture has condensed on the cuticle in extremely fine particles, which then run together, and the drop may then be held by capillary attraction to the now wetted surface.

A method which promised to obviate some of the drawbacks referred to was that of placing minute swabs of cotton-wool or paper-pulp—scraped filter-paper fibres—saturated with spore-laden water on the leaves; such swabs stick well and as they dry mark the spot infected: but although their presence does not hinder the germination of the spores, the method was not particularly successful, for in some cases the germ-tubes ran into the damp interspaces of the cotton-wool and there lost themselves, as it were.

Returning now to the treatment of the seedlings. Having sown the spores, each pot was covered with a large inverted beaker lined with moist filter-paper, and placed in the west window. After 24–48 hours the beakers were removed, and the pots placed under very large bell-jars in zinc trays, and these bell-jars were usually removed on the third or fourth day, and the pots placed in the open.

Of course differences in detail of procedure had to be introduced to meet exigencies of weather, and I availed myself of the cellar or area in the hottest weather, and of tables and boxes in shade and half-shade in various positions in the garden. These details are given in the tabulated results.

It is certain that these differences of temperature, illumination, drought and wet, and so forth, affecting the transpiration, assimilation, &c., of the seedlings, also affect the period of germination, inoculation, and incubation, and difficulties in explaining various phases can be overcome only when this is understood.

8. The Results of Infection.

Successful inoculation is followed by a period of incubation usually about a week to ten days in duration, during which period the hyphae are spreading in the intercellular spaces.

We have seen that the germination of the spore is ruled by certain factors of which temperature is very important, perhaps the most important—it being always understood that sufficient moisture is present.

The effects to be looked for, about the tenth day, on those parts of the leaves on which Uredospores have been sown, are outbreaks of the well-known sienna-brown or orange-brown tufts of Uredospores similar to those sown. These appear first as minute yellow pimples or pustules, pushing up the epidermis and then bursting through as they rupture it at the stomata. The outbreak of such pustules is the proof of successful infection.

Preceding the actual outbreak of pustules, often by several days, we have a pale yellowish discoloration of the leaf, at the spot infected, and it not unfrequently happens that such pale flecks are alone formed, and never advance so far as to develop spores. Sections of these infection-flecks show the presence of the mycelium in the tissues, and the loss of colour is due to two causes—the destruction of chlorophyll in the attacked cells, and the filling up of the intercellular spaces by the hyphae, thus rendering the mass more translucent than when filled with air.

In yet other cases I find an active discoloration of another kind produced at the infected spots. The tissues turn yellow and then brown or black, rapidly shrivelling as if corroded. This is due to the actual death of the cells and withering of the tissues at the infected spots, and at first I thought it must be owing to some other fungus having got in. It is so in some cases, but in the majority of those to be considered it appears to be due, rather, to the infecting tubes and hyphae being too destructive to adapt themselves to the host-tissues, and must be regarded as a sign of failure of infection, because the Uredo-mycelium is unable to advance in the dead area, and of course no pustules are developed. We might compare the unsuccessful mycelium here to a pot-plant placed in unsuitable soil, and therefore incapable of flowering.

It will thus be intelligible that four cases may occur as the incubation period runs its course. At the one extreme we may find no visible effect at all: the spores have either not germinated on the epidermis, or the infection has failed, owing to the germ-tubes being unable to enter the stomata and establish a mycelium in the intercellular spaces.

At the other extreme we have successful entry and infection, and the mycelium in the leaf gives rise to the pustules of Uredospores in due course.

Thirdly, we may have the intermediate stage where pale flecks betray the presence of a mycelium in the intercellular spaces, but circumstances prevent this coming to maturity as a spore-producing organism, and so no pustules of Uredospores are formed.

Whether this internal mycelium[1] eventually lives or dies depends on several factors ; the point here is that it remains barren of spores.

The fourth case is met with when the tissues turn brown and die, the destructive action of the infecting tubes having killed the cells too rapidly. The affected patch thus appears corroded, and since the dead cells are unsuitable as a medium for further growth of the mycelium, the parasite dies.

In the following tables I record the infection as successful or positive (indicated by the sign +) only when the spore-bearing pustules are developed at the infected spots. In all other cases it is unsuccessful or negative (indicated by the signs O or –) and only when necessary is the remark added that the infected spots show 'flecks' or 'corrosion' respectively. The histological details and figures are held over for the present, with other continuations of the work, and will form the subject of further communication.

9. EXPERIMENTS WITH POT-PLANTS.

The first set of experiments of which I propose to give the results here, was simply planned to see whether seedling plants, of manageable size and in small pots, were suitable for the purposes of the investigation. The procedure adapted was as follows.

Seedling plants of the species of *Bromus* referred to below

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[1] Internal, that is to the leaf as a whole, but really in the intercellular spaces.

were removed from their seed-beds in the Gardens, after having been weeded out and exposed for several weeks, and were potted off into small pots of soil, with no extraordinary precautions. Each plant had three to five leaves, and the infection was carried out by simply placing spores on the lamina and marking the leaf with silk.

The results seemed to show that spores taken from leaves of *B. mollis*, infected *B. mollis* and *B. secalinus* freely, but refused to infect *B. inermis,* while the results were doubtful as regards *B. sterilis*, *B. asper*, and *B. arvensis*.

Repetition of the experiment gave similar results, except that here the infection sometimes failed on *B. mollis*; and yet again a third experiment yielded similar results, except that this time it was *B. sterilis* which gave the doubtful result.

It eventually suggested itself as possible that more care was necessary in keeping the spores taken from the leaves of *B. mollis* and those from the leaves of *B. sterilis* separate, for although I only employed those from *B. mollis* for the infections, I had collected both in the same tin though separated in paper wrappings, and did not at the time regard it as of such supreme importance as was subsequently found to be the case to keep them separate. It being admitted that the fungus is the same on both species this was not unnatural, at the time, but the sequel showed that all such assumptions must be avoided where these fungi are concerned. Although it is the species *Puccinia dispersa*, whether growing on *Bromus mollis* or *B. sterilis*, I now know that the infection capacity differs much in the two cases.

In this, the first set of experiments in which my attention was directed to the question of adaptation or selective infection *within the genus Bromus itself*, several sources of error are to be met with, the most serious being one to which sufficient attention has not always been paid in the past, though most careful observers must have thought of it. It depends on the recognition of the fact that Uredospores when capable of normal germination at all, are highly infectious spores, and that if the host-plants used are—as is usually the case—exposed in a garden or even in a greenhouse or laboratory already contaminated with such spores, the same kinds of difficulties and dangers may arise as in any other work where highly contaminating organisms have access to the experiments.

On putting together the total results of these preliminary infections of garden seedlings, removed from the beds to pots and then infected, we get the following:—

In no case apparently did the spores taken from the leaves of *B. mollis* infect *B. inermis*, and in no case did they fail to infect *B. secalinus*, and with a few doubtful exceptions *B. mollis.*

As regards *B. asper*, *B. arvensis*, and *B. sterilis* the results were less consistent.

Similarly with the spores from *B. sterilis.* They failed to infect *B. mollis*, *B. arvensis*, and *B. inermis* in all cases: they infected *B. asper* and *B. secalinus*, however, in the only case tried.

On looking more carefully into these preliminary trials, I found that several sources of error needed careful examination. In the first place, the seedlings themselves had been growing for some time in the open, and there was no guarantee that their leaves were free from wind-borne spores at the time of transplanting. As matter of fact, on searching the tufts of seedlings in the garden during the next two or three weeks I found the Uredo on *B. asper*, *B. secalinus*, *B. mollis*, and *B. sterilis*, and subsequently on others.

Secondly, I had collected both *B. mollis* and *B. sterilis*, with spores on them, from the same fields, and, as already stated, was not at the time fully alive to the existence of any physiological difference between the two forms: morphologically the two forms are identical. It is true I kept the two kinds separate in my collecting tins, but considering the quantity of spores already forming on *B. mollis* in the fields, it would not be surprising if the leaves of *B. sterilis* had already been dusted with them.

Thirdly, it soon appeared certain that an experimental error had crept in in the case of at least one of the experiments.

But the most irritating error of all, and one which caused much trouble in the immediate future, was the discovery—only made after the plants had come into flower—that the seedlings labelled *B. asper* were not *B. asper* at all, but *B. arvensis*—that is to say an error had been made by the seedsman who supplied the seed. In consequence of this, I had to overhaul the whole stock of seeds and seedlings myself, and in the experiments which follow believe there need be no doubt as to the authenticity of the species, except in one or two special cases to which attention will be drawn where necessary, and in regard to which further investigations are proceeding.

It becomes clear, in fact, that we have to keep our eyes open to the danger of impure cultures of the *hosts*, as well as of the *parasite*. As will be seen in the sequel, we have also to take account of variations and race-peculiarities in both.

Considering these and other possibilities of error, I was led to devise some better methods of preparation and infection of the culture-plants and spores.

In the following experiment (see Table XII) sowings in pots were made of eleven carefully selected species or varieties of *Bromus*, viz.: *B. mollis*, L., *B. secalinus*, L., *B. velutinus*, Schrad., *B. maximus*, Desf., *B. arvensis*, L., *B. racemosus*, L., *B. commutatus*, Schrad., *B. interruptus*, Hack., *B. sterilis*, L., *B. madritensis*, L., *B. erectus*, Huds. Good garden soil was used, and germination, under a hand-glass in the garden, resulted normally during the warm weather, so that in a week it was possible to start the infections. It may be noted, however, that whereas *B. mollis* showed above ground on the fourth day, and *B. arvensis* and *B. maximus* were up by the fifth day after sowing, it required six days for *B. sterilis*, *B. madritensis*, and *B. secalinus*, and seven days for *B. racemosus* and *B. interruptus* to be sufficiently high, while *B. commutatus* and *B. erectus* were not well up[1] until the eighth day.

The infections were made by placing Uredospores from

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[1] I regarded the seedlings as 'well up' when 1–3 mm. showed above ground.

B. mollis and *B. sterilis* gathered on June 1, from widely distant localities and kept in separate tin boxes till June 3, on the drops of water hanging from the water-pores at the tips of the first leaves. This method is quite successful in such cases, as direct and repeated observations have shown: the germ-tubes soon make their way to the stomata of the emerging leaf, and infection results near the apex only.

Three pots of each species (or variety) were sown. One of each was infected with Uredospores from *B. mollis*, another with those from *B. sterilis*, while the third series was not infected, but kept as a control set. Each series was kept under a large bell-jar, with damp filter-paper in it, and left thus covered at a western window for two days. After that the whole of the series was put outside, in a sheltered spot, but still covered with the bell-jars. The garden used was well away from any plants of *Bromus*, and no diseased plants were allowed in it except such as I brought there. At the end of a week they were fully exposed to the weather. The latter had been warm and sunny during the first week, but by June 12–13 it turned cold and some rain fell, and several days of dull or wet weather, often very cold, followed, varying as to wind which was sometimes bleak and dry. The principal assumptions entertained here were: (1) that carefully selected clean ‘seeds,’ germinated in new pots under glass at a distance from any known source of infection, would give me host-plants free from contamination; (2) that by gathering the spore-material from places some distance apart, and keeping it in each case quite separate in closed boxes, tubes, &c., it should be possible to ensure freedom from accidental infection; (3) that by keeping the inoculated plants under glass until infection was well assured, it should be possible to avoid accidental infection; because, even assuming that wind-blown spores reached the plants after subsequent exposure, the resulting pustules would appear so late that I could discriminate between the consequences of the primary and of the secondary infection; (4) there was the further assumption that the artificially induced infection would occur normally in the tips of the young leaves just emerging from the first leaf-sheath, although the seedlings were of different heights at the moment of inoculation.

Further experience has shown that these assumptions, carefully checked, do not vitiate the conclusions drawn from the experiments.

There was, nevertheless, a possible source of error in the large number of plants employed in these experiments. Each pot contained from 25 to 100 seedlings, according to the size of the 'seeds' sown and their germinating power. I inoculated about ten to twenty seedlings in each case, and judged of the results as merely positive or negative according to the subsequent discovery of pustules. I now know that it may be of some importance whether the plants are well or ill-nourished, and it is quite possible that in some of the more crowded pots the results were less convincing than in later experiments whence this source of error was eliminated. Nevertheless such plants show normal infection.

The question as to the height of the 'spear' above ground need not concern us, since subsequent experiments, where the heights were duly measured and recorded, showed that a given species will be infected readily when only 10-20 mm. high, whereas the infection fails on another 50-100 mm. high.

The results are given in the following Table XII.

These results point to the conclusion that while the Uredo grown on *B. mollis* can quickly and readily infect *B. mollis*, *B. velutinus*, *B. arvensis*, *B. secalinus*, and *B. racemosus*—all, be it remarked, closely allied forms—it is unable to infect *B. sterilis*, *B. madritensis*, *B. maximus*, *B. erectus*, *B. commutatus*, or *B. interruptus*, or does so with difficulty.

On the other hand, while the Uredo grown on *B. sterilis* can readily infect *B. sterilis* and *B. madritensis*—also closely allied—it appears to fail on the other Bromes, except possibly on *B. maximus*.

In all cases the control series gave negative results.

As the Table XIII (p. 284) shows, substantially similar results were obtained on repeating this experiment on seed-

TABLE XII.

Exp. No. 706, June 4, 1901. 'Seed' sown May 27. Bromes infected on tips of seedlings just (2–15 mm.) above ground, germinated under hand-glass in garden. Infected plants put outside, under bell-jars, after 48 h., in N. light, then (after a week) exposed. Get sun about 2 hours at mid-day. Normal plants, though small.

Species.	*Origin of spores.*	*Results.*	*Approximate No. of plants infected.*	*Incubation period.*	*No. of leaves with pustules on 19th day.*	*Period of observation.*
B. mollis	B. mollis	+	20	11 days	10	21 days
,,	B. sterilis	—	20		0	,,
B. velutinus	B. mollis	+	20	11 ,,	19	,,
,,	B. sterilis	—	20		0	,,
B. maximus (1)	B. mollis	+	?*	19 ,,	1	,,
,, (2)	B. sterilis	+	?	19 ,,	1	,,
B. sterilis (3)	B. mollis	+	?	19 ,,	3	,,
,,	B. sterilis	+	?	10 ,,	18	,,
B. madritensis	B. mollis	—	20		0	,,
,,	B. sterilis	+	15	10 ,,	14	,,
B. erectus (4)	B. mollis	+	10	19 ,,	1	,,
,, (5)	B. sterilis	—	10		0	,,
B. commutatus	B. mollis	—	20		0	,,
,,	B. sterilis	—	20		0	,,
B. arvensis	B. mollis	+	12	11 ,,	10	,,
,,	B. sterilis	—	12		0	,,
B. secalinus	B. mollis	+	8	11 ,,	6	,,
,,	B. sterilis	—	15		0	,,
B. interruptus (6)	B. mollis	+	20	19 ,,	2	,,
,,	B. sterilis	—	20		0	,,
B. racemosus	B. mollis	+	10	11 ,,	6	,,
,,	B. sterilis	—	10		0	,,

(1–3) Must be regarded as doubtful?
(4) Must be regarded as doubtful? (5) 10 infected.
(6) Must be regarded as doubtful?
* About 20, but not exactly recorded.

lings slightly forced in the intermediate pit, and kept during incubation in a damp shady corner where they never got direct sunlight at all. The plants were much drawn, slightly pale in colour, and very succulent—i.e. they were more or less slightly etiolated. The principal differences were the very poor pustules developed and fewer positive results. In some cases—e.g., *B. arvensis* and *B. secalinus*—the period of incubation seemed to be lengthened, while in others no comparison seems possible.

As the Table XIII shows, the spores of *B. mollis* infected *B. mollis* readily and *B. arvensis* and *B. secalinus* more slowly, but they did not successfully attack *B. velutinus* and *B. race-*

TABLE XIII.

Exp. No. 707, June 8, 1901. 'Seed' sown June 1. Seedlings germinated in intermediate pit one week, then infected at tips and kept under glass 48 hours. Then outside under glass, in damp shady corner. Very damp and drawn plants.

Species.	*Origin of spores.*	*Results.*	*Approximate No. of seedlings infected.*	*Incubation period.*	*No. of leaves with pustules on 16th day.*	*Period of observation.*
B. mollis (1)	B. mollis	+	20	10 days	2	21 days
„	B. sterilis	—	20		0	„
B. velutinus	B. mollis	—	20		0	„
„	B. sterilis	—	20		0	„
B. maximus	B. mollis	—	20		0	„
„ (2)	B. sterilis	+	20	13 „	1	„
B. sterilis	B. mollis	—	20		0	„
„ (3)	B. sterilis	+	20	10 „	10	„
B. madritensis	B. mollis	—	20		0	„
„	B. sterilis	+	20	10 „	3	„
B. erectus	B. mollis	—	10		0	„
„	B. sterilis	—	10		0	„
B. commutatus	B. mollis	—	20		0	„
„	B. sterilis	—	20		0	„
B. arvensis	B. mollis	+	12	16 „	2	„
„	B. sterilis	—	12		0	„
B. secalinus	B. mollis	+	8	16 „	2	„
„	B. sterilis	—	10		0	„
B. interruptus	B. mollis	—	20		0	„
„	B. sterilis	—	20		0	„
B. racemosus	B. mollis	—	10		0	„
„	B. sterilis	—	10		0	„

(1) 11 other leaves have spots not burst, owing to drying up of tips.
(2) Perhaps doubtful? (3) Several other leaves show spots.

mosus as they did in the previous experiment. As before, *B. sterilis*, *B. madritensis*, *B. maximus*, *B. erectus*, *B. commutatus*, and *B. interruptus* seemed to resist the fungus.

Again, we see that the spores from *B. sterilis* readily infect in *B. sterilis* and *B. madritensis*, but not others, except in the doubtful case of *B. maximus*.

This series undoubtedly raises questions as to how far the physiological condition of the host affects the question of infection, a question to which I shall return subsequently.

In another series, Table XIV, the seedlings were raised as in the previous series, and the infected plants were kept in the laboratory at a west window under damp bell-jars. Thus the general temperature was considerably higher than before, and bright sunlight reached the plants for several hours during the afternoon. On the whole, this seemed to shorten the incubation period and to enhance the number and rapidity of the infections. The plants were somewhat drawn, owing to the damp close atmosphere, but the pustules developed were larger and more numerous than in the last series.

From this Table XIV may be gathered confirmation of

TABLE XIV.

Exp. No. 708, June 10, 1901. 'Seed' sown June 3. Seedlings germinated in open under hand-glass, and infected when one week old, and just above ground (2–5 mm.). The infected plants kept in laboratory, under glass, in W. window. Plants damp and somewhat drawn.

Species.	*Origin of spores.*	*Results.*	*Approximate No. infected.*	*Incubation period.*	*No. of leaves with pustules on 14th day.*	*Period of observation.*
B. mollis	B. mollis	+	20	9 days	16	21 days
„	B. sterilis	—	20		0	„
B. velutinus	B. mollis	+	20	12 „	1	„
„	B. sterilis	—	20		0	„
B. maximus	B. mollis	—	20		0	„
„	B. sterilis	—	20		0	„
B. sterilis	B. mollis	—	20		0	„
„	B. sterilis	+	20	8 „	19	„
B. madritensis	B. mollis	—	20		0	„
„	B. sterilis	+	20	9 „	16	„
B. erectus	B. mollis	—	10		0	„
„	B. sterilis	—	10		0	„
B. commutatus	B. mollis	+	20	12 „	5	„
„	B. sterilis	—	20		0	„
B. arvensis	B. mollis	+	10	9 „	8	„
„	B. sterilis	—	10		0	„
B. secalinus	B. mollis	+	8	15 „	3	„
„	B. sterilis	—	8		0	„
B. interruptus	B. mollis	+	20	10 „	7	„
„	B. sterilis	—	20		0	„
B. racemosus	B. mollis	+	10	12 „	3	„
„	B. sterilis	—	10		0	„

the readiness with which spores from *B. mollis* infect that species and *B. arvensis* and *B. velutinus*; *B. secalinus* and *B. racemosus* being also successfully attacked, as are, moreover, *B. interruptus* and *B. commutatus*, all closely allied species, be it noted. *B. sterilis*, *B. madritensis*, *B. maximus*, and *B. erectus*, on the other hand seem immune, as in previous cases.

Here, too, spores from *B. sterilis* readily infected only that species and *B. madritensis* but not the others; results quite in accordance with previous experience.

If now we summarize the results of the infections in these three series—remembering that the method of infection and age of the plants used was the same in all, the only differences being in the dates of sowing and the after-treatment of the plants—some suggestive facts come to light, as the following Table XV shows.

TABLE XV.

Summary of Exp. Nos. 706–8.

Species.	*Origin of spores.*	*Results.*			*Incubation period.*	*No. of infected plants showing pustules.*
		706	707	708		
B. mollis	B. mollis	+	+	+	9–11 days	28
,,	B. sterilis	–	–	–		0
B. velutinus	B. mollis	+	–	+	11–12 ,,	20
,,	B. sterilis	–	–	–		0
B. maximus (1)	B. mollis	+	–	–	19 ,,	1
,, (2)	B. sterilis	+	+	–	13–19 ,,	2
B. sterilis (3)	B. mollis	+	–	–	19 ,,	3
,,	B. sterilis	+	+	+	8–10 ,,	47
B. madritensis	B. mollis	–	–	–		0
,,	B. sterilis	+	+	+	9–10 ,,	33
B. erectus (4)	B. mollis	+	–	–	19 ,,	1
,,	B. sterilis	–	–	–		0
B. commutatus	B. mollis	–	–	+	12 ,,	5
,,	B. sterilis	–	–	–		0
B. arvensis	B. mollis	+	+	+	9–16 ,,	20
,,	B. sterilis	–	–	–		0
B. secalinus	B. mollis	+	+	+	11–16 ,,	11
,,	B. sterilis	–	–	–		0
B. interruptus (5)	B. mollis	×	–	+	10–19 ,,	9
,,	B. sterilis	–	–	–		0
B. racemosus	B. mollis	+	–	+	11–12 ,,	9
,,	B. sterilis	–	–	–		0

(1–5) Doubtful as to the positive result?

The three experiments leave little room for doubt that under circumstances in which *B. mollis* is rapidly and easily infected by the spores from *B. mollis* (the incubation period being nine to eleven days), *B. sterilis* is either immune or only with difficulty and slowly infected by this fungus—e. g., after nineteen days in three cases out of about twenty (see Table XII).

The spores from *B. mollis* also infect *B. arvensis* readily, and *B. secalinus*, *B. interruptus*, *B. racemosus*, and *B. velutinus* less readily.

On the other hand, while the spores of *B. sterilis* rapidly and easily infect that species (incubation period ten days), they are unable to successfully attack *B. mollis* even after twenty-one days.

Now this, put in other words, seems to mean that the spores of the brown Uredo (*P. dispersa*) if grown on *B. mollis* are able to infect successfully practically any member of the group *Serrafalcus*, and but rarely or not at all any member of the other sections so far examined of the genus *Bromus*; whereas the same fungus grown on *B. sterilis* readily infects members of its own group *Stenobromus*—e.g., *B. sterilis*, *B. madritensis*, and *B. maximus*—but is debarred from the *Serrafalcus* group.

The matter appeared so important that I proceeded to try to get results even more conclusive and free from possible sources of error.

I here add the results given in Table XVI, though they teach nothing new except to show the kind of error which may creep into such experiments, in the case of the one plant of *B. erectus* which appeared to have been successfully infected by spores from *B. mollis*, which it was practically certain was not the case.

The procedure adopted in the next series of experiments was to start the germination in new pots under glass in the garden[1], as before, but to allow only a small definite number of plants to each pot. When old enough to infect—i.e. when at least one leaf was completely formed and expanded —I infected a certain definite proportion of the seedlings at known spots on marked leaves, and recorded the results. The uninfected seedlings thus served as controls. In most cases also I carefully tested the germinating power of the spores used in two ways: in cells and in open watch-glasses,

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[1] It has been already stated that there were no Bromes or Brome Rust in the garden here referred to, except such as I had under experimental control.

TABLE XVI.

Expt. No.	*Date.*	*Host.*	*Origin of spores.*	*No. of seedlings in pot.*	*No. in-fected.*	*Method of infection.*	*No. succeeded on*					*Period of incubation.*
							July 4	*July* 5	*July* 6	*July* 10	*July* 12	
726	June 23	B. mollis	B. sterilis	20	4	On tip drops						
,,	,,	B. sterilis	,,	18	2	,,		2	2	2	2	12 days
730	June 25	B. mollis	,,	10	10	,,						
,,	,,	B. sterilis	,,	11	11	,,	3	5	6	Tips dry		9–11 days
731	,,	B. mollis	,,	12	2	On second leaf						
,,	,,	B. sterilis	,,	12	2	,,	1	1	2	2	2	9–11 days
723	June 23	B. erectus	B. mollis	3	2	On first leaf						
724	,,	B. erectus	,,	6	3	,,	1*	1	1	1	1	

* This pustule showed up on June 29 and was probably not due to the artificial infection.

and employed all care in the selection of mature spores from unexhausted leaves.

These series differ from the preceding, further, in that the infections were always made on the flat upper surface of the leaf, the stomata being more numerous there than on the lower surface. In the later cases I also recorded the heights of the seedlings employed, to see if that factor was important, and used fewer seedlings in the pots, in order to get better root-development.

TABLE XVII.

Exp. Nos. 727 and 728, June 24. Pot plants—'seed' sown June 10 kept carefully under cover in green-house, plants bright green but somewhat drawn. Spores good. In the series No. 728 the spores were from another source, and proved to be vigorous and germinating well.

Expt. No.	*Species.*	*Origin of spores.*	*No. of plants.*	*No. infected.*	*No. succeeded.*		*Results.*
					July 5	*July* 12	
727	B. velutinus	B. sterilis	24	3	0	0	None
„	B. maximus	„	24	3	0	0	„
„	B. madritensis	„	24	3	0	0	„
„	B. commutatus	„	24	3	0	0	„
„	B. arvensis	„	24	3	0	0	„
„	B. secalinus	„	24	3	0	0	„
„	B. interruptus	„	24	3	0	0	„
„	B. racemosus	„	24	3	0	0	„
728	B. velutinus	B. sterilis	10	3	0	0	„
„	B. maximus	„	10	3	0	0	„
„	B. madritensis	„	10	3	0	0	„
„	B. commutatus	„	9	3	0	0	„
„	B. arvensis	„	10	3	0	0	„
„	B. secalinus	„	10	3	0	0	„
„	B. interruptus	„	10	3	0	0	„
„	B. racemosus	„	10	3	0	0	„

Table XVII shows once more how incapable are spores from *B. sterilis* of infecting Bromes from the *Serrafalcus* group, but we must not overlook the fact that *B. madritensis* also escaped.

The three series Nos. 747, 752, and 754 (Table XVIII) were instituted to test a different set of Bromes. As before, pots of seedlings a week old were employed and the infection was at the tips of the spears, the spores being laid on in wet

TABLE XVIII.

Seedlings in pots, infected at the tips—pulp method.

Exp. No.	*Date.*	*Host.*	*Origin of spores.*	*No. in pot.*	*No. inoculated.*	*Height when inoculated.*	*Treatment, &c.*	*No. of infected plants on.*					*Remarks.*
								July 17	*July* 19	*July* 20	*July* 21	*July* 27	
747 *a*	July 6	B. mollis	B. mollis	7	4	10–20 mm.	Spores kept indoors 24 hours. Germinating fairly freely.	0	0	0	0	0	No positive results at all.
„ *b*	„	B. tectorum	„	7	5	2–8		0	0	0	0	0	
„ *c*	„	B. ciliaris	„	10	5	2–3		0	0	0	0	0	
„ *d*	„	B. brizaeformis	„	4	3	2–3		0	0	0	0	0	
„ *e*	„	B. secalinus	„	7	4	2–8		0	0	0	0	0	
„ *f*	„	B. sterilis	„	6	4	10–20		0	0	0	0	0	
„ *g*	July 7	B. inermis	„	10	6	2–6		0	0	0	0	0	
752 *a*	„	B. mollis	B. mollis	8	6	20	Spores kept overnight, and taken from a different source. Germination excellent.	0	0	0	1	1	
„ *b*	„	B. tectorum	„	7	5	10–20		0	0	0	0	0	
„ *c*	„	B. ciliaris	„	6	4	5–15		0	0	0	0	0	
„ *d*	„	B. brizaeformis	„	6	4	10–20		0	2	3	3	3	
„ *e*	„	B. secalinus	„	7	4	15–25		0	1	2	2	2	
„ *f*	„	B. sterilis	„	7	4	10–30		0	0	0	0	0	
„ *g*	„	B. inermis	„	8	6	2–5		0	0	0	0	0	
754 *a*	July 8	B. mollis	B. sterilis	9	5	20–30	Spores kept overnight. Germinated freely in 2 hours.	0	0	0	0	0	No positive results at all.
„ *b*	„	B. tectorum	„	9	5	20–30		0	0	0	0	0	
„ *c*	„	B. ciliaris	„	9	6	15–20		0	0	0	0	0	
„ *d*	„	B. brizaeformis	„	8	6	10–20		0	0	0	0	0	
„ *e*	„	B. secalinus	„	8	5	20		0	0	0	0	0	
„ *f*	„	B. sterilis	„	7	4	30–40		0	0	0	0	0	
„ *g*	„	B. inermis	„	7	6	5–15		0	0	0	0	0	
„ *h*	„	B. Schraderi	„	4	3	2–3		0	0	0	0	0	

pulp obtained by scraping sterilized filter-paper. In all cases the tested spores gave good and in some cases excellent results as regards germination.

The infection was made under wet beakers, as usual, and the plants left thus at the west window for two days. Then they were put outside under bell-jars, and freed from these on the fourth day, and placed fully exposed to the sun, the pots standing in saucers and kept properly watered.

The temperature on July 6 to 13, the week of inoculation and infection, was high, the maximum being about 29° C and the minimum 15° C in the shade, and in the west window between 3 and 6 p.m. it would occasionally be higher, though a shade blind is always used there.

It is to the high temperature, I think, that the delay or failure of infection and incubation must be attributed. The question arises how far the failures are due to it alone. In considering these failures we must not forget that each pot in each series received the same treatment, however, so that we still have comparative results.

Nevertheless it seems significant that rain brought down the temperature of July 7 to about 14–20° C from 16–30° C the minima and maxima of July 6. On July 8 the temperature rose again. It was these series which directed my attention more particularly to the question of temperature, and no doubt much work will be needed before its full importance in infection is understood. When we find that the thermometer registers 38–36° C in the sun, and that (see Table X, p. 270) the spores will not germinate much above 25° C, it seems likely that the young mycelium in the leaf will also be inhibited by the high temperatures, though we are ignorant of what the exact temperature inside the leaf may be.

In view of the evident failure of Nos. 747 and 754 it seemed necessary to examine somewhat more closely what conditions could be supposed to have affected the matter. Three points are concerned: the germination of the spores, the infection, and the incubation periods.

The spores were tested and were known to be vigorously

TABLE XIX.

Exp. Nos. 766, 767, 768. Seedlings in pots, a week old.

No.	*Date.*	*Host.*	*Origin of spores.*	*No. of plants.*	*No. inoculated.*	*Height.*	*Results.*						
							July 26	*July* 27	*July* 28	*July* 29	*July* 30	*July* 31	*Aug.* 1
766 *a*	July 17	B. sterilis	B. mollis	7	4	50–60	0	0	0	0	0	0	0
,, *b*	,,	B. Schraderi	,,	9	4	25–30	0	0	0	0	0	0	0
,, *c*	,,	B. pratensis	,,	5	3	20–65	0	0	0	0	0	0	0
,, *d*	,,	B. racemosus	,,	7	4	20–60	0	0	0	0	0	1	1
767 *a*	,,	B. sterilis	B. sterilis	10	7	55–65	2	3	5	5	5	6	7
,, *b*	,,	B. Schraderi	,,	11	5	25–50	0	0	0	0	0	0	0
,, *c*	,,	B. pratensis	,,	5	3	15–50	0	0	0	0	0	0	0
768 *a*	July 18	B. pratensis	B. secalinus	6	4	40–80	0	0	0	0	0	0	0
,, *b*	,,	B. Schraderi	,,	11	5	50–70	0	0	0	0	0	0	0
,, *c*	,,	B. sterilis	,,	9	5	40–60	0	0	0	0	0	0	0
,, *d*	,,	B. racemosus	,,	5	4	50–65	0	0	0	0	0	0	0

TABLE XX.

Exp. Nos. 735, 736, and 738, June 27. Seedlings exactly as in Nos. 727, 728, and 732, but seeds sown June 17, and on July 1 the plants were put out under bell-jars. Spores tested: very vigorous.

Species.	*Origin of spores.*	*No. of plants.*	*No. infected.*	*Average height of plants.*	*Results.* *Number of pustules succeeded.* *July* 5	*July* 6	*July* 7	*July* 8	*July* 9	*July* 11	*Period of observation.*
B. mollis	B. sterilis	11	8	1·5–2 cm.	0	0	0	0	0	0	21 days
,,	B. mollis	12	7	1·5–3	1	3	5	6	7	7	,,
,,	,,	17	7	2–4	1	2	5	6	6	6	,,
B. velutinus	B. sterilis	7	5	2–5	0	0	0	0	0	0	,,
,,	B. mollis	9	5	3–5	0	4	5	5	5	5	,,
,,	,,	12	7	2·5–4·5	4	6	7	7	7	7	,,
B. maximus	B. sterilis	11	6	5–10	0	0	0	0	0	0	,,
,,	B. mollis	6	4	4·5–5	0	0	0	0	0	0	,,
,,	,,	11	6	3·5–5	0	0	0	0	0	0	,,
B. sterilis	B. sterilis	17	6	10–12	6	6	6	6	6	6	,,
,,	B. mollis	7	5	2·5–3·5	0	0	0	0	0	0	,,
,,	,,	17	6	3–4	0	0	0	0	0	0	,,
B. madritensis	B. sterilis	9	5	2–5	5	5	5	5	5	5	,,
,,	B. mollis	12	7	2–4	0	0	0	0	0	0	,,
,,	,,	14	6	4–5·5	0	0	0	0	0	0	,,
B. commutatus	B. sterilis	10	6	2–3	0	0	0	0	0	0	,,
,,	B. mollis	6	4	1·5–3	2	4	4	4	4	4	,,
,,	,,	9	6	1–2	0	3	5	5	5	5	,,
B. arvensis	B. sterilis	10	6	2–3	0	0	0	0	0	0	,,
,,	B. mollis	13	5	3–4	1	1	1	1	1	1	,,
,,	,,	13	5	1–4	0	3	3	3	3	4	,,
B. secalinus	B. sterilis	12	6	3–5	0	0	0	0	0	0	,,
,,	B. mollis	11	6	3–5	2	6	6	6	6	6	,,
,,	,,	5	3	1·5–4	2	3	4	4	4	4	Probably one leaf had touched another.
B. interruptus	B. sterilis	12	6	2–5	0	0	0	0	0	0	,,
,,	B. mollis	10	7	3–4	1	3	4	6	6	6	,,
,,	,,	9	5	2–4	1	2	3	3	3	4	,,
B. racemosus	B. sterilis	12	6	1·5–2·5	0	0	0	0	0	0	,,
,,	B. mollis	10	6	1–2	2	4	5	5	5	5	,,
,,	,,	4	2	1–2·5	0	0	0	0	1	1	,,

germinating at 20–22° C, so we may assume that no source of error existed there.

The infection was done by sopping up spores in paper pulp, as I found them stick so much better. Each infected plant was then put in the west window under a beaker kept wet with filter-paper—my usual method.

July 6—the day of infection of No. 747—opened dull and cool, the shade temperature being 16–19·5° C and it rained hard in the later part of the day.

July 7 was warm, close and dull, with sunny intervals later. Shade temperature 22° C at 10 a.m.

July 8 was bright, hot with cool easterly breezes.

July 9, overcast and dull muggy morning, t. = 19·5° C at 11 a.m. Hot and sunny bursts later.

July 10, 11, 12 and onwards were scorching hot days.

It seems impossible to find any source of error in the temperature from July 6–8. No. 747 was put out on the 8th. It remained under the bell-jar till the 10th. Then free in the blazing sun.

No. 752, similarly infected (but with better spores) on July 7, was put outside on the 10th. Its bell lifted on the 11th and on the 13th free in the sun.

Similarly with No. 754. Hence we must conclude either that the paper pulp method is bad, or that the temperature during incubation was so high that the mycelium in the leaf was killed.

The weather during incubation was extremely hot—July 10–21—and several other seedlings were badly scorched when left under bell-jars, and the suspicion arose that the plants may have got so hot that the Fungus could not withstand it, and its growth was inhibited.

Of course it might be urged that there is the possibility that, after all, these species of *Bromus* are resistant—but if so why did *B. mollis* in 747 and 752 resist the *B. mollis* spores, or *B. sterilis* in 754 those of *B. sterilis*? Previous experiments have shown over and over again that such a result is not to be looked for.

That it was really the high temperature, and not the method of infection, however, seemed clear after the following experiments.

Three series (Nos. 759, 763, and 764) of the same hosts, &c., as in the preceding lists, were infected by placing the spores in the tip-drops and on the face of the leaf, in water only. The temperature was very high, and all failed.

On the other hand, by adopting the precaution of carrying out the infection in a cool cellar, and allowing the incubation to take place in a well-lighted but cool area, where the temperature did not rise above 25° C, I found the results quite comparable to those of the previous experiments before the very hot weather set in. See Tables XIX and XX, and Table XXII, p. 297. Similar successful infections were then obtained in a number of other cases, some of which have been shown in results already published[1], and which are quite conclusive as to the state of affairs when the external conditions for infection are satisfactory.

10. DISCUSSION OF THE FOREGOING RESULTS.

There seems to be no doubt from the evidence now accumulated that the Uredospores of *Puccinia dispersa* are capable of germinating upon any leaf of any species of *Bromus* and putting forth the germ-tubes which seek the stomata. Here the tip of the germ-tube behaves differently according to the species of *Bromus* attacked and the species of host-plant whence the Uredospore has been derived.

If these species are identical—e. g., if Uredospores derived from *Bromus mollis* find the conditions for germination on leaves of *Bromus mollis*—the tip of the Uredospore swells up over the stoma, and soon puts forth a branch into the intercellular spaces beneath, and there ramifies as a mycelium which, in ten days or so, again puts forth pustules of Uredospores. Even here, however, the success of the mycelium depends on circumstances. If the temperature, light, supply of water and minerals, &c., are unfavourable, and the leaf is

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[1] Proc. Cambridge Phil. Soc., vol. xi, Pt. V, p. 307.

TABLE XXI.

Exp. No. 741 June 30, and 744 July 2. Pot-seedlings 20 days and 8 days old sown with spores from *B. secalinus*. No. 741 kept under bells outside, the others in open sun. All spores separately tested and known to be vigorous.

No.	*Date of inoculation.*	*Species.*	*Origin of spores.*	*No. of plants.*	*No. inoculated.*	*Results. Number succeeded.* *July* 10	*July* 11	*July* 12	*July* 13	*July* 14	*July* 17	*July* 21
741 *a*	June 30	B. mollis	B. secalinus	10	4	0	0	0[1]	0[1]	0[1]	0[1]	0[1]
744 *a*	July 2	”	”	7	4	0	0	2	2	3	3	3
741 *b*	June 30	B. velutinus	”	9	4	0	0	0	0	0	0	0[2]
744 *b*	July 2	”	”	9	7	0	0	0	0	0	0	0
741 *c*	June 30	B. maximus	”	11	4	0	0	0	0	0	0	0
744 *c*	July 2	”	”	8	5	0	0	0	0	0	0	0
741 *d*	June 30	B. sterilis	”	9	4	0	0	0	0	0	0	0
744 *d*	July 2	”	”	7	5	0	0	0	0	0	0	0
741 *e*	June 30	B. madritensis	”	7	4	0	1	1	1	1	1	1[3]
744 *e*	July 2	”	”	8	5	0	0	0	0	0	0	0
741 *g*	June 30	B. commutatus	”	12	4	0	0	0	0	0	0	0[4]
744 *g*	July 2	”	”	10	5	0	0	0	0	0	0	1
741 *h*	June 30	B. arvensis	”	12	4	2	4	4	4	4	4	4
744 *h*	July 2	”	”	10	4	0	0	2	2	2	2	2
741 *i*	June 30	B. secalinus	”	10	4	2	4	4	4	4	4	4
744 *i*	July 2	”	”	7	5	4	5	5	5	6	6	6[5]
741 *k*	June 30	B. interruptus	”	12	4	0	0	0	0	0	0	0
744 *k*	July 2	”	”	16	5	0	0	0	1	1	1	1
741 *l*	June 30	B. racemosus	”	11	4	0	1	1	1	1	1	1
744 *l*	July 2	”	”	10	4	0	0	0	0	0	0	0[6]

[1] There are flecks on three leaves.

[2] Several flecks.

[3] Doubtful if due to inoculation.

[4] Several flecks.

[5] Assume that one leaf was accidentally infected?

[6] Several flecks.

TABLE XXII.

Exp. Nos. 774 and 775. Seedlings a week old infected on first leaf with tested vigorous spores at temperature near optimum.

No.	*Date of infection.*	*Host.*	*Origin of spores.*	*No. of plants.*	*No. infected.*	*Results.*				
						July 30	*July* 31	*Aug.* 1	*Aug.* 2	*Aug.* 4
774 *a*	July 21	B. mollis	B. mollis	10	5	3	4	5	5	5
,, *b*	,,	B. tectorum	,,	8	4	0	0	0	0	0
,, *c*	July 22	B. ciliaris [1]	,,	8	5	0	0	0	0	0
,, *d*	July 21	B. brizaeformis	,,	11	5	2	2	2	2	2
,, *e*	,,	B. secalinus	,,	10	5	3	3	4	5	5
,, *f*	,,	B. macrostachys	,,	9	5	0	4	4	4	4
,, *g*	July 22	B. inermis	,,	10	5	0	0	0	0	0
,, *h*	,,	B. pratensis [2]	,,	9	5	0	0	0	0	0
,, *i*	July 21	B. velutinus	,,	7	4	0	2	3	3	3
,, *k*	,,	B. sterilis	,,	6	4	0	0	0	0	0
,, *l*	,,	B. maximus	,,	7	4	0	0	0	0	0
,, *m*	,,	B. madritensis	,,	9	4	0	0	0	0	0
,, *n*	July 22	B. Schraderi [3]	,,	11	5	0	0	0	0	0
,, *o*	,,	B. unioloides [3]	,,	3	2	0	0	0	0	0
,, *p*	,,	B. canadensis	,,	2	2	0	0	0	0	0
,, *q*	,,	B. erectus	,,	4	2	0	0	0	0	0
,, *r*	,,	B. giganteus	,,	1	1	0	0	0	0	0
775 *a*	,,	B. mollis	B. secalinus	7	4	0	0	0	0	0
,, *b*	,,	B. tectorum	,,	6	4	0	0	0	0	0
,, *c*	,,	B. ciliaris	,,	9	5	0	0	0	0	0
,, *d*	,,	B. brizaeformis	,,	8	5	0	0	3	3	3
,, *e*	,,	B. secalinus	,,	9	6	3	4	6	6	6
,, *f*	,,	B. macrostachys	,,	9	5	5	5	5	5	5
,, *g*	,,	B. inermis	,,	8	5	0	0	0	0	0
,, *h*	,,	B. pratensis	,,	6	4	0	0	0	0	0
,, *i*	,,	B. velutinus	,,	10	5	0	3	4	4	4
,, *k*	,,	B. sterilis	,,	6	4	0	0	0	0	0
,, *l*	,,	B. maximus	,,	6	4	0	0	0	0	0
,, *m*	,,	B. madritensis	,,	7	4	0	0	0	0	0
,, *n*	,,	B. Schraderi	,,	8	4	0	0	0	0	0
,, *o*	,,	B. unioloides	,,	2	2	0	0	0	0	0
,, *p*	,,	B. canadensis	,,	2	2	0	0	0	0	0

[1] Species needs further examination. [2] Species needs revision. [3] Synonyms.

thereby rendered an unsuitable medium, the infecting tube may fail to gain a successful entry, or the mycelium may be starved and unable to form a new crop of spores, or it may remain dormant for a time until the tissues regain their normal capacity for supporting it. It is even probable that the mycelium may be starved out by the, in a sense, dominant tissues of the host-plant, when itself very feeble, if the latter regain their vigour, and thus the infection becomes abortive.

If the Uredospores germinate on a leaf of some other species of *Bromus* than the one which bore them,—e.g., if spores from *B. mollis* germinate on leaves of *B. sterilis*—the infection may be rendered abortive, owing to the non-adaptation of the parasite to the host, in other ways. Thus the infecting tube may attack the stomata and underlying cells too vigorously, as it were. In this case the cells first attacked die, and the dead tissues are so unsuitable as pabulum for the incipient mycelium, that the latter dies off from starvation, a corroded patch showing where the injury is localized. This appears to be a common event when the tips of the young leaves of *B. sterilis*, *B. madritensis*, or *B. maximus* are invaded by vigorous spores derived from *B. mollis*.

In such cases the non-adaptation of the parasite to its new host is shown, not by any active resistance of the latter, but by the too vigorous onslaught of the former producing such disastrous results that the mycelium cannot advance through the ruined tissues its ill-timed ravages have brought about.

In sections of such, the short stumpy mycelium, with fatty contents suggesting a starved condition, may be observed among the dead and dying cells of the leaf-tissue, evidently unable to grow.

Yet another case of non-adaptation of the parasite appears to occur when the Uredospores from one species attack a species unsuitable to them, e.g., when spores from *B. mollis* germinate on the leaves of *B. inermis* or of *B. erectus*, &c.

In these cases it seems that the infecting tubes reach and penetrate the stomata, but are unable to form a mycelium in the tissues, evidently because the living cells are really resistant. How the latter prevent the hyphae from putting haustoria into their cell-cavities is not yet clear, but it looks as if they exerted some deleterious influence on the delicate tips and thus brought their efforts to abortion.

It will be obvious that the foregoing explanation of the phenomena differs entirely from Eriksson's *Mycoplasm* hypothesis. The dormant mycelium is dormant not because it has established a *symbiosis* with the host, but because it *has failed to establish any such relations.* It is like a plant in poor soil, or in a medium too dry or too cold, &c., for its welfare. It drags on a starved, stunted existence which will end in death unless the environment improves, and nurses it again into vigorous growth. We must rather consider the flourishing mycelium, fully adapted to its host-plant, as having established successful symbiotic relations, for, as I pointed out long ago, a Uredine when flourishing in a leaf does not act as a devastating parasite, but as one which slowly taxes its host, and even stimulates the cells for some time to greater activity. This is often shown by the persistent green colour and activity of the cells immediately round a pustule at a time when the rest of the leaf is yellow and faded. The same conclusion is borne out by the well-established fact that the best developed pustules and Uredospores are derived from the most flourishing green leaves. In other words, we get a better nourished and better developed mycelium in a leaf which can supply it with plenty of food ; just as we get a finer plant by cultivating it highly in good soil and surroundings.

It will be observed that I lay some stress on the origin of the spores, a point far too much overlooked in all discussions regarding these parasites. Most observers have seemed to regard adapted parasitism as if it concerned chiefly the Fungus. I look upon the influence of its host as an equally important factor: though here and there the Fungus also varies from the normal.

The Uredospores derived from *Bromus mollis* attack the leaves of another plant of *B. mollis* so successfully because their food-supplies and previous environment have affected their protoplasm in some way which makes it easier for their germ-tubes and mycelium to grow in tissues which afford them the same nutriment and present the same obstacles, &c., as they have hitherto enjoyed, or been confronted with.

They can also flourish in *B. secalinus*, *B. racemosus*, *B. commutatus*, because here also the food-supplies, &c. offered are nearly the same—these species being so closely allied as to be regarded by some authorities as mere varieties.

But matters are different when it comes to attacking *B. maximus*, *B. sterilis*, &c. We may suppose the food and the resistances offered to the mycelium by these species to differ considerably from those which existed in the tissues of *B. mollis*, though not perhaps sufficiently so to present a barrier incapable of being overcome by an odd spore varying from the normal here and there.

I regard this matter as exactly similar in kind (however different in degree it may be) to that where a carbo-hydrate-loving Fungus is sown on a proteid, or when a Yeast adapted to one kind of sugar is placed in another kind, or where we attempt to rear dung-fungi on gelatine, wood-fungi on potato, and so forth. Numerous other illustrations can be given, but, not to multiply analogies unnecessarily, I will merely refer to the well-known case of Bacteria, distinct races of which can be produced by slight differences of nutrition and training.

Such cases also remind us that it is possible to educate a given Fungus or Bacterium to feed on very different media by gradually accustoming it to the changed conditions; and I suppose that when the Uredospores from *B. mollis* are sown on *B. secalinus* and *B. racemosus* as well as *B. mollis*, and find that it does best on the latter, next best on *B. secalinus*, and worst on *B. racemosus*, that such 'education' is substantially what is occurring, because if I now take the Uredospores developed in consequence of this infection on *B. secalinus* and sow them on the same three species, it is *B. secalinus* which proves the best host for them.

It is indeed very probable that by *gradual* variation and adaptation the Fungus can pass to all or nearly all the species of Bromes in turn, even to such as have hitherto appeared immune.

That by gradual passage from variety to variety, and from one species to a closely allied one, such spores may be gradually adapted to different hosts in nature, seems an obvious corollary from the facts.

To sum up, then, I should place in the foreground the fact that three phases must be considered in infection:

(1) The germination of the Uredospore.

(2) The act of inoculation or infection; and

(3) The incubation period or growth of the mycelium in the tissues.

Each of these phases has its vicissitudes. The germination depends on the vigour and previous nutrition of the spore, as well as on the factors of the environment active during the process; and the nature and vigour of the resulting germ-tube are determined especially by these.

The act of inoculation, or entry of the germ-tube into a stoma, brings into play new factors; for the living cells attacked, with their known capacities for producing acids, enzymes, food-stuffs, chemotactic substances, &c., cannot be regarded as passive. It depends on these whether the germ-tube can gain a safe entrance. It may be so well adapted that this is easy, e.g., from *B. mollis* to *B. mollis*, or it may be that the over-energetic germ-tube destroys the guard-cells, &c., and so ruins the affair at the start, e.g., from *B. mollis* to *B. sterilis*.

Once inside, the young mycelium is still by no means assured of successful development and growth. Even in a host-species naturally accommodating, e.g. *B. mollis* to the Fungus from *B. mollis*, a lack of minerals, especially potassium or phosphorus, may bring about slow starvation; or the temperature may be too high for the Fungus, though the grass itself withstands it well; or the host is so shaded that it assimilates badly and so forth. All these and similar events will have their effect, and the starved mycelium may die or lie dormant till the leaf dies, or possibly be resuscitated again if affairs improve before the life of the leaf is ended.

It seems to me that many cases of delayed outbreak of the Fungus, of apparent failure of attack, of poorly developed pustules, and of feebly germinating spores are to be explained by the above considerations.

When the invading germ-tube finds itself in the leaf of a species which differs so much from the one on which the Fungus giving rise to the Uredospores was raised, that the incipient mycelium has to accept food-supplies differing considerably from those on which it was brought up, and to face antagonistic influences of other kinds, enzymes and possibly anti-toxins, &c., on the part of the cells it is in contact with, it may be dominated entirely, and the infection fails. Or it may just manage to struggle along and even to develop a few feeble spores, and it may depend on the vigour of these latter whether the reinfection of this species can occur, and so on.

11. FACTORS IN THE HOST.

It is evident that some factor or factors on the part of the host-plant must be concerned in rendering infection successful, or the reverse; because, as we have seen, even when the external conditions are favourable to germination, and even when spores have successfully germinated on the leaf, and the germ-tubes reached the stomata, infection only follows in the case of certain species or varieties, while others are 'resistant' if not 'immune.' The question thus arises, In what does this capacity for 'resistance,' or 'immunity,' consist?

Several possibilities may be suggested in answer. The cell-walls might be supposed to be too thick for the hyphae, even when safely ensconced in the inter-cellular passages, to penetrate them; or the stomata may be imagined to be too small for the tip of the tube to force its way in; or the hairs on the epidermis may be a hindrance, and so forth. In most of the few cases where such questions have arisen, some such anatomical hindrances to infection have been suggested, and in at least one similar instance—that of wheat-rust, such anatomical hindrances to infection have been asserted[1] and denied[2] by different observers.

But it is obvious that no mere direct examination of the structure can be expected to supply a sufficient answer to such questions, and still less that speculative suggestions

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[1] Cobb, Agric. Gaz. N. S. Wales, vol. iii, 1892, p. 1.

[2] Eriksson, Die Getreideroste, 1896, p. 351.

should do so. I have accordingly gone into this question of the structural peculiarities of the host-plant in a manner more searching and thorough than hitherto, and have, I believe for the first time, devised methods of attacking the question which promise accurate results, which results, moreover, are perhaps somewhat surprising in their nature.

This part of the investigation has, as will readily be understood from the sequel, proved a very laborious, not to say tedious, business, but it was obvious that it had to be done; and although I am not prepared to state that all the numerous measurements and calculations are accurate and final, it will be seen that they hang together sufficiently firmly to make a chain of evidence which seems to support the main conclusion, which is, that the resistance to infection of the 'immune' or 'partially immune' species and varieties is not to be referred to observable anatomical or structural peculiarities, but to internal, i. e. intra-protoplasmic, properties beyond the reach of the microscope, and similar in their nature to those which bring about the essential differences between species and varieties themselves.

The problem which I set myself was, to investigate as thoroughly as possible the sizes, numbers, and distribution of the stomata, hairs, chlorophyll-tissue, vascular bundles, sclerenchyma and other structural units of the leaf, and to see if in any two or more species or varieties of Brome such structural relations showed differences at all compatible with differences in their predisposition to the disease or to their immunity from infection.

In order that no avoidable complications should be introduced owing to variations on the part of individuals grown under different conditions, or in different leaves or parts of leaves, I adopted the precaution of selecting for examination of these structural factors the same part of the same leaf, grown under the same conditions. Not only so, I took this leaf from the pots of two of the most conclusive sets of experiments, viz. Nos. 774 and 775 (see Table XXII), in the following manner.

When, on August 4, I made the last records of the results of infection of the two series named, the first green leaf of both the infected and uninfected seedlings from each pot was removed, and put into tubes of absolute alcohol and of Fleming's solution. Each tube received also a cardboard slip with the serial experiment-number, name of the species, and date. These tubes were then put aside (the specimens in Fleming's solution having been properly hardened, washed and transferred to absolute alcohol) to await examination during the autumn and winter. Meanwhile, notes were accumulated as to the length, breadth, number of ribs, thickness, height of ridges and so on of the fresh leaves, in order that future comparisons could be made, in case any question arose during the examination of the preserved material.

In due course, the examination was made as follows. The upper part—three centimetres or so in length—of each leaf was taken, and examined as follows. The uppermost centimetre (apex) was removed and the rest cut into short lengths of about three to four millimetres. One of these was mounted with its upper face upwards, and its next segment with its lower face upwards on the same slide. Various methods—balsam, glycerine, glycerine-jelly, warming in eau-de-javelle, &c., were tested, but the most satisfactory results were obtained by transferring through warmed glycerine and alcohol to glycerine jelly.

These translucent preparations were then examined for such details as the breadth of the leaf, the number of ribs and their distances apart, the number and size, distribution, &c., of hairs, stomata, and so forth.

The remaining segments were employed to obtain transverse sections, similarly mounted and used for measurements of the thickness, breadth, &c., of the leaf, the vascular bundles, chlorophyll-tissue, &c., as well as to check the preceding measurements.

The results are set forth in the accompanying Tables. I may here state that no measurable differences in the thickness of the cell-walls, cuticle, waxy bloom, &c., were obtained, and these factors are omitted from the Tables.

12. GENERAL ANATOMY OF THE FIRST GREEN LEAF.

In all the species examined the first green leaf of the seedling is ligulate, acute, and slightly hooded at the apex, varying in length from 40–50 to 80–100 mms. and inrolled at the base. The length is not sufficiently constant to be of service as a character, but the breadth, from 1–3 mms., is remarkably so, as the table of measurements shows.

The mid-rib always contains the strongest vascular bundle, and has a keel—which may be very slight however—subtending it. This is flanked by one, two, or three ribs on each side, according to the species, in each of which a weaker bundle runs. Thus *B. mollis*, *B. arvensis*, *B. interruptus*, &c., have usually three ribs in all, *B. secalinus*, *B. sterilis*, &c., have five, while *B. maximus*, *B. unioloides*, &c., have seven. It appears to be constantly the case also that each alternate rib contains a feebler vascular bundle; for instance, where there are three in all, the strong mid-rib is flanked by a weaker one on either side; when five are present, those nearest the margins are stronger than those between them and the mid-rib; and when there are seven in all, the second from the margin on each side is stronger than those on either side of it.

Corresponding to each rib is a ridge, i. e. the tissue of the leaf is thicker especially above (but also below) than in the intervals, and we thus have a series of intervening grooves alternating with ridges, especially on the upper surface of the leaf. It is in the tissue beneath these grooves that the chlorophyll is aggregated.

It is on the flanks of these ridges, and only there, that the stomata occur. These are arranged in longitudinal series, usually a single series on each flank of the ridge, but occasionally double (and, rarely, even triple) on one flank of one ridge on each half of the lamina.

There is no exception, in the cases examined, to the rule that the stomata are more numerous on the upper surface than on the lower, the increased numbers being due to closer packing of the stomata in each longitudinal series, and occasionally to an increase in the number of series above. The stomata are large, and always placed with the long axis coinciding with that of the longitudinal series. As a rule the stomata are somewhat larger on the lower than on the upper surface, and account has to be taken of some variation in the extremes of size: the majority, however, are of an average size between these extremes.

Hairs are never totally absent, though they vary enormously in abundance, and the rule is almost without exception that they are more numerous and often much more numerous below than above, thus reversing the order of events found in the case of the stomata.

As regards the length of the hairs, considerable variation is also evident, though sufficient constancy as regards average length is found in each species to make it worth while noting the character. The hairs are always simple and usually stiff and tapering, and arise from the crests of the ridges on the upper surface of the leaf, but from the flanks or from the intervals (grooves) between the ridges on the lower surface. On the latter, moreover, there is no recognizable order in their arrangement, and beyond a sort of general rule that a stoma and a hair do not usually occur close together I have been unable to observe any very definite relation between these organs. At the same time it appears probable that in their inception there is some more or less definite order of succession, but since I have paid very little attention to the youngest stages, the matter must remain undecided.

All the Bromes examined have motor-cells in the grooves between the ridges on the upper surface; there are none on the lower. These motor-cells are merely enlarged and turgescent epidermal cells, the contraction and expansion of which draws together or drives apart the ridges of the upper surface, thus bringing about corresponding infolding or expansion of the leaf. The mechanism is easily seen in the behaviour of

TABL

Dimensions of leaf. The black lines in col

Species of *Bromus.*	(1) *Width of leaf: direct measurement.*	(2) *No. of ribs.*	(3) *Distances between the ribs measured from axis to axis direct (low power).*									
			Margin to No. 1	1–2	2–3	3–4	4–5	5–6	6–7	*No.* 7 *to margin.*	*Total μ.*	*M to*
B. mollis	1·2 mm.	3	192	390	▌402	210					1194	1
B. tectorum	1·7	5	162	358	358	▌312	325	143			1657	2
B. ciliatus	1·8	5	169	357	390	▌325	325	143			1709	2
B. brizaeformis	2·0	5	162	325	338	▌345	338	175			1683	1
B. secalinus	2·4	5	260	455	455	▌455	455	260			2340	2
B. macrostachys	1·9	5	221	357	390	▌390	325	195			1878	1
B. pratensis												
B. inermis	1·2	5	143	293	292	▌292	293	98			1411	1
B. velutinus	2·0	5	227	390	390	▌391	390	227			2015	2
B. sterilis	2·0	5	228	377	351	▌325	364	195			1840	2
B. maximus	3·0	7	195	325	520	520	▌520	520	390	169	3159	19
B. madritensis	1·7	5	182	338	325	▌325	351	169			1690	19
B. Schraderi	2·1	7	130	292	325	325	▌325	325	260	130	2112	1
B. unioloides	2·5	7	162	293	338	332	▌326	390	299	163	2303	19
B. racemosus	1·75	5	196	365	330	▌330	360	220			1801	3
B. commutatus	1·1	3	160	416	▌420	190					1186	1
B. interruptus	1·0	3	160	371	▌352	160					1043	20
B. arvensis	1·2	3	192	360	▌384	172					1108	19
B. canadensis	1·7	5	195	325	325	▌325	325	162			1657	20

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II.

l 4 indicate the position of the mid-rib.

(4) nces between ribs measured on transverse sections of leaf.							(5) *Average total breadth of ribs (sections).*	(6) *Depth of mid-rib.*	(7) *Depth at Sinus.*	(8) *Mean sectional area of chlorophyll tissue per mm. of breadth.*	(9)
2–3	3–4	4–5	5–6	6–7	*No. 7 to margin.*	*Total μ.*					
▌423	188					1241	237	260	150	110	88,990
455	▌435	423	324			2300	224	325	152	238	214,200
423	▌429	422	140			2083	224	260	130	195	174,030
337	▌337	345	162			1720	198	260	127	193	171,770
461	▌448	442	241			2314	300	325	151	238	207,060
325	▌325	325	195			1710	210	293	146	219	192,063
305	▌311	305	182			1584	218	260	117	188	155,358
409	▌390	390	260			2184	236	342	133	237	201,190
423	▌468	455	253			2294	243	293	101	197	176,315
520	520	▌520	507	338	182	3192	410	325	147	236	205,685
305	▌325	325	195			1670	192	214	120	203	179,655
312	325	▌338	292	260	130	2067	333	188	100	144	120,808
390	403	▌390	390	325	162	2606	327	260	149	204	178,402
371	▌345	384	262			2059	249	288	120	204	179,316
▌350	160					1035	134	224	109	166	144,420
▌439	198					1263	147	268	122	195	172,303
▌371	192					1145	134	262	96	179	155,857
312	▌306	312	195			1697	269	273	162	217	182,497

TABLE XIII.

Dimensions of leaf. The black lines in colum and 4 indicate the position of the mid-rib.

Species of *Bromus.*	(1) *Width of leaf: direct measurement.*	(2) *No. of ribs.*	(3) *Distances between the ribs measured from axis to axis direct (low power).*									(4) *Distances between ribs measured on transverse sections of leaf.*									(5) *Average total breadth of ribs (sections).*	(6) *Depth of mid-rib.*	(7) *Depth at Sinus.*	(8)	(9) *Mean sectional area of chlorophyll tissue per mm. of breadth.*
			Margin to No. 1	1–2	2–3	3–4	4–5	5–6	6–7	*No.* 7 *to margin.*	*Total μ.*	*Margin to No.* 1	1–2	2–3	3–4	4–5	5–6	6–7	*No.* 7 *to margin.*	*Total μ.*					
B. mollis	1·2 mm.	3	192	390	402	210					1194	195	435	423	188					1241	237	260	150	110	88,990
B. tectorum	1·7	5	162	358	358	312	325	143			1657	234	429	455	435	423	324			2300	224	325	152	238	214,200
B. ciliatus	1·8	5	169	357	390	325	325	143			1709	227	442	423	429	422	140			2083	224	260	130	195	174,030
B. brizaeformis	2·0	5	162	325	338	345	338	175			1683	195	345	337	337	345	162			1720	198	260	127	193	171,770
B. secalinus	2·4	5	260	455	455	455	455	260			2340	247	475	461	448	442	241			2314	300	325	151	238	207,060
B. macrostachys	1·9	5	221	357	390	390	325	195			1878	195	325	325	325	325	195			1710	210	293	146	219	192,063
B. pratensis																									
B. inermis	1·2	5	143	293	292	292	293	98			1411	163	318	305	311	305	182			1584	218	260	117	188	155,358
B. velutinus	2·0	5	227	390	390	391	390	227			2015	280	455	409	390	390	260			2184	236	342	133	237	201,190
B. sterilis	2·0	5	228	377	351	325	364	195			1840	260	435	423	468	455	253			2294	243	293	101	197	176,315
B. maximus	3·0	7	195	325	520	520	520	520	390	169	3159	195	410	520	520	520	507	338	182	3192	410	325	147	236	205,685
B. madritensis	1·7	5	182	338	325	325	351	169			1690	195	325	305	325	325	195			1670	192	214	120	203	179,655
B. Schraderi	2·1	7	130	292	325	325	325	325	260	130	2112	130	280	312	325	338	292	260	130	2067	333	188	100	144	120,808
B. unioloides	2·5	7	162	293	338	332	326	390	299	163	2303	195	351	390	403	390	390	325	162	2606	327	260	149	204	178,402
B. racemosus	1·75	5	196	365	330	330	360	220			1801	307	390	371	345	384	262			2059	249	288	120	204	179,316
B. commutatus	1·1	3	160	416	420	190					1186	185	340	350	160					1035	134	224	109	166	144,420
B. interruptus	1·0	3	160	371	352	160					1043	204	422	439	198					1263	147	268	122	195	172,303
B. arvensis	1·2	3	192	360	384	172					1108	198	384	371	192					1145	134	262	96	179	155,857
B. canadensis	1·7	5	195	325	325	325	325	162			1657	208	364	312	306	312	195			1697	269	273	162	217	182,497

transverse sections, not too thin, in alcohol and glycerine to which water or eau-de-javelle are added in various proportions.

The margins of all the species examined are strengthened by sclerenchyma-cells arranged in a long thin band, and a similar feeble band runs down the crest of the keel below the mid-ribs. In very rare cases a much feebler strand runs below the two stronger secondary bundles. In no case does the amount of sclerenchyma approach the dignity of a girder, as it so often does in the broader leaves of mature plants.

The margins of all species examined, with the exception of one which is probably not a true Brome, have short sharp asperities with the points turned upwards, sometimes with some turned downwards. Similar asperities occur also on the mid-rib or stronger ribs of *B. unioloides*, in addition to the hairs proper, but in no other Brome examined has this character been found to occur.

13. DIMENSIONS OF THE LEAF.

Although differences of some value as regards length of leaf are attainable, so long as we confine our attention to seedlings growing under the same conditions, I pass them by as of relatively little importance in the present connexion. In Table XXIII are set forth the measurements of (1) the average breadth of the whole leaf; (2) the number of ribs; (3) the intervals between the ribs as measured on the translucent solid pieces of leaf; (4) the same intervals as measured with a higher power on transverse sections; (5) the average total breadth of the vascular bundles of the ribs, as measured on transverse sections; (6) the depth of the mid-rib from the crest of its ridge above to the crest of the keel below; (7) the depth of the leaf at the middle of the sinus between a pair of ridges, also, like the last, measured on the transverse section; and lastly (8 and 9) the calculated sectional area of chlorophyll-tissue in each interval, and its volume for each square millimetre of leaf-surface.

Columns 1 to 4 explain themselves. It is only necessary to remark that precautions were taken to compare any shrinkage in breadth due to the action of the reagents employed in preserving and mounting. The danger is a real one, because the contraction of the motor-cells under certain circumstances may vitiate the measurements by drawing together the whole upper surface of the leaf. I found, however, that with the properly hardened material relaxed in glycerine jelly and measured at once, this danger was reduced to a minimum, and the measurements compare very accurately with those made on fresh specimens. Nevertheless, I took the precaution to institute check measurements (see columns 3 and 4) of the rib-intervals throughout by two different methods, and it will be noticed how closely the results set forth in column 1 (measurement with a lens direct) usually agree with the totals in columns 3 and 4. Moreover, it should be noted that exactly the same treatment throughout was accorded to all the species.

In measuring the intervals, in column 3 the micrometer scale[1] was made to travel from the axis of one rib to that of the next, or (column 4) from the centre of one vascular bundle to that of the next. It will be noticed that the distance from rib to rib is often greater on one side of the mid-rib than on the other. This inequality in the breadth of the two halves of the lamina of grass leaves has often been observed, but, so far as I am aware, no explanation has been given of it. It appears to be due to the fact that the smaller half-lamina was the innermost in the involuted state of the leaf in the bud, and thus had less room for lateral extension, its growth being hindered by the pressure of the surrounding parts—the enveloping outer half-lamina and sheath—between which it is trapped, as it were. The same mechanical pressures help to arrest the longitudinal growth also, and so induce the twist[2] in the lamina by rendering one edge shorter than the other.

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[1] I used a Zeiss 'Mess-ocular' with travelling scale, and a mechanical stage.

[2] This twisting of adult grass leaves has often been noticed. See an interesting paper by Max Wichura in *Scientific Memoirs*, Parts III and IV, 1853, p. 262, where, however, the author failed to give any satisfactory explanation of the phenomenon.

Columns 5–7 were introduced in order to give the data for obtaining the approximate calculations in columns 8 and 9, viz. calculations of the mean area of chlorophyll-tissue and epidermis divested of the vascular tissue and alone attackable by the Fungus. I tried several methods of more direct measurement of this tissue before deciding that the irregular shape of the leaf defeated all attempts to obtain such. But it appeared so necessary to ascertain, however approximately, whether any relation exists between the volume of attackable tissue per square unit of leaf-area, and the susceptibility or immunity of the species, that I hit upon the following device.

Having subtracted the width of the vascular bundles (column 5) from the total width of the leaf (column 4) as measured on sections, I took the mean depth of the leaf-section from columns 6 and 7, and then treated the whole as a rectangle. The area of this gives us the result shown in column 8, reduced to a rectangle with its longer side equal to one millimetre. This sectional area multiplied by 1,000 gives us the volume of tissue per 1 sq. mm. of leaf surface.

It must be admitted that these areas and volumes cannot be exact. The ideal object of attainment would be the volume of the cells and inter-cellular spaces, numbers of chlorophyll-grains and their sizes, and so on, but I found it hopeless to expect any success in carrying out such estimations as were attempted in this connexion.

One point that has to be attended to is to allow for the inter-osculations of vascular bundles by lateral bundles. It is quite a mistake to suppose that the 'veins' of grasses are all parallel; they are netted, and the only device I could think of for allowing for the lateral connexions was to deduct the tissues immediately above and below the much-predominating main ribs. In any case, this is the least attacked of all the non-vascular tissue.

Perhaps all I can claim for this part of the subject is to have suggested a method which can be improved upon in future measurements. If the latter were made on a sufficiently large scale I think average results of value could be obtained and tested.

14. STOMATA.

I have elsewhere[1] published the details of my examination of the stomata, showing that there is no discoverable relation between their sizes and numbers, and may refer to that demonstration for information as to the methods of estimation and of checking pursued. It was natural to expect that, since the germ-tubes enter the leaves via the stomata, the sizes and numbers of the latter would be important factors: on the contrary, they seem to be of no importance whatever in connexion with the question here raised.

15. HAIRS.

It is conceivable that the degree of hairiness of the leaf may be a factor in hindering the access of the germ-tubes to the stomata. In any case I found that in certain series of experiments where spores were kept in place on the leaves by fluffy masses of cotton-wool, the germ-tubes frequently ran into the interstices and appeared to lose themselves there instead of finding their way to the stomata. Too much stress must not be laid on these observations, however, since such wet pads of cotton-wool may have altered the conditions considerably—e. g., impeding access of oxygen, light, gas interchange and so on—and it is probable that the natural hairs never become thoroughly wetted as were these saturated cotton fibres.

Be this as it may, it seemed worth while to obtain measurements of the length and the relative numbers of the hairs, and the results—obtained simultaneously with those of the stomata and hence by similar methods—are set forth in Table XXIV.

The columns explain themselves. In column 1, in addition to the extreme lengths, I have added the commonest averages.

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[1] Proceedings of the Cambridge Philosophical Society, vol. xi, Part V (1902), pp. 318–323.

TABLE XXIV.

HAIRS.

Species of *Bromus*.	1					2		3		4		5	
	Average length in μ.					*Average No. in a field = 900 μ diam.*		*Average No. on a transv. section of leaf.*		*No. on the sq. mm. calculated from col. 2.*		*No. per sq. mm. actually counted and plotted.*	
	A.		*B.*		*Mean.*	*A.*	*B.*	*A.*	*B.*	*A.*	*B.*	*A.*	*B.*
B. mollis	450–1400	850	440–770	600	920	5	6·6	1·5	3	8	10	9	10
B. tectorum	500–650	500	280–300	290	468	5·6	10·6	2·2	2·8	9	16	9	21
B. ciliatus	240–650	450	330–960	375	600	4	10·2	1	2·3	6	16	8	19
B. brizaeformis	300–760	600	450–830	600	560	6·8	23	2·2	7·4	10	36	24	46
B. secalinus	250–550	250	250–380	300	400	6·8	12·2	1·4	4·3	10	19	12	22
B. macrostachys	200–550	250	200–700	250	450	3·8	10·8	1·1	4·3	6	17	5	21
B. pratensis	60		0					0·6	0			25	0
B. inermis	400–750	450	800–1000	800	700	5·2	5·5			8	9	8	9
B. velutinus	300–600	350	300–600	350	450	6	12·4	1·3	3·3	9	19	11	18
B. sterilis	600–850	650	250–1400	450	825	4·2	8	0·6	2·1	6	13	5	15
B. maximus	380–700	450	320–550	450	510	3·4	5	0·9	1·5	5	8	5	9
B. madritensis	65–550	250	60–130	60	305	5·2	5·6	1·5	2·2	8	9	11	10
B. Schraderi	200–400	400	200–1000	675	600	5	8·8	1·0	1·4	8	14	6	14
B. unioloides	350–500	380	220–350	300	360	4·8	3	1·7	2·4	7	5	6	4
B. racemosus	250–550	360	100–230	200	325	3·2	5·4	0·3	2·1	5	8	4	17
B. commutatus	200–300	220	100–200	150	200	3	6·6	1·1	1·3	5	13	5	14
B. interruptus	360–380	370	0			2·2	0	0·9	0	3	0	3	0
B. arvensis	250–350	300	160–200	180	255	4·4	8·0	0·3	1·2	7	12	5	22
B. canadensis	250–840	600	800–1000	900	625			0·5	2·0			12	27

Columns 2 and 4 are useful checks on column 5, as in the case of the stomata already referred to. Also as before, the numbers in column 3 have only a relative value, as establishing the general fact that the number of hairs on the lower surface is greater than that on the upper, thus reversing the rule for the stomata. There are one or two discrepancies, but I am inclined to regard the results given in column 5 as most reliable.

16. IS THERE ANY RELATION BETWEEN INFECTION AND THE VISIBLE STRUCTURAL FEATURES?

It now remains to see whether any of the structural peculiarities referred to stand in relation to the comparative immunity from the susceptibility of the species or varieties of Bromus examined. In order to test this, I adopted the following argument and method.

If the volume of the chlorophyll-tissue, for instance, is a factor of importance, then the curve obtained by joining the apices of ordinates of lengths proportional to the volumes of the chlorophyll-tissue in the various species, ought to bear some definite relation to the curve obtained by joining ordinates proportional to the percentage of successful infections.

In order to understand the nature of this 'infection-curve,' it is necessary to refer to my previous summary of results[1], from which I take the part referring to *B. mollis* (Table XXV). It will be seen that with spores from *B. mollis* seedlings of the same species (*B. mollis*) were successfully infected 60 out of 85 times—i. e. 70·6 per cent.; whereas *B. secalinus* was infected only 31 out of 61 times—i. e. 50·7 per cent., and *B. maximus* only once out of 74 times—i. e. 1·3 per cent., and so on. It will be noticed how the successful infections with these spores reared on *B. mollis* all group in the *Serrafalcus* sub-genus, the few exceptions (*B. sterilis*, *B. erectus*) not seriously interfering with this statement.

Now, if we join the apices of ordinates proportional to these percentages, we have a graphic representation which

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[1] Proc. Cambridge Philos. Soc., vol. xi, Part V, pp. 323–328.

TABLE XXV.

Summary of results of infection in 843 experiments in which spores from *B. mollis* were used as inoculating material.

Species infected.	*No. of plants.*	*Results + in.*	*Per cent. successful.*
B. erectus	37	1	2·7
B. inermis	32	0	0
B. ciliaris (1)	20	0	0
B. tectorum	21	0	0
B. sterilis	90	4	4·4
B. madritensis	77	0	0
B. maximus	74	1	1·3
B. secalinus	61	31	50·7
B. velutinus	62	35	56·4
B. arvensis	76	28	36·8
B. mollis	85	60	70·6
B. racemosus	56	15	26·8
B. commutatus	45	14	31·1
B. interruptus	49	19	38·8
B. brizaeformis	18	5	27
B. macrostachys	12	4	33
B. unioloides	2	0	0
B. Schraderi (2)	9	0	0
B. canadensis	2	0	0
B. giganteus (3)	1	0	0
B. pratensis (3)	14	0	0

(1) Species needs examining. (2) Synonym of preceding.
(3) Species requires further examination.

I term the 'infection curve.' And just as this is possible for the case given, so also different curves are obtainable for the infections with spores from *B. sterilis*, *B. secalinus*, &c.[1]

On drawing these two curves, the result shows there is no resemblance between them: nor is there any resemblance between the infection curve—as it may be termed—and the curves of the sizes or of the number of stomata, of the sizes and numbers of hairs (Tables XXVI and XXVII), of the area of the leaves (Table XXVIII), or in short the curves of any of the structural factors of the leaf.

In similar comparison of the curves of stomata and of infection, it is obvious at a glance that while spores from *Bromus mollis* infect that species readily, as also they do

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[1] See Proc. Cambridge Phil. Soc., l. c., Tables VI and VII.

B. secalinus and *B. velutinus* with larger stomata, they refuse to infect *B. inermis* with equally large stomata, and only once (out of 74 trials) infected *B. maximus* with far larger ones.

Or, again, if the small size of the stomata were the explanation of the immunity of *B. unioloides* and *B. Schraderi*, how are we to reconcile this with the only partial immunity of *B. brizaeformis*, where they are much smaller?

Similarly, supposing it were suggested that *B. macrostachys* is as readily infected as *B. secalinus* by spores derived from the latter, because the stomata are approximately identical in size and numbers; we have still to explain how it is that *B. inermis*, with equally large and numerous stomata, is immune, as is also *B. maximus* with much larger but fewer stomata.

Or again, spores from *B. sterilis* readily infect *B. madritensis*, which has larger but fewer stomata than the former species. How is it that *B. maximus* is almost immune to these spores, although its stomata are far larger? Is it because they are also fewer? If so, it seems queer that *B. tectorum* should also have proved immune, because its stomata are more numerous than those of *B. madritensis*, and hardly smaller than those of *B. sterilis*. And the results are similar with the other factors. It is useless to reproduce all the curves of the various factors, and it may suffice that I have tried all sorts of combinations and can discover no relations between them and the curves of infection. We are hence driven to conclude that the factors which govern predisposition on the one hand and immunity on the other, are similar to those which govern fertility and sterility of stigmas to pollen, and I have elsewhere[1] shown that parallels between the behaviour of pollen (which is after all a kind of spore) towards the stigma of the receptive plant in cross-breeding, and of these Uredospores towards their host-plants, multiply as we examine them. The importance of all this is, I think, that it justifies the hopes of those who believe that the con-

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[1] Proc. Cambridge Phil. Soc., l. c., pp. 326-328.

TABLE XXVI.

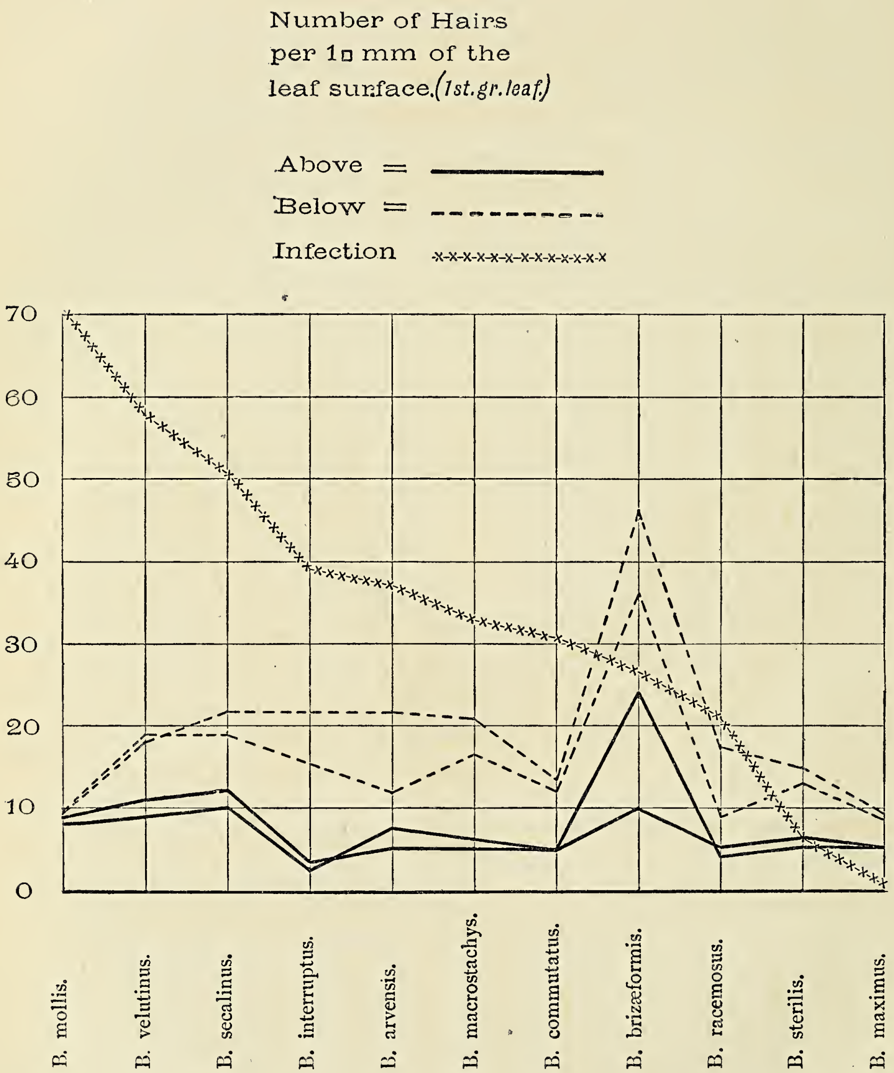
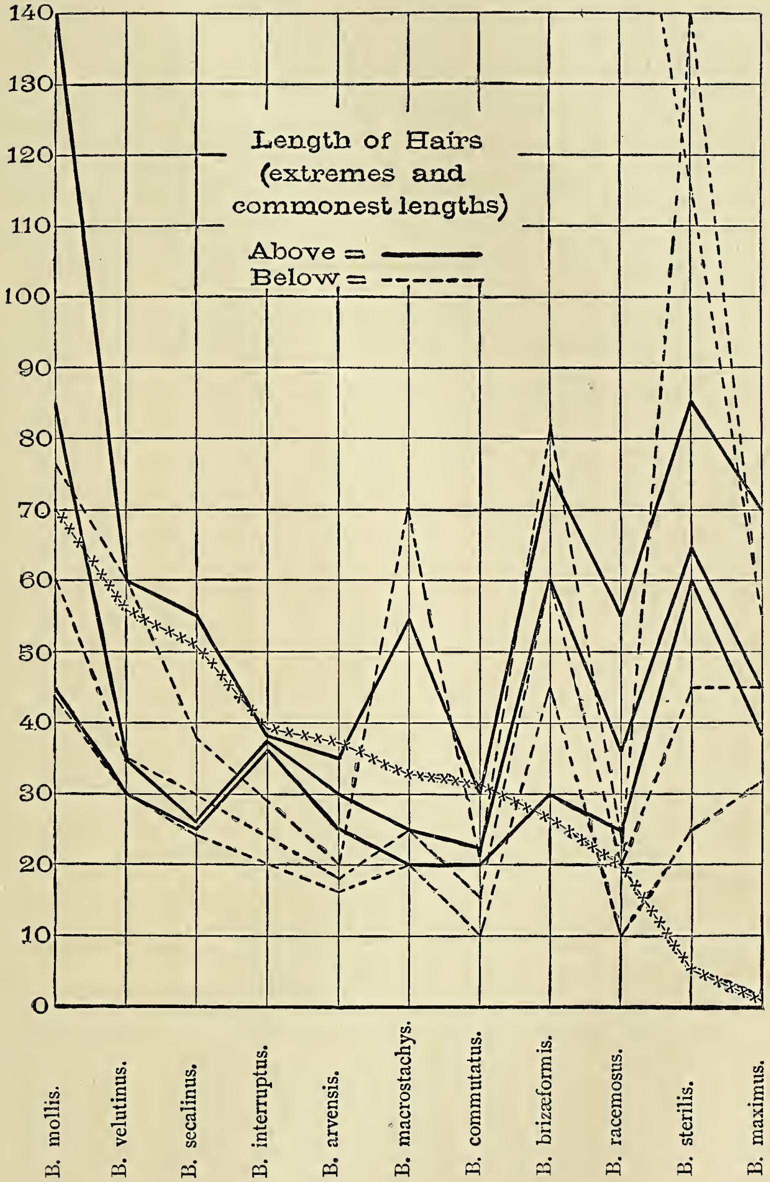

Number of Hairs
per 1□ mm of the
leaf surface.(1st.gr.leaf.)
Above =
Below =
Infection
70
60
50
40
30
20
10
0
B. mollis.
B. velutinus.
B. secalinus.
B. interruptus.
B. arvensis.
B. macrostachys.
B. commutatus.
B. brizæformis.
B. racemosus.
B. sterilis.
B. maximus.

TABLE XXVII.


140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Length of Hairs (extremes and commonest lengths)
Above =
Below =
B. mollis.
B. velutinus.
B. secalinus.
B. interruptus.
B. arvensis.
B. macrostachys.
B. commutatus.
B. brizæformis.
B. racemosus.
B. sterilis.
B. maximus.

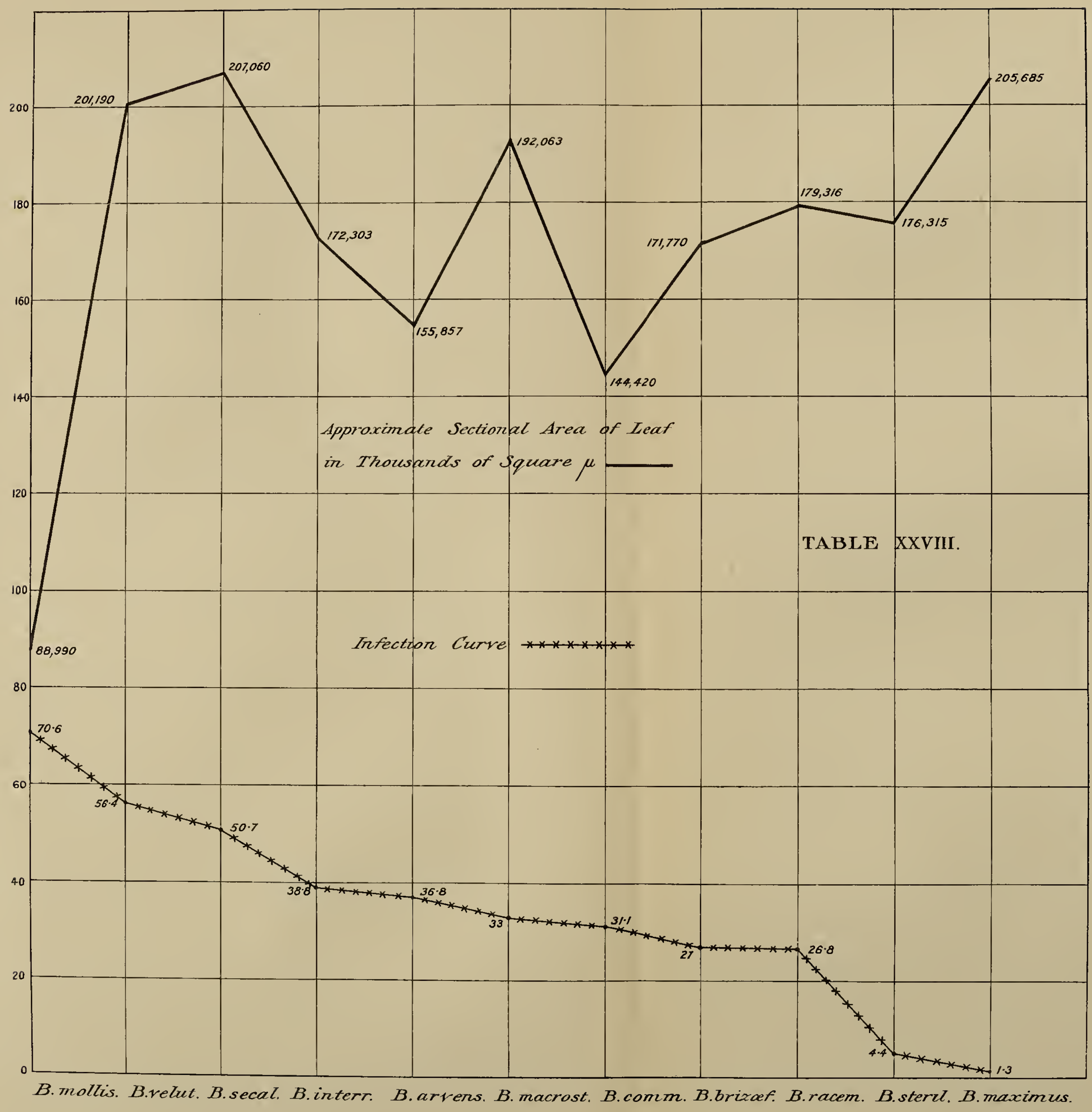


TABLE XXVIII.

University Press, Oxford.

stitution of plants can be so modified by breeding and selection, that disease-resisting varieties should be no more difficult to evolve than varieties which refuse to cross with the pollen of certain other forms. Only, we must not forget that the Fungus is also capable of being bred and selected, and prepotent varieties of spores are just as much realities as prepotent pollen.

On Variation in the Flowers of certain Species of Primula.

BY

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With a Figure in the Text.

MUCH has been written concerning the Primulaceae, which in part is due to the interest taken by botanists in the morphological significance of the pistil, the position of the stamens, and origin of the petals. As regards abnormal flowers, we find that many monstrosities, &c., have been recorded; thus Masters[1] describes cases of dialysis, meiophylly, proliferation, polyphylly, petalody of pistil and stamens, &c.

It does not appear, however, that any detailed observations have been published as to the numerical variations of the different floral parts such as have been carried out in other natural orders, e.g., Burkill[2] on *Stellaria media* and other plants, and Pledge[3] on *Ranunculus repens*.

When this work was commenced some few years ago (1898) it was intended to keep under observation for a number of years one particular species of the genus gathered from

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[1] Masters, Maxwell, Vegetable Teratology. Ray Society, 1869.

[2] Burkill, I. H., On some Variations in the Number of Stamens and Carpels. Journ. Linn. Soc. Bot., vol. xxxi, 1895-7.

[3] Pledge, J. H., Numerical Variation of Parts of *Ranunculus repens*. Nat. Sci., vol. x, 1897, p. 323.

[Annals of Botany, Vol. XVI. No. LXII. June, 1902.]

different localities, in order to ascertain whether there obtained years of maximum and minimum variation, and also to see whether it would be possible to acquire data which would afford any indications as to the laws, if any, which govern variation.

This somewhat ambitious but excellent intention, like so many others, was not carried out, chiefly owing to the lack of time and the writer's attentions being occupied by other branches of botanical science.

But although the original scheme was practically abandoned, still several interesting facts were ascertained: so that it was resolved to tabulate and publish the somewhat fragmentary results in the hope that some interested in this line of research, and having the necessary time at their disposal, might find it possible to carry further the results embodied in this paper.

The plants used were the primrose and cowslip. The majority of the former were collected in the woods, &c., around Stone Street, a small hamlet situated on the Lower Greensand, some four and a half miles east of Sevenoaks in Kent. Flowers were also obtained from the top of Polhill, a few miles east of Knockholt on the North Downs in the same county. The cowslips, the only other species examined in quantity, were gathered in the meadows at the foot of the North Downs, quite close to the village of Kemsing, which is again situated in Kent. Here the soil is argillaceous in character (Gault). It is almost unnecessary to add that the flowers were picked quite indiscriminately; no attempt being made to select those showing variations more than others.

The numerical variations of the outer whorls—calyx, corolla, and androecium—proved disappointing, inasmuch as they lead to no definite conclusion; hence it is proposed merely to draw attention to the more important features as briefly as possible.

Observations on the cowslips only extended over one season (1898), so that it will be as well to deal with this plant first.

Primula veris, Linn., 1898. Of this plant 1,250 flowers were examined, and of these 3·52 °/₀ deviated from the normal type. The majority of abnormal flowers were heteromerous (53·66 °/₀), and it was also seen that the short-styled flowers were more variable than the long-styled. The androecium proved the most aberrant whorl, although the total number of variations only showed a percentage of 2·48. The range of numerical variation in the different whorls was from 4 to 6. The gynoecium was always normal.

It was sometimes noticed that the flowers having parts less than five in number were the youngest in an inflorescence, which corresponds to what Burkill[1] found to obtain in many plants examined by him.

Primula vulgaris, Huds., 1898. The blossoms of this season were less variable than the cowslips, for out of a total of 830, but 2·65 °/₀ were aberrant. Of these variations the majority (75 °/₀) were heteromerous, and the long-styled flowers varied slightly more than the short-styled. The range of numerical variation was the same as in *P. veris*, viz. from 4 to 6, and the individual parts of numerically anomalous whorls of organs were generally above the normal number 5.

The calyx was the most variable whorl, and, as before, the gynoecium was normal throughout.

1899. In the spring of this year 2,483 flowers were examined, of which number 11·3 °/₀ were variable; a much higher proportion than in 1898. The short-styled blossoms varied more than the long-styled by more than 2 °/₀, and it was observed that those flowers collected during the height of the flowering season were the most abnormal. The majority (57·36 °/₀) were heteromerous.

As regards the range of numerical variation, it was found in the flowers of this year to be much wider than in those examined hitherto, being no less than from 3 to 8 in the case of the calyx, 4 to 8 in the corolla, and 4 to 10 in the androecium. In the long-styled flowers, taken by themselves, this range was not so wide, never being more than from 3 to 7. Of the different whorls, the calyx varied more than the

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[1] Loc. cit.

corolla, which in turn was slightly more aberrant than the androecium.

It has been noted that the flowers of *P. vulgaris* examined in the spring of '98 were all normal as regards their pistils. On the other hand, those of this year ('99) showed many interesting abnormalities: these variations, however, were confined to the styles and stigmas, in no cases were any aberrations discovered in the ovary itself.

Dealing with the stigma first; twenty-eight flowers were seen having these organs definitely lobed, while in three cases they were lobed in a more irregular manner. That is, thirty-one variations were found out of a total of over 2,000 (Table I).

TABLE I.

LOBED STIGMAS.

	2-lobed.	*3-lobed.*	*4-lobed.*	*Irregularly lobed.*
Short-styled flowers	3	4	0	2
Long-styled flowers	18	1	2[1]	1

TABLE II.

STYLES.

No. of styles.	2	3	4
Short-styled	0	1	0
Long-styled	6[2]	3	1

The stigmas lobed in a definite manner were constricted into two, three, or four lobes, the exact proportion of each kind being indicated in the accompanying Table (I), and illustrated by Nos. 1 and 2 (Fig. 20).

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[1] One slightly so.

[2] Of these one had two flat stigmas and another one stigma longer than the other.

Mac Nab[1] has recorded a bilobed stigma. In describing a specimen, he states: 'The whole of the flower is perfectly normal, except that the stigma is markedly bilobed. The ovary does not seem to consist of more carpels than usual.' The flowers, with the anomalous stigmas, had but a single style; a certain number of blossoms, however, were observed which possessed more than one; thus there were seen six cases of two styles, four of three, and one of four (Table II). It was often noticed that when the number of styles was more than one, these organs were shorter than is normally the case (Nos. 3 and 4, Fig. 20). It may also be stated that in cultivated plants of *P. floribunda*, a comparatively high proportion of flowers examined showed lobed stigmas; but in all cases a single style was present. It is also worthy of note that in these instances of lobed stigmas, excepting one flower in which the number of parts was normal throughout, there was an increase in the number of the members of each whorl. The exception had a two-lobed stigma, but the calyx, corolla, and androecium each had five component parts. Of the other cases the following held:—C_9 Co_9 An_{10} stigma two-lobed, C_6 Co_6 An_6 stigma two-lobed, C_6 Co_6 An_6 stigma irregularly lobed and somewhat peltate.

Comparing these numbers with what obtained in those flowers of *P. vulgaris* having lobed stigmas, it is found that in the latter plant the majority of such flowers had their normal number of sepals, &c.; never was there a marked increase as in the case of *P. floribunda*.

It is true that the proportion of these variations in the style and stigma is very low: they are of interest, however, when the discussion as to the number of carpels present in the ovary is borne in mind.

It might be argued from these abnormalities that the ovary is composed of more than one carpel: but it has to be borne in mind that teratological evidence, taken by itself and without reference to the facts of development, is, according to

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[1] Mac Nab, On some Abnormal Flowers of Primula. Proc. Roy. Dublin Soc., vol. ii, 1878–80.

many botanists, somewhat dangerous and apt to be misleading. The published evidence as to the development of the pistil may or may not lead to the conclusion that only one carpel is present.

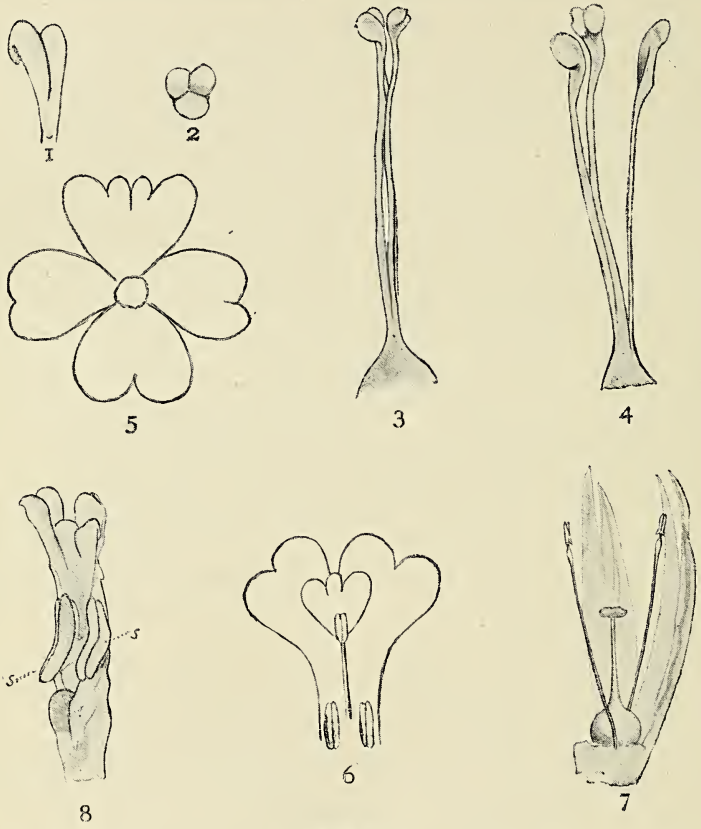

Fig. 20.

All the illustrations are of *Primula vulgaris*. 1. Side view of a two-lobed stigma. 2. A three-lobed stigma viewed from above. 3. Part of a pistil showing two styles. 4. An ovary with three styles. 5. A flower with four petals, one of which is doubly lobed. 6. A blossom having a small petal more internally situated than the others, and showing one stamen carried up to the corolla throat. 7. Dissection of a flower with two free stamens inserted on the receptacle. 8. Pistil showing a curiously lobed stigma with two adnate stamens (*s*).

Masters[1], writing of *Primula*, states that 'On its (the re-

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[1] Masters, On some Points in the Morphology of the Primulaceae. Trans. Linn. Soc., Ser. 2, Bot., vol. i, 1877.

ceptacle's) raised edge five small tubercles sometimes appear simultaneously, which are the carpels. These five tubercles are gradually raised from below by the lengthening of the receptacle in a tubular manner, so that we have soon a flask-shaped pistil with its narrow neck and open mouth.' On the other hand, in a footnote appear the following remarks: 'Quite as frequently, as far as I have observed in *Lysimachia* and *Primula*, the pistil originates as a ring, which grows upward from beneath so as to form a tube, upon whose edge the five tubercles are not formed till quite late in development, and in some cases, especially in monstrous flowers, not at all.'

Pfeffer[1] states that in *Glaux* the ovary raises itself as an annular wall of uniform height, as is usually the case in *Lysimachia quadrifolia*. As regards the latter plant, he observes that sometimes one sees three, rarely four or five, portions of the wall project as humps. This occasionally appears still more evidently in *Primula elatior* and *P. chinensis*. From these facts he concludes that one has here to do with five foliar organs alternating with the stamens.

No other author, as far as has been seen, makes mention of the ovary arising from five protuberances ultimately fusing to form the characteristic ovary. Thus Duchartre[2] states: 'Vers le moment où le bourrelet corollin se montre à la base des jeunes anthères, l'organe femelle commence à manifester son apparition. La partie supérieure et centrale de la fleur primitive, celle qu'entoure l'androcée et qui possède une surface assez large, commence à se relever, dans toute sa circonférence, d'un leger bourrelet circulaire continu; ce bourrelet circonscrit un petit enfoncement dont le fond ne reste pas uni ni creux, mais se bosselle lui-même et un petit mamelon arrondi qui occupe le centre de toute la fleur.'

Payer[3] writing about the development of *Samolus Valerandi*

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[1] Pfeffer, W., Zur Blüthenentwicklung der Primulaceen und Ampelideen. Pringsheim's Jahrb. f. wiss. Bot, vol. viii, p. 194.

[2] Duchartre, Observations sur l'organogénie de la fleur et en particulier de l'ovaire chez les plantes à placenta central libre. Ann. des Sci. Nat., Bot., 3^{e} sér., tom. ii, 1844.

[3] Payer, Traité d'Organogénie Comparée de la Fleur. Paris, 1857.

makes the following statements: 'Peu de temps après la naissance des étamines, le centre de la fleur se déprime et il en résulte une petite excavation, qui est l'origine du pistil. Cette petite excavation n'occupe pas tout le centre de la fleur; il y a entre elle et la base des étamines une sorte de chemin de halage sur lequel on voit bientôt poindre un bourrelet circulaire qui grandit rapidement, et forme une sorte de tuyau de cheminée au-dessous de l'excavation qui, de son côté, est devenue de plus en plus profonde.'

My own observations show that in the plants examined[1] the ovary arises invariably as a ring of tissue, and nothing has been seen either in *Primula* or the other plants which could be interpreted as five carpels. Once only, in *Anagallis arvensis*, Linn., the top of a young ovary was seen to be somewhat crenated.

Up to the present, then, it appears from the facts of development that the tubular upgrowth is either a single carpel, or, if it represents a number of carpels, the rudiments are generally indistinguishable owing to the simultaneous upgrowth of the tissue between them. On the other hand, there are many points in favour of the ovary being multicarpellary in nature.

The increased number of styles and stigmas tends to show that there are present more than one carpel, and then the dehiscence of the capsules of many plants of the Order into five or ten teeth points in the same direction, or of the structure in question being derived phylogenetically from one with five carpels.

Again, if the other Orders of the Cohort to which the Primulaceae belong are examined, it is found that the Plumbaginaceae are characterized by the possession of five styles, which is in favour of the ovary of Primulaceae being composed of five carpels.

The Myrsinaceae having but a single style do not afford evidence of a definite character.

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[1] *Primula veris*, Linn., *Hottonia palustris*, Linn., *Glaux maritima*, Linn., *Anagallis arvensis*, Linn., and *Samolus Valerandi*, Linn.

Variations other than numerical. It was only to be expected that abnormalities, other than have been considered up to the present, would be seen during the examination of a large number of flowers.

It is proposed to mention them briefly now.

Primula veris, Linn. No striking monstrosities were observed in this plant. A few flowers were seen in which one member of a whorl, either calyx or corolla, was smaller than its fellows. More frequently the filament of a stamen was divided into a Y-shaped structure, each branch bearing an anther.

Primula vulgaris, Huds. In 1898 the only other abnormalities seen were as follows. Single sepals or petals were sometimes (five instances) smaller than the others, and in one case the petals of a flower were in three distinct sizes.

The style varied much in length, thus the stigma in long-styled flowers was sometimes protruded out of the corolla tube, and sometimes was only just above the stamens. In the short-styled flowers two instances were noted in which the stigma was about level with the stamens.

1899. Monstrosities were much commoner this year. The corolla frequently had a petal lobed in the manner illustrated in No. 5) Fig. 20). The exact number of such instances was six, three cases occurring in the long-styled flowers, and three in the short. Of the former two specimens possessed six petals and one five; and of the latter one corolla had four petals, one five, and the other six.

Two flowers were seen in which one petal was inserted in front of another. No. 6 illustrates a similar peculiarity, but here the small and more internally placed petal was alternate: in this flower (No. 6, Fig 20) there was a further abnormality consisting in one stamen being carried up to the irregularly placed petal on a filament partly adnate to the corolla tube, thus forming a rough transition between the long and short-styled flowers. (It will be seen from the figure that the flower was of the long-styled type.) This particular blossom possessed six sepals, the numbers of the other parts were normal. The other instance of superposed petals showed no peculiarity in its androecium, and had five sepals, eight petals, and seven stamens.

No. 7 (Fig. 20) illustrates a portion of a very interesting short-styled flower which had eight sepals, eight petals, and ten stamens, eight of which were situated at the throat of the corolla and the other two inserted upon the receptacle. These two had long free filaments, so that their anthers were carried up to the level of the others.

A parallel instance to this was seen in another flower which had the normal number of sepals and petals but seven stamens, two of which were inserted lower down on the corolla tube and had long filaments. The pistil of this flower also was very abnormal. It was of a curious shape, broad and short; the stigma was lobed and the style was partly staminal, two very pronounced stamens being sessile upon it.

This is illustrated in No. 8.

The remaining abnormalities were less interesting, and consisted of sepals and petals being of an abnormal size, thus making the flower zygomorphic. Branched filaments of stamens were not uncommon, twenty instances being noted. The styles of some flowers were longer or shorter than is normally the case in the manner already pointed out above.

The Mechanism of Stomata.

BY

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Stanford University, California.

With Plate XIII.

THE movements of stomata have been familiar to botanists for more than a century. From all points of view, anatomical and physiological, the stomata have received more constant and lasting attention probably than any other single vegetative structure in the plant. And yet recent literature on the subject is most contradictory, not only as to the mechanism of their movements, but even as to the conditions which influence their opening and closing. On the theme proper of this paper—the relation between the structure of stomata and their movements—our knowledge is incomplete but harmonious, and I am therefore happily spared the necessity of controversy. But as this takes for granted the occurrence of movement under certain conditions, we must first determine what these conditions are, and how, aside from the structure of the stomata, the conditions are met.

The earliest attempt at a solution of these problems seems to have been that of von Mohl[1], who described the thickening of the walls of what he regarded as a typical stoma, and

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[1] H. v. Mohl, Welche Ursachen bewirken die Erweiterung und Verengung der Spaltöffnungen? Bot. Zeit., xiv (1856), 697, 713.

[Annals of Botany, Vol. XVI. No. LXII. June, 1902.

added (p. 702): 'Diese ungleichförmige Wanddicke muss auf die Veränderungen dieser Zellen, wenn sie Wasser endosmotisch einsaugen oder abgeben, von Einfluss sein.' He determined that stomata freed from pressure of neighbouring cells opened in light and closed in darkness; but did not believe that stomata on uninjured leaves moved likewise by their own activity. Passing over Müller's[1] work, most of which has not stood the test of time, the next important contribution is Schwendener's[2], which described in detail the thickening of the walls of several stomata, and showed clearly the relation of their structure to their movements: the structure being constantly such as to permit an increase in turgescence of the guard-cells to open the pore; and the movements of the guard-cells being made more independent by thinner parts of the outer wall, next to the guard-cells, acting as hinges.

Leitgeb[3], as von Mohl had less emphatically done, ascribed greater activity to the surrounding, and less to the guard-cells; his view being that if stomata closed at night the guard-cells were forced together by the increasing turgescence of the subsidiary or epidermal cells. But Leitgeb found stomata shut on brightly illuminated plants which had transpired freely, when the pressure against the guard-cells was presumably not greatest; and also observed a disappearance of solid matter in guard-cells before the pore opened. Schaefer[4] showed conclusively for certain stomata (*Amaryllis*, *Aconitum*, &c.) that their movements were independent of the surrounding cells; for they closed in darkness and remained closed even if isolated from other cells; and opened in a saturated atmosphere, when the pressure of the neighbouring cells must

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[1] N. J. C. Müller, Die Anatomie und Mechanik der Spaltöffnungen, III. Jahrb. f. wiss. Bot., viii (1872), 75–116.

[2] S. Schwendener, Ueber Bau und Mechanik der Spaltöffnungen. Monatsber. d. Akad. d. Wiss. zu Berlin, 1881, p. 833.

[3] H. Leitgeb, Beiträge zur Physiologie der Spaltöffnungsapparate. Mitth. Bot. Inst. Graz, i (1886), 123–184.

[4] R. Schaefer, Ueber den Einfluss des Turgors der Epidermiszellen auf die Function des Spaltöffnungsapparates. Jahrb. f. wiss. Bot., xix. (1888), 178–205. Berlin Dissertation.

have been at its maximum. As my own experiments will show, stomata open in bright light when under water. Von Mohl's assumption, that light influenced the stomata by photosynthetically increasing the amount of osmotically active material in the guard-cells, has usually been concurred in by those who ascribed to them the chief activity in their movements. Schellenberg[1] maintains that absence of CO_2 suspends the action of light; but Darwin's[2] results are the direct opposite.

As to the factors which directly affect stomata, it is generally agreed that abundant moisture, in the plant and in the air, tends to open the pore. When the plant transpires too actively the stomata begin to close, before the wilting is discernible (Leitgeb, Darwin). Von Mohl's statement, that if the epidermis of most plants, with the stomata open, be mounted in water the stomata promptly close, is not true of all with motile stomata (for instance, not of *Medeola*, nor, as von Mohl saw, of many Orchids). When it occurs it is because the structure of the epidermal cells lets them take up water more rapidly than the guard-cells can, and after a time the pore reopens (Schaefer, l. c., p. 189), with sections thick enough to include some of the mesophyll, so that the water does not come into immediate contact with the inner wall of the epidermis, this preliminary closing is prevented. According to Müller, Kohl[3], and Darwin, closed stomata are opened by a rise in temperature; Schwendener could not substantiate this, and Leitgeb found it true in light but not in darkness.

The influence of light is to open the pore, which tends to close in darkness, and the closure at night has sometimes been regarded as wellnigh universal. The most generally recognized exceptions to this rule are halophytes, hydro-

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[1] H. Schellenberg, Beiträge zur Kenntniss von Bau und Function der Spaltöffnungen. Bot. Zeit., liv (1896), 169–185.

[2] F. Darwin, Observations on Stomata. Proceedings of the Royal Society, lxiii. (1898), 413–417. Philos. Trans., Royal Soc., cxc (1898), 531–621: pp. 608–610.

[3] F. G. Kohl, Zur Mechanik der Spaltöffnungsbewegungen. Bot. Beibl. z. Leopoldina, 1895.

phytes, and plants with nyctitropic leaves (Stahl[1], Darwin). The stomata of such hydrophytes as have them must, in general, be regarded as at least slightly motile (Leitgeb, Haberland[2], Darwin); Kohl and Schellenberg would regard most of them as entirely closing the pore. Stahl[3] is the most positive supporter of the view that even among terrestrial plants nocturnal closure is no general rule. For the study of transpiration, his method—testing for escaping water—is certainly better than direct microscopic examination of the stomata. But when the stoma is itself the subject of study, direct observation is the only conclusive method; and comparatively few stomata have as yet been *seen* open at night. We owe these largely to Leitgeb. I shall assume then that most stomata are motile, and that the pore is more or less completely closed in darkness.

Greater precision than has hitherto been observed in the use of terms is prerequisite to an analysis of the mechanism of the movements. Turgescence and turgor have been used in this connexion indiscriminately for the osmotic pressure which the dissolved material in the cell-sap can exert, and for the condition of turgidity. Restricting turgescence to the latter sense, let us distinguish the former as turgor; the word is already most familiar in that use—to indicate the osmotic power of the cell-sap, usually measured by plasmolysis. The turgor in the guard-cells must vary, being increased by light[4] or heat. The turgescence depends upon the turgor and also upon the available supply of water. In direct sunlight and proper warmth, in spite of the increasing turgor, the evaporation of water may lessen the turgescence of the guard-cells,

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[1] E. Stahl, Ueber den Pflanzenschlaf und verwandte Erscheinungen. Bot. Zeit., lv (1897), 71–109.

[2] G. Haberlandt, Zur Kenntniss des Spaltöffnungsapparates. Flora, lxx (1887), 97–109.

[3] E. Stahl, Einige Versuche über Transpiration und Assimilation. Bot. Zeit., liii (1894), 117–145.

[4] This assumed variation in turgor needs careful study: a difference in turgor by day and by night has never been measured. Nor are the osmotically active substances known. Kohl tells us that the action of diastase opens the pore; but diastase, like sugar, is unknown in guard-cells.

causing the pore to close. The turgescence of the subsidiary and other epidermal cells must vary, but there is no reason to suspect that their turgor does so, except inappreciably with the temperature.

To distinguish between the entire opening between the guard-cells and the narrowest part of this opening, where it closes, I have decided, reluctantly, to call the former the rift, and the latter the pore. To use 'pore' for one and 'pore proper' for the other is quite unsatisfactory. 'Centralspalte' serves for the pore, when it *is* central, but it forced Haberlandt[1] to the negative description of the stoma of *Polytrichum* as 'ohne Centralspalte,' and no English word will translate it.

Hinges in the outer wall, next the guard-cell, were recognized by Schwendener (1881) as necessary to permit the lateral movement of the guard-cell. A similar thin line on the inner wall is called an inner hinge (Haberlandt, 1887). Besides these lateral hinges, which may extend a part or the whole of the side of the guard-cell, Westermaier[2] recognizes similar thin places at the ends as polar hinges. In all of these places it is most necessary, from the mechanical standpoint, to distinguish between mere thin lines, which will bend but not give way, and therefore are fixed axes of revolution—real hinges—and broad bands of thin wall, often the entire wall of the subsidiary cells, which permit movement by the guard-cells, but which are not fixed axes deserving to be called hinges at all. The difference in the movements permitted by the hinge and by the thin band is obvious. More details as to the hinges and their relation to the mechanism of stomata will accompany the treatment of the stomata themselves.

The pressure that may be exerted against stomata is of two very different kinds. That of the neighbouring cells,

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[1] G. Haberlandt, Beiträge zur Anatomie und Physiologie der Laubmoose. Jahrb. f. wiss. Bot., xvii (1886), 359–498.

[2] Max Westermaier, Ueber Spaltöffnungen und ihre Nebenapparate. Schwendener Festschrift, 1889, p. 63–80.

increasing with their turgescence, cannot be guarded against by a hinge, for the latter must permit movement in one direction as well as in the other; this is true even in the possible case that the wall acts as a spring, because any movement is from a temporary state of equilibrium, disturbable in either way, else the motility of the stoma is interfered with. In many leaves, chiefly succulents, the stomata would be subjected to much greater, and probably irresistible pressure resulting from shrinking of the entire leaves with *loss* of turgescence; but this pressure would be exerted against the guard-cells by the walls, and they (the guard-cells) are protected against it by thin bands[1]. Without such protection the stomata would be forced to shut, as probably occurs in the instance of *Chrysoma*[2], whose cross-section shows only a hinge.

In stomata whose outline changes with their movements, and only in these, the turgescence of the contiguous cells must be a factor in determining the state of equilibrium, open, closed, or intermediate. But because the pore closes with excessive transpiration when turgescence in the leaf is least, because the contents of the guard-cells furnish a clue to changes in turgor which is wanting in the neighbouring cells, because some stomata do not change their outline (surface view) in their movements, because isolated stomata usually move like those on uninjured leaves, and because the forms and structures of the guard-cells are explicable and intelligible on this ground only, the conclusion cannot be escaped that the turgescence of the neighbouring cells is a passive factor, the active one being, as Schwendener and his students have maintained, the turgescence of the guard-cells.

We are now ready to turn to a study of the structural devices by which an increase in the turgescence of the guard-cells accomplishes the opening of the pore. The types

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[1] W. Benecke, Die Nebenzellen der Spaltöffnungen. Bot. Zeit. (1892), 521, 537, 553, 569, 585, 601.

[2] F. E. Lloyd, Some points in the anatomy of *Chrysoma pauciflosculosa*. Bull. Torr. Bot. Club., xxviii (1901), 445–450.

already familiar—those of *Amaryllis*, *Helleborus* and the Gramineae[1], described by Schwendener, Haberlandt's *Mnium* type, and the peculiar case of *Azolla* as explained by Schaefer—will be taken up in appropriate places in a sequence intended to show their relations to one another and to the various other forms to be described.

When we say that the guard-cell becomes more turgescent we mean that its volume is forcibly increased. As the cell begins to take up water, the pressure against all units of area of the wall is the same. Therefore the greater walls sustain the greater pressure; or in other words, the greatest pressure is exerted in the direction of the least diameter of the cell. To bend a wall requires less pressure than to stretch it, because in bending only one of its faces is stretched. If, then, the wall of an anisodiametric guard-cell be reasonably thin throughout, or in large part, an increase in turgescence will be accommodated without any stretching of the wall, by an equalization of the diameters, the cell becoming more nearly spherical. Stomata meeting these conditions should be regarded as structurally simple because the lack of great local thickening leaves them in so far like cells of the epidermal tissue. We will consider first stomata of little depth, which enlarge, with increasing turgescence, at right angles to the surface of the leaf.

MEDEOLA VIRGINICA, L.

The stomata of *Medeola* are irregularly scattered over both surfaces of the leaves. The epidermal cells are very large, with remarkably sinuate walls. The stomata are likewise large, of rather irregular outline, usually not quite as wide as long, though occasionally wider, as in Fig. 1. The very obtuse angles making the irregularity seen in surface view mark either the points of connexion with the stoma of the walls between the epidermal cells, or more often peculiar outgrowths or folds of the wall into the lumen of the epidermal

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[1] S. Schwendener, Die Spaltöffnungen der Gramineen und Cyperaceen. Sitzber. Berl. Akad. Wiss., 1889, i, 65–77.

cell. Such folds occur only where the cells are in contact with stomata, and more often from the sides of the latter. The folds frequently leave what appear to be intercellular spaces next the guard-cells or in the end of the fold: I have been unable to determine the extent of these spaces in cross-section, even with serial sections cut in paraffine, but they certainly do not pass the external wall. In cross-section (Fig. 2) the stomata are conspicuously shallow. The walls are equally thin throughout, except for a narrow ridge of entrance and a place which cannot nearly always be detected, representing the ridge of exit. In very thin sections it appears that the lumen projects somewhat toward the ridge of entrance.

To study the changes in guard-cells with variations in the width of the pore, I cut surface sections of the leaf with the razor. Such sections keep the stomata subject to any tensions the underlying mesophyll may exert upon it, directly or indirectly; and spare them the violence inflicted by stripping the epidermis off alone. The leaf of *Medeola* is so spongy throughout and the stomata are so large that a little less accuracy in measurement is the only objection to studying them in place. Their appearance and behaviour are exactly the same in the sections. This is not necessarily true of all stomata, but it helps me to believe that the objections of Benecke and Kohl to work done with sections are not practically important. At any rate, on plants where it cannot be determined that there is or is not a difference it is because they cannot be studied in place, so that resort to sections, when one would measure all dimensions, is compulsory. The sections were made from leaves in bright diffuse light. They were mounted in water, drawn very carefully with a camera lucida, closed by running glycerine under the cover, and drawn again: the drawings were measured. All measurements are stated in mikrons. Even approximately accurate measurements of depth, by focussing with the micrometer screw adjustment as is feasible with many stomata, are impossible with *Medeola* for want of marks to focus on. And I was unable to make satisfactory use of Schellenberg's method, using thick cross-sections. It is very easy to make certain that there is a decrease in depth when the pore closes, but not to measure it. The dimensions determined were:—

	I.		II.	
	Open.	Closed.	Open.	Closed.
Length of stoma	62	62	59	59
Width of stoma	46	46	47·5	47·5
Width of guard-cell	20	22 +	21	23 +
Width of pore	6	1·5	5 +	1
Width of outer vestibule . .	11	10		

The pore of most of the stomata does not quite close: so transpiration through the stoma must take place at night. Still it is a motile stoma the width of whose pore varies more than 4 μ. The length and width of the entire stoma do not change. But the closure of the pore is effected entirely by a flattening out of the guard-cells. In this process the outer vestibule is narrowed; and, as may be seen on sections viewed from within the leaf, the lines representing ridges of exit move nearer together. The whole process when the pore opens is therefore a becoming round of each guard-cell, in which all parts of the wall except the very narrow back seem to be equally concerned.

Since the pore opens at most only as much as the guard-cells become narrower—the dorsal wall being subject not to a push but to a pull from the guard-cell—it is essential that this wall be quite rigid. Though the walls are thin, this is accomplished by the outgrowths already described, which are therefore a most important feature of the apparatus. The rigidity of the ends is insured in part by the wall between the guard-cells, and by the walls between the epidermal cells, which strike the guard-cells irregularly, and in part by folds of the wall, which, however, are of much less frequent occurrence here than on the dorsal walls. The rigidity of the ends seems more essential to stomata of some other mechanical types than to these, and will be found provided for in various ways. But reinforcement of the dorsal wall is a want peculiar to stomata of fixed outline. Solereder[1] describes what I take for a similar peculiarity of the wall of *Erodium cicutarium* and *Geranium Londesii*, figuring the latter. On California material of *E. cicutarium* however I find no such structure. The stomata of *Pyrola secunda*, L., bear a superficial resemblance, but the mechanism is altogether different. Linsbauer[2] describes and figures what seems to be the same structure on *Lycopodium complanatum*, L., var. *thyoides*, H. B. K. It is not present on our American *L. complanatum*, the dorsal wall of whose guard cells is too thick to require reinforcement. Leitgeb (l. c.) describes projections from the wall into the lumen of the guard-cell, of *Galtonia* and some other plants.

It may be of interest to add to this account of the stoma of *Medeola* that while only a part of the guard-cells show plasmolysis in 4 per cent. KNO_3 (tested during day), the pore begins to narrow in 1 per cent., and in 1·5 per cent. closes entirely if it does so at all.

The nearest approach to the stoma of *Medeola* hitherto described is that of

MNIUM CUSPIDATUM,

made familiar by Haberlandt[3]. The *Mnium* stoma approximates mechanically that of *Medeola*, agreeing in that the total area is constant, the pore opening with an increase in the depth of the guard-cells: but it falls short of the type, as Haberlandt's measurements and diagram show, in that the outer (upper) wall is rigid, so that the width of the anterior vestibule is fixed, the movement being executed entirely by the ventral and inner walls.

The stoma of

FUNARIA HYGROMETRICA

differs from that of *Medeola* to the same extent as does that of *Mnium*, but in this case the inner wall is rigid (Fig. 3),

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[1] H. Solereder, Systematische Anatomie d. Dicotyledonen. Stuttg., 1898–9, p. 193.

[2] K. Linsbauer, Beiträge zur vergleichenden Anatomie einiger tropischen Lycopodien. Sitzungsber. d. k. Acad. d. Wiss. Wien, cvii. i (1898), 995.

[3] L. c., 1886: Physiol. Pflanzenanat., 2nd ed., p. 390.

leaving the movement to be performed by the ventral and outer walls. The closure is incomplete, and is effected about equally by the central part of the ventral wall and by the ridge of entrance. I measured the pore from ridge to ridge. These measurements were made on a rather small stoma.

	Open.	Closed.
Length of stoma	45	45
Width of stoma	35	35
Width of pore	5	3
Depth of guard-cell	13·7	8·4

The chief peculiarity of this stoma, as is well known[1], consists in the partial resorption of the wall between the guard-cells, leaving them in open contact at both ends of the rift. As Haberlandt pointed out (l. c. p. 465), and direct observation shows, this does not interfere with the mechanism of the stoma. As practically all stomata are symmetrical both shut and open, the variations in turgescence must be the same in both guard-cells. So far as movements are regulated by variations in the turgescence of the guard-cells alone, it can therefore make absolutely no difference in their movements whether or not the guard-cells communicate.

It is surprising that the relation between the shape of the stoma in surface view and the mechanism should hitherto have been overlooked. In those that we have been considering, the width of the guard-cells was necessarily in considerable excess over the depth. The length was limited because any possible variation in volume at the ends is wasted, and so interferes with the sensitiveness of the stoma. For these reasons, stomata with this mechanism are conspicuously broad: the limit to the ratio of breadth to length is fixed by the danger that the bulging of the outer and inner walls should be interfered with by the end walls. There are a vast number of stomata so shaped that the depth increases with

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[1] W. Ph. Schimper, Recherches anatomiques et morphologiques sur les mousses, Strassburg, 1848; Haberlandt, l. c., 1886. Similar stomata occur on various other mosses.

an increase in turgescence; and so long as the total width of the stoma does not decrease, the increase in depth contributes to the opening of the pore. But there are comparatively few whose pore is opened by this factor alone. In many stomata of the types next to be considered there is some increase in depth, but it is not considerable and may be neglected in describing them.

SAGITTARIA VARIABILIS, ENGELM (Figs. 5, 6).

The stoma of *Sagittaria* is conspicuously narrow. The one drawn is a fair specimen; the ratio of width to length is 1 : 2·6. Looking at the stoma as a whole, which I have sought to justify by the discussion in connexion with *Funaria*, it is evident that with increasing turgescence this stoma would widen, and if possible shorten. In cross-section it is seen that closure is effected by the middle of the ventral wall and by the ridge of entrance. If the guard-cell were to be regarded as composed of two halves, one of them having thick, the other thin walls, the halves would be an outer and an inner, rather than a ventral and a dorsal. If now the entire stoma widens as its turgescence increases, the outer wall, instead of stretching, will draw back the sides of the pore, opening it. While the wall between the guard-cells does not prevent them from acting as if it were not present when the action depends on excess of length over breadth, it does, by refusing to stretch so long as an increasing volume can be accommodated more easily by a change in shape of the stoma, make it necessary to consider the guard-cells individually with respect to depth: they are deeper than wide. A limited shortening of the stoma is possible without compressing or distorting this wall, from the shortening of the rift as it widens. Schwendener (l. c. p. 845) says the outer vestibule of the stoma of *Amaryllis* shortens in widening; if this does not shorten the entire apparatus, the wall between the guard-cells must be singularly elastic. Leitgeb reports a considerable shortening of the stoma as it widens. Schaeffer (l. c. pp. 199–204) has justified the assumption that the presence of this wall is inessential, and spared me the obligation to give statistics in this case of *Sagittaria* by making an apparatus representing a stoma of

AZOLLA CAROLINIANA

on the same mechanical principles, except that it had corners which were withdrawn as the sides bulged out. It is obvious that only a widening of the middle part of the stoma will result in opening the pore. An increase in the width of the ends would be disadvantageous, and the thick walls at the ends of the guard-cells of *Sagittaria*, as compared with their other walls, may be construed as to prevent this. The stoma of *Canna* has the ridges a little more thickened than those of *Sagittaria*: according to Weiss[1], its ratio of breadth to length is 1 : 3·49. His table contains three others more slender than that of *Sagittaria*, but I cannot speak for their mechanism. The ratio of axes of the stoma of *Luzula campestris* is 1 : 2·84. It and that of *Lilium superbum* represent a transition to the type of

AMARYLLIS.

In the stomata hitherto considered some stretching of the walls was possible, and in *Sagittaria* undoubtedly occurred. In the type to which we have now come, the stretching of the dorsal wall is the most conspicuous feature. I can add nothing to Schwendener's exposition of its mechanism (l. c. 1881). The stomata of this type are broader than that of *Lilium superbum*, deep, usually large, and freely motile. *Amaryllis formosissima* (Schwendener's subject) is stated by Weiss to have the ratio of breadth to length 1 : 0·93, it being the broadest stoma in his table; but his material must have been unusual in that respect. The thickening of the wall of the guard-cell is almost confined to the angles of the ventral face, so that with increasing turgescence the dorsal wall alone will be stretched and become more convex, drawing open the pore as in the case of *Sagittaria*. The stoma

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[1] A. Weiss, Untersuchungen über die Grössen- und Zahlenverhältnisse der Spaltöffnungen. Jahrb. f. wiss. Bot., iv, 196.

of *Smilax glauca*, Walt. (Figs. 7, 8), represents this type very well. As is true of *Amaryllis*, the dorsal wall is so thin that it readily collapses in glycerine[1]. The stoma of the stem of *Polygonum sagittatum*, L. (Fig. 15), also belongs here; the presence of a thin outer wall on the adjoining cell, instead of a thick wall with a hinge, makes the stoma more freely motile. The stomata of *Dracaena* sp. and of *Euonymus atropurpureus*, Jacq. (Fig. 10) are also of this type, in that the thickening is largely confined to the ventral half of the guard-cells, but the thickening is so excessive that motility is comparatively limited.

A great number of stomata combine the features of the types of *Medeola* and *Amaryllis*, so that in opening the pore the depth increases and at least a part of the dorsal wall becomes more convex. Most commonly the inner part of the stoma executes the movement, the outer walls moving little if at all. These are features of the type of

HELLEBORUS,

whose mechanism has also been fully explained by Schwendener (l. c. 1881, pp. 856-7). The stoma of *Aplectrum hyemale*, Nutt. (Fig. 11), represents this type, which is most familiar because, though one of the most complicated, it is used in various general texts as a plan from which to explain the mechanism of stomata in general. It differs most conspicuously from *Amaryllis* in that the entire inner wall, as seen in median cross-section, is strongly thickened, so that it will neither stretch nor bend. The dorsal is thin, somewhat convex, and oblique, slanting in and toward the pore. The greater diameter of the lumen—not necessarily of the entire cell—as seen in cross-section is parallel to the surface: accordingly with increasing turgescence the greatest pressure is exerted to deepen the cell. This can be done at first without stretching any wall, but merely by bending them where they are thin, if the inner wall moves backward until

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[1] Not however, in my experience, until it has ceased to be stretched; cf. Leitgeb, p. 152.

the dorsal wall is straighter and perpendicular to the surface: as the inner wall moves backward and inward the pore of course opens. The inner wall of the subsidiary or other contiguous cell is usually thin throughout, and attached to the inner dorsal angle of the guard-cell, more or less at a right angle to the surface. This provides that it shall offer no considerable resistance to the movement of the guard-cell; and also, as Schwendener (1889) observes with reference to the Gramineae, by giving the deep subsidiary cell a free and elastic inner wall, removes its turgescence as an obstacle to the movement of the guard-cell (cf. Fig. 55).

It has usually been assumed that a hinge belonged to the wall of the subsidiary cell. Haberlandt (l. c., 1886, p. 466) says that a hinge is often present on the outer wall of the guard-cell of Mosses, near the dorsal side; but the rest of the description—walls inequally thickened, thicker ventrally, and back walls more or less thin—fits the type of *Amaryllis*, with which a hinge in such a place would be useless. Linsbauer (l. c., p. 1000, Fig. 7) figures the guard-cell of *Lycopodium Phlegmaria* with a hinge on the inner wall. In stomata of the type of *Helleborus*, as the pore opens by an inward and downward movement of its sides, the hinge representing the axis of a cylinder in whose periphery the side of the pore moves, it is evident that the nearer to the ridge of entrance the hinge is placed the more the sides of the pore will move backward, and the less, inward. Accordingly the hinge is practically always brought forward on to the outer wall of the guard-cell, the dorsal part of which remains thin for this reason. This is well illustrated by *Ipomoea hederacea* (Figs. 54, 55). The same advantage is gained if the pore is situated deep down in the rift, as far as possible inside the level of the hinge. In *Helleborus* and other stomata of its type the pore is therefore well inside the middle of the rift, almost down to the beginning of the inner wall. This principle is carried still farther in the stoma of *Viburnum prunifolium*, L. (Fig. 14), in which closure is effected by the ridge of exit.

ACHILLEA MILLEFOLIUM (Figs. 15, 16, 17).

Achillea and many other plants have stomata strikingly like those of *Helleborus*, but different in the one very important particular that the breadth of the lumen of the guard-cell does not exceed the depth. In the thickening of the walls and in the hinges they agree with *Helleborus*, and sometimes in a moderately oblique dorsal wall as well. The stomata of this pattern are all very small, and, while motile, do not open wide, and are therefore not good subjects for experimental study. As I would construe these stomata, they operate in part by a stretching of the dorsal wall, as in *Amaryllis*; but another factor must be recognized, at the ends of the guard-cell. The lumen there is deeper than broad, and hence widens with increasing turgescence. On its ventral face each guard-cell opposes the other, so that the increase in breadth must be by the retreat of the dorsal wall. When both ends of the dorsal wall are forced backward all of it must go, opening the pore; but as there is a hinge in the outer wall only, the inner alone is free to move bodily backward, and the resulting movement is exactly as in *Helleborus*. The responsibility of the union of the ends of the guard-cells in this mechanism demands a considerable size there, and the result is that the pore is short compared with the length of the stoma.

The study of numerous examples has convinced me that in stomata of the *Helleborus* type the ends almost always act somewhat in this same way, except as the direction of the axes makes the movement of the dorsal wall be obliquely backward and inward. Thus in the stoma represented by Fig. 12, the longest axis being a–a', the greatest pressure will be at a right angle to it, and the dorsal wall will be forced in the direction of β. While the operation of the *Helleborus* stoma would be intelligible without this assistance from the ends, it is probably no inconsiderable factor. Haberlandt is right in recognizing that the type of *Helleborus* is a combination of those of *Mnium* and *Amaryllis*; it may also contain elements of that of the Gramineae. Only the (dynamic) characters of the types of the Gramineae and of *Amaryllis* are present in that of *Achillea.* In some stomata of both of these types, in *Aplectrum* and *Lobelia* for instance, the inner wall is thickened at least dorsally very nearly to the end of the guard-cell. This gives the ends an advantage in controlling the middle part of the cell; and *Aplectrum* has a longer rift in proportion to the length of the stoma than any other of its type that I have seen.

POLYGONATUM BIFLORUM (Figs. 18, 19)

has stomata whose mechanism is such as has just been described—probably intermediate between *Helleborus* and *Achillea*—but which is entirely inverted. The outer wall is the more evenly thickened across its surface. The outer walls of the adjacent cells are at a right angle to the surface of the leaf where they strike the guard-cells; the dorsal walls incline ventrally towards the surface; and the pore is above the middle of the rift.

The restriction of the active part of the guard-cells to their ends, which is partly accomplished in *Achillea,* is complete in the stomata of

THE GRAMINEAE

and Cyperaceae, which have been thoroughly treated by Schwendener (1889). In median cross-section (Fig. 20) the outer and inner walls of the guard-cells are very thick, the lumen being reduced to little more than a mere slit. The subsidiary cells are much deeper than the guard-cells, and have thin outer and inner walls. In longitudinal section (Fig. 21) the guard-cells are seen to be enlarged and thin-walled at the ends; cross-sections there (Fig. 22) show the depth to be much greater than the width. With increasing turgescence the ends of the guard-cells widen, and the retreating dorsal wall carries with it the thick, passive middle part of the cell, opening the pore. In surface view (Fig. 23), these stomata are usually slender and straight-backed. Near each end of the guard-cell is a well-marked area, always easily recognized, which represents the thin-walled part of the cell. The dorsal and polar walls are usually not far from perpendicular to the surface, though the dorsal are sometimes inclined a little inwardly towards the rift, and the polar in the other direction. The inward inclination would give the guard-cell an inward as well as a backward movement in opening the pore; which will be an advantage when the outer wall of the subsidiary cell is considerably thicker than the inner, or attached at less of an angle to the surface. But the movement of the guard-cells is typically horizontal.

In the Ericaceae the dorsal and usually the polar walls incline strongly ventrally inward; and in mature stomata, when the thickening is such that the median part must be quite rigid, they retain a slight motility, which is then mechanically of the type of the Gramineae. But, as will be shown later, they are of the type of *Achillea* when more active. *Euphorbia dentata*, Mx., has stomata on the back of the leaf very suggestive of those of the Gramineae, except in not being deep at the ends. The deep, thin-walled epidermis makes subsidiary cells unnecessary. The stomata of the stem are as near *Amaryllis* as to *Achillea*, while those of the upper surface are intermediate in structure between those of the stem and those on the back of the leaf, making a fair series of connecting forms on the one plant.

Among the Gramineae themselves it is common for the outer wall of the subsidiary cell to be thicker than the inner, as in Fig. 30, and it is always attached at an angle less favourable to free movement. The result must be that the inner part of the guard-cell is forced backward more easily than the outer. If this difference in the ease of movement becomes very considerable, the result will be a stoma standing in the same relation to the grass type that *Mnium* does to *Medeola*. The *Achillea* type will be midway between this stoma and that of *Amaryllis*, as the *Helleborus* is a combination of those of *Mnium* and *Amaryllis*.

THE GYMNOSPERMAE.

From the work of Hildebrand[1], Kraus[2], Strasburger[3], Mahlert[4], and Klemm[5], it has long been recognized that the stomata of all Gymnosperms constitute a well-defined morphological type. They occur individually at the bottom of depressions, the wall just above them showing a more or less thin hinge. In median cross-section (Fig. 24) the lumen is shallow, and there can be distinguished, as Kraus says, only an outer thick and an inner thinner wall. Both walls are too thick to be bent—not to suggest stretched—by a pressure from the contents. They are strongly lignified and, where exposed to the air, cutinized. The part remaining cellulose varies in different genera. It does not look probable to me that there is any considerable movement of water through this wall (cf. Schwendener, 1881, p. 836), the ends of the guard-cells affording a readier passage. A cross-section at the end of the stoma throws the needed light on the mechanism. The outer wall is narrow, and the dorsal wall inclined about 45°, making the cell almost a right-angled triangle in section, the dorsal wall being the hypotenuse. The walls are thin throughout, except for a part of the dorsal. When the guard-cell takes up water the dorsal wall will be forced in the direction indicated by the arrow in Fig. 25, carrying with it the thick-walled part of the cell and opening the pore. The thickened line running along the dorsal wall helps the active ends to move the passive middle zone, and so permits a longer rift. The very oblique polar walls and hinges already mentioned facilitate the free movement of the guard-cells in the manner just described.

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[1] F. Hildebrand, Der Bau der Coniferen-Spaltöffnungen und einige Bemerkungen über die Vertheilung derselben: Bot. Zeit. xviii (1860), 149-152.

[2] G. Kraus, Ü. d. Bau d. Cycadeenfiedern: Jahrb. f. wiss. Bot. iv (1865), 305–346.

[3] E. Strasburger, Ein Beitrag zur Entwickelungsgeschichte der Spaltöffnungen: Jahrb. f. wiss. Bot. v (1866), 297–342.

[4] Mahlert, Beiträge zur Kenntniss der Laubblätter der Coniferen, mit besonderer Berücksichtigung des Spaltöffnungsapparates: Bot. Centralb. xxiv (1885), 54, 85, &c.

[5] P. Klemm, Ueber den Bau der beblätterten Zweige der Cupressineen: Jahrb. f. wiss. Bot. xvii (1886), 498–540. I have been unable to see Strübing's Königsberg thesis, of 1888, on this subject.

That the mechanism of the Gymnosperm stomata has remained so long unexplained is probably due to the difficulty of directly observing their movements. Their being overlapped by other cells is less of an obstacle to direct measurement than the bubble which persistently clings in the depression outside the pore, where the waxy surface prevents its removal by water. Moreover, on old evergreen leaves the walls become so thick even at the 'hinge' that movement is impossible; this is the case on the leafless stems of *Ephedra*. The deciduous leaves of *Gingko* and *Larix* have motile stomata, whose movement can be observed and measured if a surface-section is exposed to the light for several hours in water from which the gas has been partly driven off, so that it will dissolve the air from the outer respiratory chamber. They will close in alcohol or glycerine. The widest open pore I have observed measured 3·5 μ; they close completely. Measured by focussing from the outer wall of the adjacent cell to the dorsal line of the lumen of the guard-cell—from *x* to *x* in Fig. 27—the depth of *Larix Europaea* was found to be 15·2 μ in water, 19 μ in alcohol. The dorsal wall of the guard-cell moved downward at the same time as towards the rift in closing. Another stoma changed depth a little more.

Stomata of similar mechanical structure are not confined to the Gymnosperms. It seems to me, as it does to Westermaier (l. c. p. 77), that the stoma of *Iris*, as it is described by Schellenberg (l. c. p. 172), is more like that of a Conifer than like that of *Helleborus*. The stoma of *Allium vineale* (Figs. 28–30) is in all essentials—hinges, shape of guard-cells, pitch of walls, and distribution of thickening—like that of a Conifer: the walls are not so much thickened and not lignified. Schwendener figures the stoma of *A. Cepa* as between this one and *Amaryllis*. In the pitch of the walls, the stoma of *Polygonatum*, described above, approaches the Coniferae. The stomata of *Botrychium* will be described later.

The grass type is more motile than the Gymnosperm, because in it the direction of enlargement of the active ends is vertical to the sides of the pore, while the movement in the Gymnosperm stoma is inclined perhaps 45°. The plan of *Medeola* presented by a stoma whose activity is restricted to the ends of the guard-cells will evidently permit no great motility. I have found it fully worked out, so that the greatest diameter of the thin-walled end is quite horizontal, only in *Osmunda Claytoniana*, L. (Figs. 31–33), and *O. regalis*, L. Stahl (l. c. 1894, p. 123), from his cobalt test, decided that the stoma of *O. regalis* was non-motile; but, while the pore does not close, its width varies somewhat. What movement occurs is an increase in the depth of the cell, in which, judging from the sections, the ends must be the active part.

In the stomata which have now been described I have intended to include a sufficient number of forms so that the various mechanical devices by which the width of the pore is made subject to the turgescence of the guard-cells should be illustrated by individual stomata, which it is convenient to call types: and also to make clear the relation of these types. As is to be expected, there are complete series of intermediate forms connecting all these types—a limit to the profitable description of which might easily be reached. There are, however, a number of individual peculiarities, as of the stoma of *Equisetum*, which have so far been passed over only for the sake of consecutiveness in types. The ecological grounds for the development of the different types can be estimated, except *a priori*, only by ascertaining in a considerable number of instances what types occur under various environments. It will also be of some interest to see to what extent any relation can be traced between the taxonomic position of plants and the mechanism of their stomata.

The Mosses, so far as they have motile stomata, seem generally to rely on an increase in the depth of the guard-cells to open the pore, agreeing in mechanism with *Mnium* or *Funaria*, more often the latter. They have been best studied by Haberlandt (1886) and Bünger[1], in whose work there is nothing to criticize, unless it be that Haberlandt did not seem

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[1] Bünger, Beiträge zur Anatomie der Laubmooskapsel, Bot. Centralbl. xlii (1890): 193, 225, 257, 289, 321, 352.

to quite appreciate the general occurrence among them of the mechanical type he was first to explain.

The stomata of *Anthoceros laevis*, L., and *A. punctatus*, L. (Figs. 34, 35), have walls of rather uniform thickness, except dorsally, where the wall is too thick to be likely to be displaced by any pressure from the guard-cell. The depth of the lumen is equal to the width. I fixed my material without examining it fresh, and can only suppose from the structure of the stoma that it is inactive. The thin polar areas and the absence of hinges make it likely that the width of the pore is influenced by the shrinking or swelling of the entire sporogonium, with variation in its turgescence. These stomata are usually exceptions (Fig. 35) to De Bary's general rule[1] that at most the guard-cells are of equal height with the epidermal cells.

The stomata of *Botrychium ternatum*, Swtz., *B. simplex*, Hitchcock, and *B. Lunaria*, Swtz., are strikingly like those of the Coniferae. *B. ternatum* has the same form in all sections, with the characters a little less extreme. The wall is cellulose; and the outer respiratory chamber is just deep enough to make a place for the characteristic hinges. The stomata become rigid in autumn. The following measurements were obtained on a grown leaf in spring:—

	Open.	Closed.
Width of stoma	38	36
Width of guard-cell	17	16·5–17
Width of pore	4	2·5
Length of stoma	55	55

At the same time there was the same downward movement of the dorsal wall as in the stoma of *Larix*. In one extreme case of a stoma whose pore changed 4 μ, this perpendicular movement was 5 μ. These stomata of *B. ternatum* are noticeably straight-backed in surface view; and those of *B. simplex* are even more so, like the conifer type. *B. Lunaria* rivals many Conifers in the thickness of the walls in median cross-section.

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[1] Comparative Anatomy, English translation, p. 36.

The restriction of the active part of the guard-cells to the ends in *Ophioglossum pendulum* is illustrated by Figs. 36 and 37, made from a stoma which had probably become rigid with age. Campbell[1] says of this species, 'The upper walls of the guard-cells are thickened irregularly': as his figure shows, this irregularity consists in leaving the thin areas at the ends, familiar in the Gramineae. The same restriction of motility to the ends, with a most excessive thickening of the middle, characterizes the stoma of *Angiopteris* (Figs. 38, 39). The deep and narrow ends would permit such a movement as in the Gramineae, insured more perfectly by the thick lines running to the ends: but the insertion of the outer and inner walls of the subsidiary cells is such that the outer part of the guard-cell, where the ridge of entrance constitutes the pore, will execute most of the movement.

In the Polypodiaceae I have examined there is in all an approach to what Haberlandt[2] calls the type of swimming plants, in that the ridge of entrance is well developed, while the ridge of exit is inconspicuous or not present. In *Dennstaedtia punctilobula*, Bernh. (Figs. 40, 41), this thickening of the ridge of entrance has gone far enough to give the stoma a rigid appearance, but it is really motile. Opening seems to be effected by a movement of the ridge of entrance outward as well as backward, such as must occur in lesser degree in the case of *Angiopteris*. The guard-cells of *Dennstaedtia* are thin-walled and shallow at the ends. In the following table the depth is measured from the ridge of entrance down to the deepest dorsal focus. The stoma was closed by displacing water with alcohol.

	Open.	Closed.
Width of stoma . .	30	28·5
Width of guard-cells . .	13·5 and 14	14 and 14·5
Width of pore . . .	2·5	0
Length of stoma . .	44	45
Depth	17	14

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[1] D. H. Campbell, Mosses and Ferns, 1895, p. 233.

[2] L. c. 1887, Physiol. Pflanzenanatomie, p. 401.

The first effect of the alcohol is to widen the pore, which then gradually closes, the sides becoming apparently straight before they meet. The increase in depth at the ends, which is partly responsible for opening the pore of this stoma, works to better advantage than in the stoma of *Osmunda*.

In other Fern stomata, with less thickened ridges, variations in depth are responsible for more of the movement. In median cross-section the guard-cells are shallower, as well as more equally thin-walled. These measurements are of the stoma of *Aspidium acrostichoides*, Swtz.:—

	Open.	Closed.
Length of stoma	57	57
Width of stoma	46·5	46
Width of guard-cell	20	23
Width, ridge of entrance	4	3
Width of pore	7 (about)	0
Width, ridge of exit	12	11

It is noticeable that while the ridge of entrance marked the narrowest part of the rift when open, the pore was closed by the thin wall inside. In other stomata of the same plant the ridges of entrance met one another in closing. And this occurs on most of our Ferns, except that the closing is often imperfect. In the stoma measured for the last table, the change in total width was less than 1 μ, which may be regarded as the share of the *Amaryllis* type in this case. The stomata of some other Ferns—*Asplenium montanum*, Willd., *A. pinnatifidum*, Nutt., *A. platyneuron*, Oakes, and *Camptosorus*—are more slender, and the walls between the adjacent cells strike their backs: and the variations in the width of the entire stoma are not quite so inconspicuous. *Pellaea atropurpurea*, Link, on the other hand, has stomata of pronounced *Medeola* type. The 'free' situation of the stomata of *Niphobolus*[1] and some species of *Aneimia*[2] makes no peculiar demands on their mechanism.

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[1] K. Giesenhagen, Ueber die Anpassungserscheinungen einiger epiphytischer Farne: Schwendener-Festschrift, 1899, p. 1; Die Farngattung *Niphobolus*, Jena, 1901, p. 85, literature there.

[2] Strasburger, l. c. 1866, p. 327; F. Hildebrandt, Ueber die Entwickelung der

The stomata of *Marsilia quadrifolia* are very like those of *Asplenium.* Two other Filicineae have stomata too well known to be entirely passed over here—*Salvinia natans* and *Azolla Caroliniana* (Figs. 42, 43). I have had fresh material of neither. The stomata of both remain open in formalin and alcohol. The mechanism of *Azolla* has been explained by Schaefer (l. c.), with whose material mine agrees in having the guard-cells as deep as broad. I agree again with Schaefer, Haberlandt (l. c. 1887), and Mettenius that the wall between the guard-cells is partly dissolved, which Strasburger[1] denied. As to *Salvinia,* it is agreed even by Kohl (l. c.), who concedes so much for no other stoma, that it is rigid.

The stomata of *Lycopodium lucidulum*, Mx., and *L. complanatum*, L., have thickened ridges which give the appearance of the *Amaryllis* type to sections. The dorsal wall, however, is thick, so that in surface view the stoma appears surrounded by an irregular heavy band—which is not quite so thick in *L. obscurum*, L. The shape of the lumen, with an observation of the movement, shows that the stoma is nearest the type of *Medeola*, but with the activity restricted largely to the dorsal half. The stoma measured was of *L. lucidulum.*

	Open.	Closed.
Length	49	49
Width of stoma	51	51
Width of guard-cell, average . . .	24	25
Width of pore	3	1
Width, between ridges of entrance . .	14	13

The decrease in depth was about 7 μ. These stomata remain motile on leaves several years old. I have not found the walls lignified (cf. Linsbauer, l. c.).

The mechanism of the stoma of *Selaginella apus*, Spring, is similar to that of *Lycopodium*, though closure is effected by the ridge of entrance, as in *Dennstaedtia.* The stoma of

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Farnkraut-Spaltöffnungen; Bot. Zeit. xxiv (1866), 245. The mature stoma was described by Oudemans in 1865.

[1] E. Strasburger, Ueber *Azolla*, Jena, 1873, p. 35.

S. rupestris, Spring, is much deeper, and with the ridge of exit well developed, being in both respects like the *Amaryllis* type.

The remarkable superficial aspect of the stomata of *Equisetum* has made them a frequent subject of note (literature in de Bary, l. c.), and some unsound speculation. In two modern texts it is stated they consist of two pairs of guard-cells, one over the other, a notion disproved by a study of their development by Strasburger thirty-six years ago (l. c., 1866, pp. 318–22). In cross-section (Fig. 46) it is at once evident that the lumen of the guard-cell has two very unequal diameters, and will therefore, like that of *Medeola*, tend to become round with increasing turgescence. The ventral and inner walls are practically all one, with a ridge of exit too little thickened to affect the mechanism. The outer wall is restricted to the ridge of entrance, which constitutes the pore, and is placed where it looks like a continuation of the wall between the guard-cell and the overlying subsidiary cell. The extensive convex dorsal wall is thin except for the thickened strips running across it from the pore, projecting into the lumen of the subsidiary cell. These strips do not stiffen the wall lengthwise of the guard-cell, and will themselves be bent by less pressure than would stretch them. Now if the pore be closed—by which I mean of course as nearly so as it becomes—and the turgor of the guard-cell increases, water will enter it from the subsidiary cell, as indicated by the arrow. To compensate for this movement of water, the wall must move in the opposite direction. This must bend the wall, but need not stretch it. Obviously the thickened strips, attached to more than one wall and presumably fixed fast at the back side, will exert a direct pull on the ridge of entrance and widen the pore. There is a conspicuous hinge in the wall above the ridge. While the guard-cells are often in contact with no other cells than their subsidiary cells, and so must be supplied with water through them, this is of course not essential to the operation of the stoma.

Of the Gymnosperms enough has been said. And of the Glumiferae it need only be stated that in the four Scirpeae[1] I have examined—*Cyperus rivularis*, Kunth, *Fimbristylis capillaris*, Gray, *Scirpus Cyperinus*, L., and *S. polyphyllus*, Vahl—median cross-sections show the thickening typical of other sedges. The stomata of *Juncus acuminatus*[2], Mx., are mechanically more like those of sedges than like those of *Luzula*, in spite of their curved dorsal wall. In some species of *Luzula*, Westermaier finds the thin polar areas in surface view, but they are invisible in my *L. campestris*, DC.

The stomata of the Liliaceae and their relatives have the one common character that they are large, and therefore convenient subjects of study, so that they were in almost exclusive use by the earlier investigators. The same character makes them an excellent subject of study from the mechanical side. That there is no particular type characterizing the Liliaceae, as might be inferred from references by Schwendener (1889) and Westermaier, is perfectly evident from the illustrations I have already used—*Medeola*, *Lilium*, *Smilax*, *Dracaena*, *Polygonatum*, and *Allium*. The enumeration of more kinds emphasizes the diversity. *Disporum lanuginosum* has the stomata broad, but also deep, combining the characters of *Amaryllis* and *Achillea*. The movement is mostly by the inner half, and is facilitated by the contour of the neighbouring cells inside the ends of the guard-cells (Fig. 47). *Uvularia perfoliata*, L., has clumsy stomata, nearest *Helleborus*. Those of *U. grandiflora*, Smith, suggest *Iris*. *Erythronium Americanum*, Ker., is nearer *Achillea* than any other type. *Clintonia umbellata*, Torr., has a mixture of *Amaryllis* and *Mnium* characters. The same is true of *Smilacina racemosa*, Desf., while *Maianthemum Canadense*, Desf., is nearer *Amaryllis*. *Convallaria majalis*, L., also has them of the *Amaryllis* type on young leaves; on leaves a year old they are thickened so as to resemble those of *Helleborus*, but are little, if at all, movable. Those of *Myrsiphyllum* are not distinguishable

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[1] Cf. Schwendener, 1889, p. 71.

[2] Schwendener, 1889, p. 77; Westermaier, l. c. p. 78.

from those of *Smilax* (Figs. 7, 8). Those of *Trillium erectum*, L., approach the *Medeola* type. *Dioscorea villosa*, L., has them similar, but the inner wall is thicker, and the dorsal wall slants as in *Helleborus*. Schmidt[1] describes and figures the stoma of *Conostylis graminea* in cross-section as like that of a grass.

Iris cristata, Aiton, has such stomata as Schellenberg describes for *Iris*, but according to Westermaier not all the species are alike. *Hypoxis erecta*, L., has stomata the slant and thickening of whose walls is suggestive of *Achillea*, though the ventral angles are noticeably thickened, and the stoma is long enough to act by its shape alone.

Lemna polyrhiza, L., has the ridge of entrance as on other floating plants, the dorsal wall thin, and the whole stoma slender, appearing motile: but I have not examined it alive and it is open after death. *Acorus Calamus*, L., and *Symplocarpus foetidus*, Salisb., have stomata of the *Amaryllis* type, but deeper than the type and narrower, and therefore needing the ventral angles less thickened. Those of *Arisaema triphyllum*, Torr., are of the *Achillea* type.

Of the Orchidaceae, *Aplectrum hyemale*, Nutt., has already been mentioned as an illustration of the type of *Helleborus*. *Goodyera pubescens*, R.Br., comes nearer the type of *Amaryllis*; which is better represented by *Spiranthes gracilis*, Big., and *S. cernua*, Richard. The latter has a notable outer hinge. *Cypripedium acaule*, Ait., approaches the *Medeola* type; and *Orchis spectabilis*, L., exemplifies it fully.

It will economize space if the stomata of Dicotyledones are merely listed, with their characters:—

Platanus occidentalis, L. Like *Quercus rubra*, L., Figs. 12, 13.

Quercus imbricaria, Mx. Different only in not being quite so wide.

Pilea pumila, Gray. Narrowed to the type of *Achillea*.

Codiaeum, sp., the green-house 'Croton.' *Helleborus* type,

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[1] K. Schmidt, Ueber den Blattbau einiger xerophilen Liliifloren: Bot. Centralb. xlvii (1891), 1, 33, 97, 164, p. 100.

with the hinge back of the guard-cell; and the line where dorsal and inner walls meet thickened to the end.

Viola ovata, Nutt. *Achillea* type.

Viola blanda, Willd., var. *palustriformis*, Gray. *Achillea* type, but thickened less than typical.

Claytonia Caroliniana, Mx. *Medeola* type; surface view almost round; in contact with several cells.

Erodium cicutarium. *Helleborus* type.

Anemonella thalictroides, Spach. *Medeola* type, in spite of thickened walls; ends and sides of guard-cells locally reinforced.

Caltha palustris, L. Slightly flatter than *Anthoceros* (Fig. 53) in cross-section, very large.

Delphinium tricorne, Mx. *Amaryllis* type.

Aconitum uncinatum, L. *Achillea* type.

Caulophyllum thalictroides, Mx. *Helleborus* type.

Capsella bursa-pastoris, Moench, *Helleborus* type, narrow.

Dentaria diphylla, Mx. Like *Capsella*, but less thickened. Both of these Cruciferae are about as near *Achillea* as *Helleborus*.

Desmodium Dillenii, Darl. Narrow: *Amaryllis* or *Sagittaria* type on leaf, with subsidiary cells.

Cassia Marilandica, L. Like *Desmodium*. Stem without stomata.

Geum vernum, L. *Helleborus* type, dorsal walls quite oblique.

Saxifraga Virginica, Mx. Nearest *Amaryllis*; but inner wall thicker than outer.

Chrysosplenium Americanum, Schwein. *Medeola* type, with suggestion of *Amaryllis*; sometimes angular.

Liquidambar Styraciflua, L. Like type of the Gramineae in the depth of the subsidiary cells; and thin ends of guard-cells very evident in surface view. In median cross-section like *Achillea*.

Hamamelis Virginiana, L. Like *Liquidambar*, but more thickened.

Cuphea viscosissima, Jacq. *Helleborus* type.

Oenothera linearis, Mx. Type of *Achillea.*

Passiflora lutea, L. Like *Anemonella.*

Eucalyptus globulus. Cotyledon. Like Halophytes: much thickened, and no part of ventral wall thin: probably rigid. Character less extreme on leaf.

Opuntia Rafinesquii, Engelm. Leaf. Many stomata rigid or abortive, but some motile. *Amaryllis* type, but with features of *Achillea.*

Hydrocotyle Americana, L. Type of *Achillea*: slender, with oblique dorsal walls.

Osmorrhiza longistylis, DC. Type of *Achillea.*

Nyssa sylvatica, Marsh. Like the Ericaceae, but thickening ceases less abruptly at ends.

The Ericaceae. With the exception of *Arctostaphylos Uva-Ursi*, Spreng., of which I have had only herbarium material whose stomata are as figured by Westermaier (l. c. Fig. 4) and are certainly very nearly rigid, the stomata of all the Ericaceae I have examined are mechanically very much alike. These subjects have been *Azalia nudiflora*, L., *Rhododendron maximum*, L., *Gaultheria procumbens*, L., *Oxydendrum arboreum*, DC (Figs. 48–51), *Andromeda polifolia*, L., *Pyrola secunda*, L., and *Chimaphila umbellata*, Nutt. In sections these agree essentially with those of *Vaccinium*, which impressed Westermaier by their resemblance to the grass type. The thickening is so distributed as to leave the thin polar areas familiar in surface view in the Gramineae. But the ends are not much deeper than the middle, the dorsal walls are not at all straight and are usually oblique in cross-section, the inner wall is much thicker than the outer, very deep subsidiary cells are not often present, and in most Ericaceae, *Oxydendrum arboreum* and *Gaultheria procumbens* being exceptions, more than one cell opposes the back side of each guard-cell. Older stomata of some of these plants are slightly motile; others apparently not at all so. Movement which is undoubtedly like that of *Achillea* is very clear when they are younger and less thickened. The following measurements were made June 1, on a young leaf of *Azalia nudiflora*, after exposure to direct sunlight, submerged:—

	Open.	Closed.
Length	25	25
Width of stoma	19	14
Width of guard-cell . . .	8	7
Width of pore	3	0

Fig. 53 shows the structure of a stoma of about the same age.

Fig, 52 is of a still younger one, the rift not yet open, but the thin areas already visible.

Cyclamen, sp. (cultivated). *Helleborus* type.

Convolvulus sepium, L. Like *Ipomoea hederacea* (Figs. 54, 55). The stomata on the stems of both of these are nearer the *Amaryllis* type.

Phlox divaricata, L. *Helleborus* type. The reinforcement of the outer part of the end walls is shown by Fig. 56.

Gentiana Andrewsii, Griseb. *Helleborus* or *Achillea* type; not very uniform, but always greatly thickened; thickenings at ends variable; most commonly as in Fig. 57.

Obolaria Virginica, L. Many abortive and angular: those which develop, somewhat like *Anthoceros*, with internal ventral corner thicker.

Chelone glabra, L. Between *Helleborus* type and the stomata on the cotyledon of *Eucalyptus*.

Physostegia Virginiana, Benth. *Achillea* type. In the stomata of the *Labiatae*, with a subsidiary cell around each end of the stoma, the wall between these, striking the dorsal wall of the guard-cell about its middle, is thin and curved, usually about 90°: in *Mentha viridis* the curve is double, 90° each way. This curve probably decreases its resistance to the movement of the stoma.

Mentha viridis, L. *Helleborus* type.

Salvia lyrata, L. *Achillea* type.

Lamium amplexicaule, L. *Achillea* type.

Nepeta Glechoma, Benth. *Achillea* type.

Mitchella repens, L. Nearer *Achillea* than to *Helleborus*.

Houstonia ciliolata, Torr. *Achillea* type.

Houstonia caerulea, L. *Achillea* type. Ends, in surface view, suggest those of *Juncus*.

Cephalanthus occidentalis, L. *Achillea* type: slender.

Campanula Americana, L. *Helleborus* type, but rather narrow.

Lobelia puberula, Mx. *Achillea* type. Thickening of dorsal edge of inner wall runs to end; rift rather long.

Taraxacum officinale, Weber. *Helleborus* type.

Senecio aureus, L. *Achillea* type. The subject was the radical leaf of a marsh variety.

Helenium autumnale, L. *Achillea* type: thickening and length of rift as in *Lobelia*.

Eupatorium ageratoides, L. f. *Helleborus* type.

Eupatorium coelestinum, L. *Achillea* type.

The number of stomata that I have had time to investigate would not warrant positive conclusions of any value in systematic botany; but it is sufficient to show that no such conclusions could be expected from a wider range of study, except in such groups, like the genus *Equisetum*, as are sharply defined in other ways, morphological and ecological. The Glumiferae and Gymnospermae are such groups. The difference between the *Achillea* and *Helleborus* types, though a very great mechanical one, is insignificant morphologically, depending on the relative depth and width of cells, which are very flat or very deep in neither case; and it is not surprising that the two should often occur in the same genera, and that there should be every intermediate stage between them. The series of divisions leading up to the formation of the stoma is sometimes a character of taxonomic value, and the mechanism must to some extent be correlated with it. Thus the presence of anticlinal walls against the dorsal wall makes desirable some type better prepared to overcome local resistance than is the *Amaryllis*.

Stomata of the *Medeola* type would not have to overcome this resistance; but they must be large in order that the necessary changes in total curvature may not involve an impracticable bending of any unit of wall; and the stomata which are surrounded by subsidiary cells formed regularly from the same initial cell are from their origin likely to be small. The stomata of the *Amaryllis* type must also be large to permit the needed curvature of the entire guard-cell, as is of course equally true of *Sagittaria.* A stoma of the Conifer type must be below the general level of the epidermis. Outside the very specialized type of the Gramineae there remain only the *Helleborus* and *Achillea* types, which on mechanical grounds could be expected to occur among the very numerous Dicotyledones with small stomata.

The size of the stoma usually corresponds somewhat to that of the epidermal cells (*Salvinia* is a conspicuous exception). And the mechanism of the stoma must be correlated with the size and the depth and the thickness of the walls of the neighbouring cells. When the subsidiary cells are small, so that a small change in volume might demand a difficult change in their form, or when anticlinal walls oppose the movement of the guard-cells, it is some advantage of the *Helleborus* and *Achillea* stomata that only the inner half must overcome this resistance; and that this inner half has a firm wall which can be forced against any single point of resistance with the whole force of the turgescence of the cell.

To some extent more direct ecological adaptations of the stomata can be seen. If Dicotyledones are examined in late summer, in the height of the season of the large gamopetalous orders, as to their stomatal mechanism, the *Helleborus* or *Achillea* type will be found with scarcely an exception. This is true of trees at all times. But if the season of study is early spring, when *Claytonia*, *Hepatica*, *Anemonella*, *Saxifraga Virginica*, &c. are collected, the *Amaryllis* and *Medeola* types will be much in evidence. The Monocotyledones with similar stomata are characteristic spring plants. *Delphinium* and *Aconitum* show a difference that I cannot construe otherwise than as an adaptation to the season. The frequent difference between the stomata of spring and summer plants suggested that by progressive thickening and a feasible change in the hinges a stoma might easily pass from the *Amaryllis* to the *Helleborus* or *Achillea* type. But this has not been found to occur. The stomata of *Quercus imbricaria*, *Dentaria diphylla*, *Lamium amplexicaule* and *Salvia lyrata*, and the *Azalea* already figured, all show their characteristic thickening before the guard-cells separate.

The ultimate ground for the difference between the predominant types of stomata in early spring and in summer lies of course in the need of protection against drought in summer. It does not follow that pronounced xerophytes can never have stomata of the *Amaryllis* or *Medeola* type. The stomata of *Equisetum* are nearest the *Medeola* type, but are protected by their position. The occasional difference between the stomata of the stems and leaves of the same plant may be partly due to the different demands on the smaller number present on the stems, and should be correlated with the larger and longer epidermal cells common on stems, instead of being ascribed altogether directly, as by Westermaier, to the tensions on the tissues of stems. This difference has already been described on *Euphorbia dentata*. Specialized subsidiary cells appear in cross-section only on the stems, or much better developed there, on many plants; for instance, *Lobelia puberula*, *Campanula Americana*, *Eupatorium coelestinum* and *Chelone glabra*. The surface-view of the *Chelone* stem shows several cells in contact with the dorsal wall of each guard-cell, in the walls between which are thin places, analogous to hinges in that they are to remove resistance to the movement of the guard-cells. The leaf of *Lobelia* shows a similar structure, but less clearly. On the stem of *Lamium* the walls between the subsidiary cells strike the dorsal wall nearer the end, instead of about midway as on the leaf. On *Ipomoea*, *Convolvulus*, *Campanula*, and *Salvia* (the species as in the list above) the stomata of the stem show a tendency toward the *Amaryllis* type, in the thickening.

It would be ridiculous to undertake to tell in detail why each plant makes use of its particular stomatal mechanism.

And to some extent the conditions under which the various types are advantageous have already been indicated. The stomata of *Mnium, Funaria, Equisetum,* the Gymnospermae, and the Glumiferae have so limited and well-defined a range of occurrence that it may reasonably be supposed that on inner grounds which have become very firmly hereditary they are not now among the devices possible to most plants. The four types of *Amaryllis*, *Medeola*, *Helleborus*, and *Achillea* have so wide and discontinuous a distribution that it is evident that in the development of individual orders or genera, or even species, there is often a possibility for selection among them. When the environment and structure of a plant are such that it is desirable that the stoma be very sensitive, then the guard-cells must be large and have thin walls, so that they can transpire and lose their turgescence before the rest of the leaf feels the loss of water. Such stomata are of the *Amaryllis* and *Medeola* types, especially the latter. Very likely the character of the epidermis most frequently determines the choice between these two types: if it is deep the *Amaryllis* type with its deep guard-cells will be natural; if shallow, the shallow *Medeola* guard-cells. Beyond this, it may perhaps be said that the *Amaryllis* stoma demands large neighbouring cells which can readily accommodate the movement of the guard-cells. And when the epidermis contains chlorophyll, as in most of our Ferns, its turgor may vary somewhat with that of the guard-cells; the *Medeola* structure makes the turgor of other cells indifferent mechanically, though it may still influence the supply of water to the guard-cells. The *Medeola* stoma has the least area of contact with other cells, by which it can receive water, and is therein most sensitive. Stomata of the *Helleborus* and *Achillea* types have the free walls of the guard-cells so reduced in area and so thickened that transpiration from them is not likely to close the pore so long as the mesophyll is well supplied with water. They will occur on plants which guard against loss of water sufficiently in other ways, so that too great sensitiveness of the stomata might result in inadequate transpiration, as well as interfere with photosynthesis. Of the two, the *Achillea* type, being narrower, has less outer and inner wall, and a narrower strip on the ventral wall is likely to remain thin. So long as other factors, ecological but not mechanical, do not interfere, it is therefore the less sensitive.

In conclusion, it may prove a convenient summary of part of the work in this paper if the mechanical types of stomata are concisely tabulated. Of the numerous combinations and intermediate forms, there are included here only the two which it is convenient to regard as types—*Helleborus* and *Achillea*.

The pore opens by—

1. A change in shape, rather than by stretching the walls, in which the change is

(*a*) An increase in the depth of the guard-cell, in which there is chiefly concerned—

The entire wall (except the dorsal)	*Medeola* (*Equisetum*).
The inner half	*Mnium*.
The outer half	*Funaria*.
The dorsal half	*Lycopodium*.
The ends	*Osmunda*.
(*b*) An increase in the width of the slender stoma	*Sagittaria*.
2. Stretching the thin dorsal wall	*Amaryllis*.

3. A change in shape, with or without much stretching, at the ends of the guard-cells which forces the dorsal wall, with the passive middle part of the cell—

Directly backward	The Gramineae.
Upward and backward	The Coniferae.

4. Combinations of the types of

Amaryllis and *Mnium*	*Helleborus*.
Amaryllis and the Gramineae	*Achillea*.

EXPLANATION OF THE FIGURES IN PLATE XIII.

Illustrating Mr. Copeland's paper on the Mechanism of Stomata.

All the figures are of stomata. Unless the contrary is stated, cross sections are across the middle of the pore.

Fig. 1. *Medeola Virginica*, L. Surface. × 380.
Fig. 2. „ ,, Cross section. × 380.
Fig. 3. *Funaria hygrometrica*, Sibth. Cross section. × 380.
Fig. 4. „ ,, „ Surface. The inner dotted line bounds the respiratory chamber. × 380.
Fig. 5. *Sagittaria variabilis*, Engelm. Surface. × 510.
Fig. 6. ,, ,, ,, Cross section. × 510.
Fig. 7. *Smilax glauca*, Walt. Surface. × 510.
Fig. 8. „ ,, „ Cross section. × 1020.
Fig. 9. *Polygonum sagittatum*, L. Cross section. × 1020.
Fig. 10. *Euonymus atropurpureus*, Jacq. Stem. Cross section. × 510.
Fig. 11. *Aplectrum hyemale*, Nutt. Cross section. × 510.
Fig. 12. *Quercus rubra*, L. Cross section. × 1020.
Fig. 13. ,, „ Cross section near end of stoma. × 1020.
Fig. 14. *Viburnum prunifolium*, L. Cross section. × 1020.
Fig. 15. *Achillea millefolium*, L. Surface. × 700.
Fig. 16. ,, „ Cross section. × 700.
Fig. 17. ,, ,, Cross section near end. × 700.
Fig. 18. *Polygonatum biflorum*, Ell. Cross section. × 760. O. W. = outer wall
Fig. 19. „ „ Surface. × 760.
Fig. 20. *Zea Mais*. Cross section at β—β of Fig. 21. × 760.
Fig. 21. „ „ Longitudinal section of a guard-cell. × 760.
Fig. 22. ,, ,, Cross section at α—α of Fig. 21. × 760.
Fig. 23. ,, ,, Surface. × 760.
Fig. 24. *Tsuga Canadensis*, Carr. Cross section. × 510.
Fig. 25. ,, „ ,, Cross section of end. × 510.
Fig. 26. „ „ „ Longitudinal section. × 510.
Fig. 27. „ ,, ,, Surface. × 510. The main focus is above the stoma.
Fig. 28. *Allium vineale*, L. Surface. × 510. The main focus is above the stoma.
Fig. 29. ,, „ Cross section. × 510.
Fig. 30. ,, ,, Longitudinal section. × 510.
Fig. 31. *Osmunda Claytoniana*, L. Cross section. × 700.
Fig. 32. ,, ,, Section across end. × 700.
Fig. 33. ,, ,, Longitudinal section. × 700.
Fig. 34. *Anthoceros punctatus*, L. Surface. × 380.
Fig. 35. ,, ,, Cross section. × 760.
Fig. 36. *Ophioglossum pendulum*. Cross section. × 380.
Fig. 37. ,, ,, Section across end. × 380.

Fig. 38. *Angiopteris*, sp. Cross section. × 760.

Fig. 39. „ „ Section across end. × 760.

Fig. 40. *Dennstaedtia punctilobula*, Bernh. Surface. × 510.

Fig. 41. „ „ „ Cross section. × 1020.

Fig. 42. *Azolla Caroliniana*, Willd. Surface. × 1020.

Fig. 43. „ „ „ Cross section. × 1020.

Fig. 44. *Lycopodium lucidulum*, Mx. Cross section. × 700.

Fig. 45. *Equisetum arvense*, L. Surface. × 510.

Fig. 46. „ „ Cross section. × 510.

Fig. 47. *Disporum lanuginosa*. Surface. × 700. The main focus is below the stoma.

Fig. 48. *Oxydendrum arboreum*, DC. Surface. × 1020.

Fig. 49. ,, „ Cross section. × 1020.

Fig. 50. ,, ,, Section across end. × 1020.

Fig. 51. ,, ,, Longitudinal section. × 1020.

Fig. 52. *Azalia nudiflora*, L. Surface. × 1020.

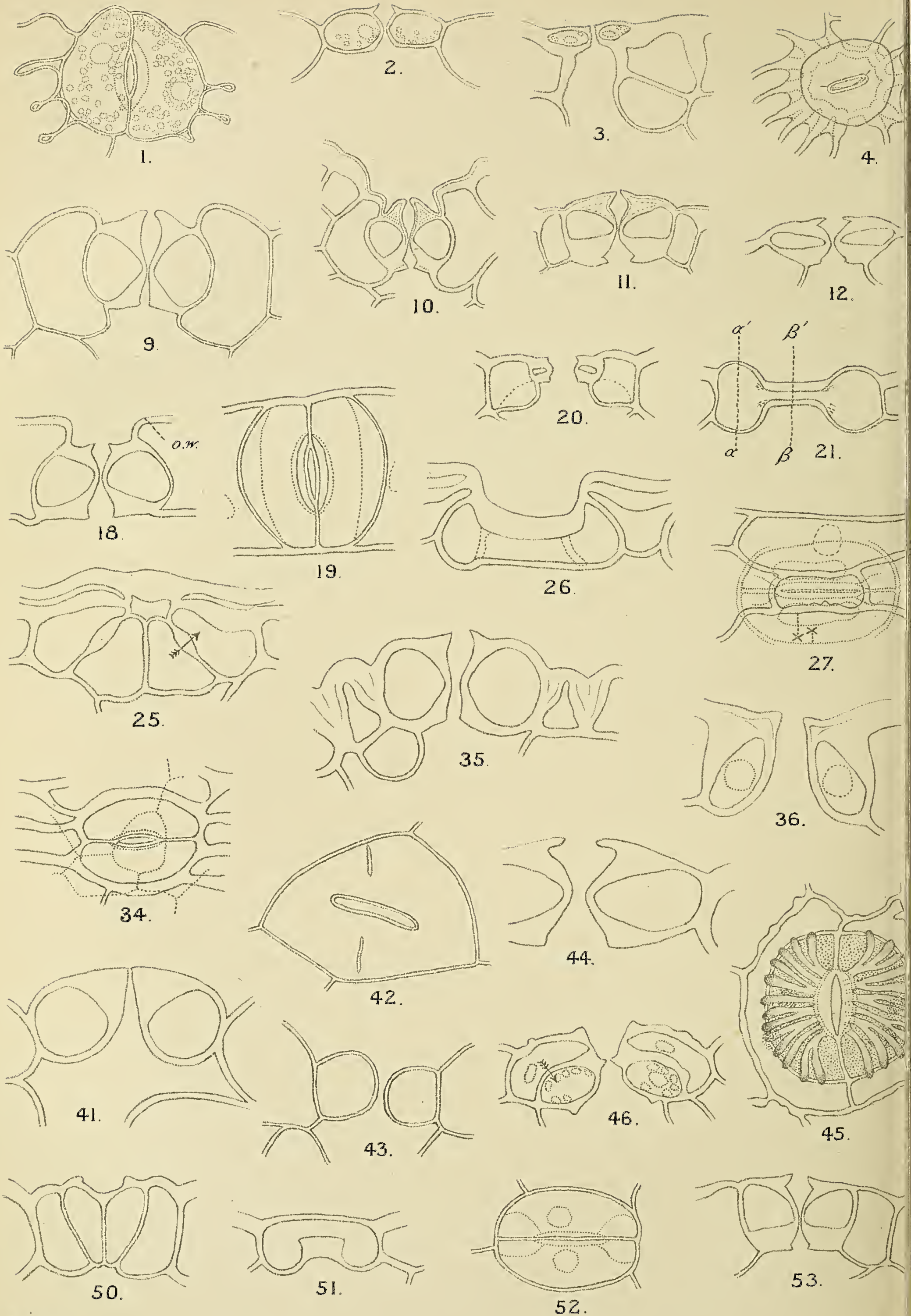
Fig. 53. ,, ,, Cross section. × 1020.

Fig. 54. *Ipomoea hederacea*, Jacq. Surface. × 760.

Fig. 55. „ ,, „ Cross section. × 760.

Fig. 56. *Phlox divaricata*, L. Surface. × 760. The focus is near the outer wall.

Fig. 57. *Gentiana Andrewsii*, Griseb. Surface. × 760.



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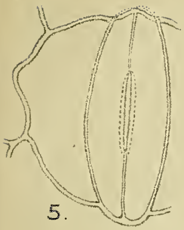
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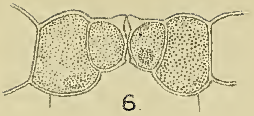
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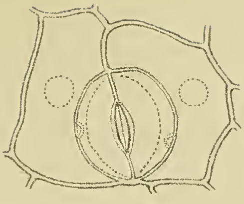
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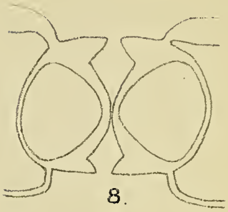
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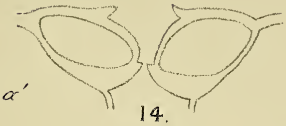
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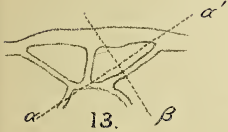

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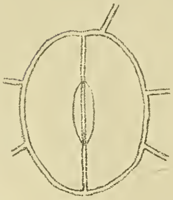
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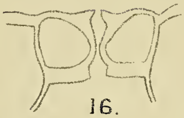
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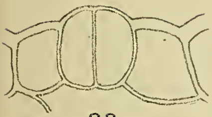
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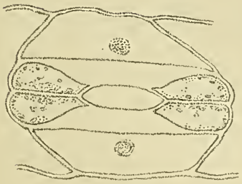
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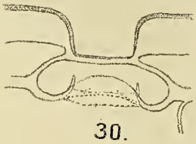
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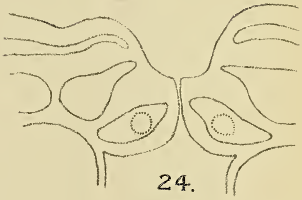
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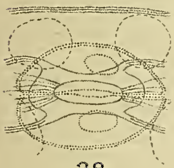
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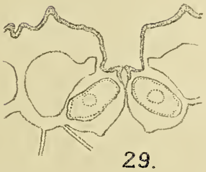
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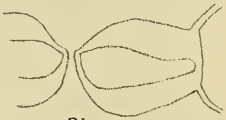
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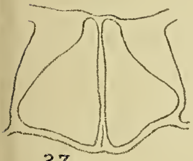
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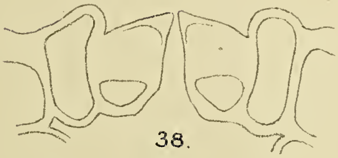
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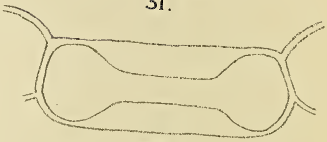
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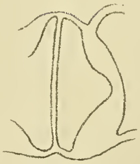
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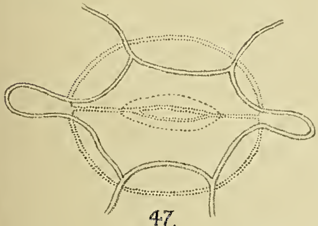
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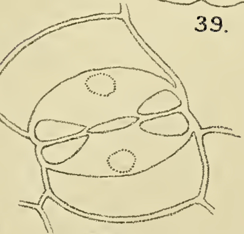
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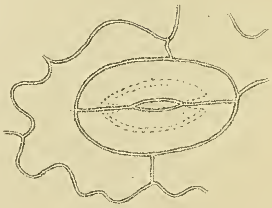
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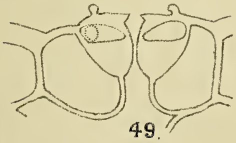
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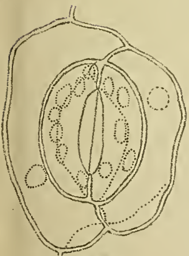
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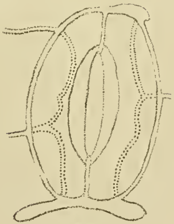
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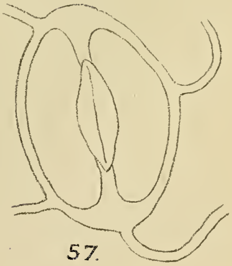
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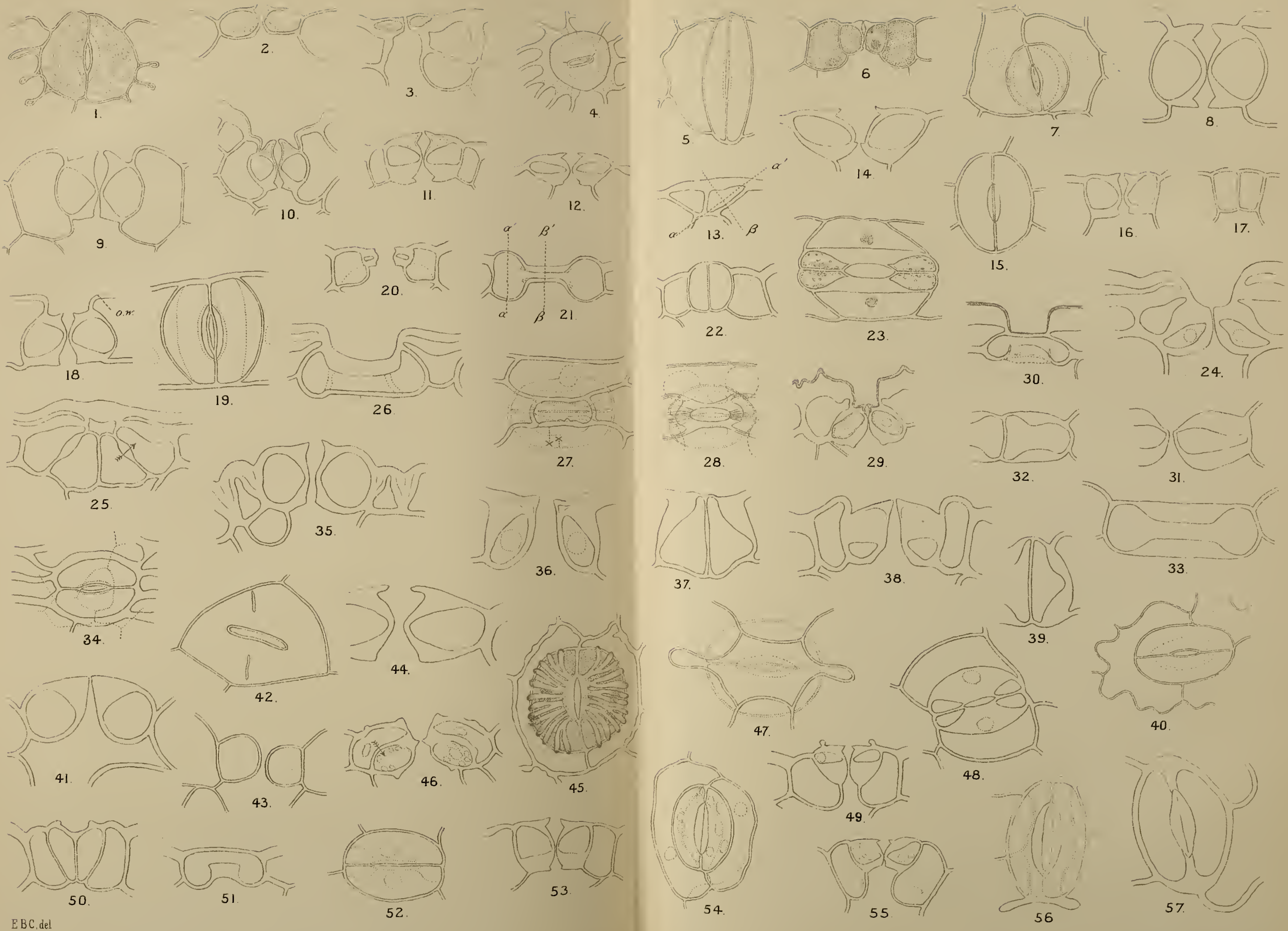

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COPELAND. — MECHANISM OF STOMATA.

University Press, Oxford

Morphological Notes.

BY

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With Plates XIV and XV.

VII. EVOLUTION OF PITCHERS IN DISCHIDIA RAFFLESIANA.

IT is a great many years ago since I derived my first knowledge of the pitchers of *Dischidia rafflesiana* from the pages of Lindley's Introduction to Botany (i, 302) and of Carpenter's classical Comparative Physiology (4th ed., 1884, 152). It had long been my ambition to have so interesting a plant under cultivation at Kew, and this, as stated in the Kew Bulletin (1892, 284), was at last accomplished in 1890 through the kindness of Dr. Treub, the Director of the Botanic Gardens, Java. Since then it has been grown at Kew continuously and with success.

Dischidia rafflesiana has been the subject of a copious literature. At first sight it might seem improbable that after the admirable and exhaustive monograph of Dr. Scott and Miss Sargant (Annals of Botany, 1893, 243–262, tt. xi, xii) any new fact could be added to our knowledge of the morphology of the pitchers. It is, however, one of the results of the change of conditions effected by cultivation to rouse latent tendencies and to develop atavistic forms which are often

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extremely instructive. Such deviations from specific stability are usually the result of seminal reproduction. In the case I am about to describe it is purely vegetative and therefore of even greater theoretical interest.

The structure of the pitcher in *Dischidia rafflesiana* is well known. Characteristic examples grown at Kew are shown on Plate XIV. As demonstrated by Treub, it is 'a modified leaf in which the inner surface corresponds to the lower surface of the normal foliage leaf' (Scott, l. c. 245). Lindley (l. c.) had erroneously conjectured that the pitchers were 'leaves, the margins of which are united.' This view was conclusively disposed of by Treub. And it is important to observe that normally the form of the future pitcher is, as it were, laid down from the first and there is no indication of any passage from the form of the normal foliar leaf to that of the pitcher. Such intermediate stages have, however, made their appearance after some ten years' cultivation in the Kew plants. A portion of one of these bearing both normal and transitional forms is shown on Plate XIV. Another shoot is represented on Pl. XV; Fig. 1, showing the under, and Fig. 2 the upper side. These indicate a complete transition from the ordinary leaf by an increasing concavity of its under surface to a pitcher, which however still differs, in its open mouth, uninflexed margins and small size, from the fully developed organ. It can hardly be doubted that these indicate the path by which the latter has been arrived at from the ordinary leaf. I can find no trace of anything of the kind having been observed in nature unless the 'partly abortive pitcher,' figured by Griffith in the Transactions of the Linnean Society, xx, t. 17, f. 2, be susceptible of this explanation.

As suggested by Sir Joseph Hooker (Flora of British India, iv, 49) 'the species of *Dischidia* all want careful study.' But as far as our knowledge extends, from a comparatively copious supply of herbarium material, supplemented by the observation of several species under cultivation, the production of pitchers is only characteristic of a small part of the genus. From this the inference may be fairly drawn that the property of producing pitchers is rather an individual adaptation, than bound up with a particular generic type as it is apparently in *Sarracenia* and *Nepenthes*. In *D. borneensis*, Becc., and *D. Collyris*, Wall. (*Conchophyllum imbricatum*, Bl.), the leaves are convex and therefore foreshadow the atavistic form described in this note. The comparison with *Dischidia rafflesiana* has not escaped Beccari, Treub, and Goebel. Scott and Sargant remark (l. c. 268) with much sagacity: 'We can scarcely doubt that from some such leaves as those of *D. Collyris*, the more highly modified root-sheltering pitchers of *Dischidia rafflesiana* have been evolved.'

I think it may be fairly claimed that this anticipation has now been realized. The interesting question, however, arises as to the teleological object achieved. Carpenter, quoting (l. c.) from Wallich the original describer, says 'The bags [pitchers] generally contain a great quantity of small and harmless black ants, most of which find a watery grave in the turbid fluid which half fills the cavity, and which seems to be entirely derived from without.' Carpenter continues: 'Thus it would seem as if the failure of the ordinary means of support in this curious plant has been compensated by the addition of an organ which, like the stomach of animals, serves as a receptacle for the supplies it may occasionally obtain.' These extracts are interesting because they show that *Dischidia rafflesiana* was from the beginning recognized as a myrmecophilous plant. This was, however, rather lost sight of when it was generally adduced some half century ago in popular physiological expositions as affording an analogue to an animal stomach.

Beccari regarded the pitchers as 'galls' which have become useful as sheltering defensive insects. This was putting their myrmecophilous origin in the most extreme form. And it is clear that it cannot be sustained. Delpino's obvious theory that the pitchers are carnivorous seems equally disposed of by the fact that their inner walls are coated with wax.

Treub's view that the pitchers are water-economizers appears most nearly to correspond with the facts. As he points out, it is only in certain, and by no means inevitable, positions that the pitchers collect rain-water. I can only conclude that on the average they pay. But under all circumstances they serve to preserve water lost by transpiration, which is one of the severest taxes the plant has to meet.

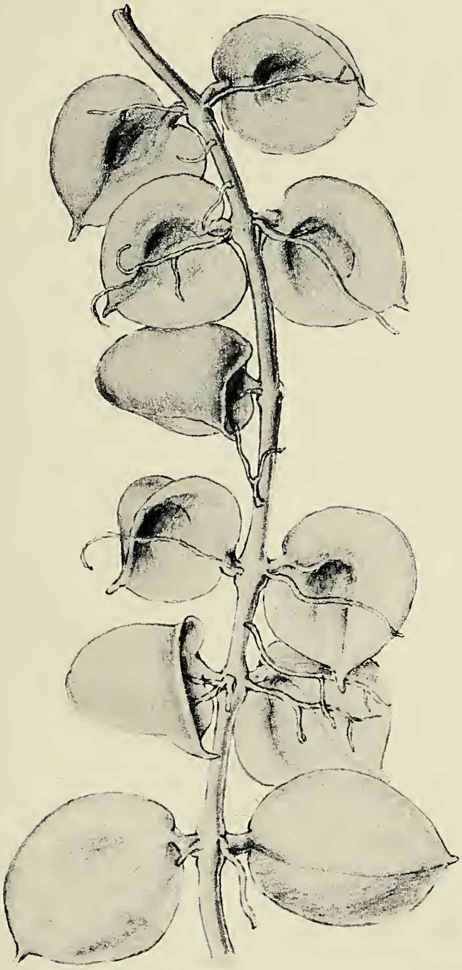
As is well known, the pitchers of *Dischidia rafflesiana* contain a copious root system. This is derived from one or more of a pair of aerial roots, which are either derived from the petiole or from the stem in close adjacence (S. and S., l. c. 259). The whole root system of the plant is adventitious. And I venture to hazard the theory that in so far as adventitious roots are not merely organs of support, their production is a response to a demand for water. In Plate XV, Fig. 1, it will be noticed that each petiolar root is applied to the concavity of its corresponding leaf, and in Fig. 3 it will be seen that as soon as the concavity becomes a pitcher the roots are included within it.

The whole, if I may say so, evolutionary data, tend to prove then that the primary object of the pitchers is the supply, or at any rate economy of water. But the copious development of the enclosed root system, which is often matted with organic débris, seems to go beyond this. The researches of Groom (Annals of Botany, 1893, 223, 242), I think, leave no doubt that the roots utilize this as if it were ordinary soil (l. c. 227). From whence is the organic matter derived? There can be no doubt that, except when in the erect position, the pitchers are usually almost dry. We are driven then to accept the suggestion of Groom based on the observations of Mr. H. N. Ridley, that the organic matter is carried in by ants (l. c. 229).

We have therefore to deal with an adaptation of a singularly complex kind. Originally destined to store and economize water the pitchers often imperfectly perform that function, and are then taken possession of by ants which supply solid in the place of liquid nutriment. Having begun as 'watercans' they, by a change of function and by the aid of ants, became 'flower-pots.'

And there is a sequel to the story scarcely less interesting. Looking through the descriptions of *Dischidia* in the Flora of British India, I came on that of *D. complex* based on a note of Griffith, which no one seems to have taken the trouble either to investigate or confirm. What excited my curiosity was that in this species a second pitcher is described internal to the primary one. This seemed to me so extraordinary that finding Griffith's solitary and imperfect specimen in the Kew Herbarium I ventured to take some liberties with it. The result seemed to me so surprising that I have asked Mr. H. H. W. Pearson to work out the promising problem which it presents.

THISELTON-DYER: ON DISCHIDIA.



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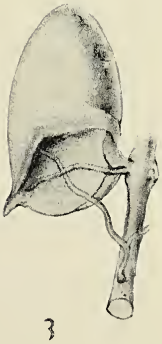

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THISELTON-DYER: ON DISCHIDIA.

On the Arrangement and Structure of the Vascular Strands in Angiopteris evecta, and some other Marattiaceae.

BY

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With Plates XVI, XVII, and XVIII, and a Diagram in the Text.

THE Marattiaceae of the present day, comprised in some five or six genera, represent the relics of a group which in the Palaeozoic age formed one of the great dominant groups of vascular cryptogams. And now, though occupying a somewhat isolated position, they nevertheless exhibit features which point more or less vaguely to an affinity with several other groups of plants. It thus becomes a matter of some interest that a family of so great palaeontological importance should be as thoroughly understood as possible, and in particular that the structural details of anatomy should be accurately and fully known and appreciated. For it is largely on the anatomical evidence as arrived at by a study of the vegetative organs, that our views as to the relationships of these ancient plants for the most part depend.

But on turning to the existing memoirs on the anatomy of the Marattiaceae, one speedily discovers many lacunae in

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our knowledge, and many discrepancies in the statements made respecting even important details. Furthermore, there is not a single species concerning which we possess anything approaching a complete account of its structure at different periods of its development. This latter circumstance is largely due to the difficulty of obtaining suitable material; and it is because we have been fortunate in possessing a fairly complete series of young plants of *Angiopteris evecta*, Hoffm., supplemented by specimens of *Marattia fraxinea*, Smith, and *Kaulfussia aesculifolia*, Blume, that we venture to endeavour to fill in some of the gaps in our knowledge of these plants.

It is not to be expected that we shall be altogether successful in this attempt. Apart from the fact that there necessarily exists a certain degree of variety in the structure, even of individuals of the same species, there is always the difficulty of correctly appreciating the relative importance of anatomical details in connexions other than with those which happen to fall more or less immediately within the purview of the investigator at the moment. Details which in one decade appear to be trivial, may in the next assume an unexpected significance, and it is perhaps hardly possible for any anatomical treatise to be otherwise than tinged with the local colour of contemporary thought.

We desire at the outset to express our indebtedness to the Regius Keeper of the Royal Botanic Garden, Edinburgh, to the Director of the Botanic Gardens at Peradeniya, to Profs. F. W. Oliver and A. G. Tansley, and to Mr. H. Wright, for their kindness in supplying us with material that has proved of such value in supplementing our own stock.

Passing over the older references to the group, the first writers who seem to have endeavoured to deal seriously with the anatomy of the group were De Vriese and Harting in 1853[1]. In this Memoir the task of working out the anatomical characters appears to have been undertaken by the latter of the two collaborators. The results were very incom-

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[1] Monographie des Marattiacées, par W. H. de Vriese et P. Harting, 1853.

plete, a circumstance partly perhaps to be ascribed to the small amount of material at his disposal.

The next paper of importance is the often quoted memoir of Mettenius (1864)[1], who in a magnificent monograph really laid the foundations of our knowledge of the intricate distribution of the vascular strands. His specimen, as is well known, was a mature plant which was in a moribund condition when he investigated it, a fact which probably accounts for some of the anomalous characters met with near the apex. He clearly distinguished the concentric funnel-shaped zones of vascular strands which form so characteristic a feature in the bulky stems of these plants, and he corrected the mistake of De Vriese and Harting of not distinguishing the intracortical roots from the foliar strands. The leaf-trace bundles were shown to form the upward and outward continuation of the funnel-shaped lattice work, and he grasped the character of the anastomoses, whereby the exit of the traces was compensated for by branches from the next internal zone of vascular strands. The details observed by him in this connexion will be discussed later on in relation to the arrangements met with in the younger sporophyte. Mettenius's account is confirmed in all important details by Miss Shove[2], who failed, however, to identify in her specimens the middle leaf-trace steles stated by Mettenius to originate from the next inner zone of bundles. This discrepancy may perhaps be explained as due to a difference in the stage of development of the plants in the two cases. Our own observations show that in young plants only the two stout lateral steles pass out to the petioles, all the rest being as yet in abeyance.

In 1889 a paper by Kühn appeared in 'Flora,' and dealt with[1] the arrangement of the vascular strands in younger plants of *Marattia* and *Angiopteris*, as well as of *Kaulfussia*.

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[1] G. Mettenius, Über d. Bau von *Angiopteris*, Abh. d. k. s. Ges. d. Wiss., ix.

[2] R. F. Shove, on the structure of the stem of *Angiopteris evecta*. Annals of Botany, xiv.

[3] V. R. Kühn, Untersuchungen ü. d. Anatomie der Marattiaceen u. Gefässkryptogamen. Flora, Bd. lxxii, 1889.

The minute anatomy of the vegetative organs was also described.

Kühn seems to have regarded as an essential character of the vascular arrangement in the stems of these plants, the presence of an axile strand or bundle which is surrounded by one or more rings of peripherally situated strands. The simplest condition is presented by *Kaulfussia.* In this Fern there is only a single ring of peripheral bundles. These anastomose with each other and give rise to the leaf-traces. Below the exit of the latter, the axile strand bends upwards and then gives off either two bundles, or a single one which immediately proceeds to fork, and the latter, by joining the peripheral ring, serve to close up the foliar gap. The axile strand from which they sprang then bends downwards, and resumes its old position nearer the ventral surface of the stem. Each leaf, situated obliquely to the right and left of the stem alternately, receives three main strands, whilst the roots spring from the lower strands of the dorsiventral stem.

Kühn regards the arrangement obtaining in *Marattia* as substantially similar to that of *Kaulfussia,* when allowance is made for the more radial character of the stem of the former. The young plant possesses a similar axile bundle situated in the middle of a ring of peripheral strands. But so far as we understand his account the mutual relation of these is not regarded as being quite alike in the two cases. In *Marattia* the axile strand is not considered as a *single* cauline bundle, but as made up of different ones at different levels. Thus the axile strand of one level passes to the periphery higher up, its (axile) place being taken by a bundle from the opposite side of the peripheral ring. The original axile strand finally passes out as one of the leaf-trace bundles. The closure of the foliar gap above, as in *Kaulfussia,* is said to be related to a strand which unites with the sides of the gap, but the details are rather more complicated. In the successive outer zones of bundles of older plants the gaps left by the exit of leaf-traces are said to be compensated in much the same way as stated by Mettenius.

We have ourselves been led to form a somewhat different conception of the relations existing between the various branches of the vascular system, as will become apparent later on. The chief respects in which we differ lie perhaps in the direction of greater simplicity, for a study of the youngest plants shows that the complex arrangements met with in the older specimens are in reality susceptible of easy explanation. The primitive type can, when once understood, be readily discerned, in spite of the disguise produced by the remarkable degree of anastomosis and branching which the vascular strands undergo in these plants.

The method adopted by us in studying the relations and the development of the vascular skeleton in the young sporophytes of various ages has been as follows. Entire plants were cut by means of the microtome into serial sections, care being taken that all the sections were preserved and retained in their proper order on slides. From these the vascular tissue has been built up in the form of wax models. Sheets of wax are prepared of a thickness appropriate to the thickness of the sections, and the degree of magnification employed, and a tracing made on successive sheets of the vascular tissue in every section in its proper order. The drawings were then cut out, due care being taken to preserve the proper orientation, and the wax sections mounted one above another were then held in their places by inserting warmed needles and by carefully fusing the edges. Models prepared in this way, and with due precautions, are extremely accurate, and there is no danger of either missing or confusing even minute details of anastomosing and branching, such as must attend the most careful dissection. And it is of course far more easy to interpret such models, all the parts of which are true to scale, than is the case with a series of drawings however carefully prepared. The actual process of tracing and building up the models often involving several hundreds of sections for one plant, is doubtless tedious, but the clearness and certainty of the results more than repay the labour expended upon them.

The vascular skeleton of the young sporophytes of Angiopteris evecta and Marattia fraxinea, and of the adult stem of Kaulfussia.

The vascular skeleton in the young plant of Angiopteris consists of an axile rod of tissue from which strands are given off to the roots and leaves respectively. The first lateral root is given off, as previously stated by one of us[1], at a point not quite opposite the formation of the first leaf-trace. It is separated from it by about 130°. The regular relation between the leaf and the corresponding root is, however, soon lost. The gaps produced by the early leaf-traces are very small and are immediately made good above. The first deeply depressed aperture or gap occurs at about the sixth or seventh leaf. The leaf-traces still continue to issue from the stele as *single* strands till a varying number have been formed, but they begin to bifurcate whilst still within the cortex of the stem. (Pl. XVI, figs. 1, 2, 3.)

As the stem increases, the leaf-traces become more numerous and crowded, and they take away a larger portion of the vascular tissue from the axile strand. The result is that the leaf-gaps become less rapidly repaired. The stele is already hollow in this region (Fig. 3), that is, it consists of a cylindrical vascular mass with perforations corresponding to foliar gaps and enclosing a core of parenchyma. Sooner or later the gap above one leaf fails to be repaired till after the exit of the trace of the next leaf, and then the original vascular cylinder becomes broken up, and assumes a condition in transverse section conforming with that of polystely or dialystely.

When once this condition has supervened, the vascular ring is never again completely repaired; on the contrary, owing to the crowding of the leaves, more and more apertures or foliar gaps are visible at any one level in the cylinder. Finally, across the intervening parenchyma commissural vascular strands are differentiated, and these connect the opposite sides of the cylinder, which now exhibits the appearance of a coarse

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[1] J. B. Farmer, On the embryogeny of *Angiopteris evecta*. Annals of Bot., vi, 1892.

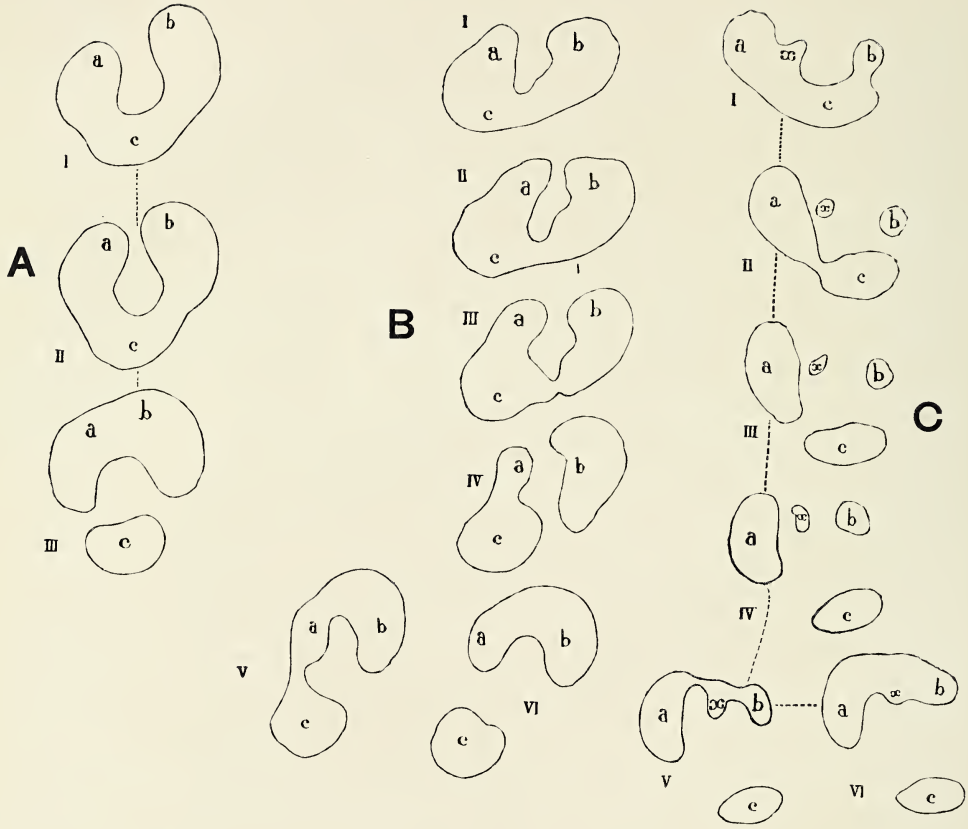

FIG. 21. The figures illustrate in consecutive horizontal (transverse) sections the changes and rearrangements that occur in the vascular strands of the stem of *Angiopteris*. The corresponding components are similarly lettered throughout.

A. The strands in a very young sporophyte; B and C the same in older plants.

a, *b*. Parts of the siphonostele at the edge of gap caused by the exit of a lower leaf trace. The reparation of the gap is shown in the later figures of the series A, B, C, respectively.

c. The leaf trace strand to be given off to the next higher leaf. *x* (in series C), a commissural strand.

To face p. 377.

lattice work differing only in the size of the mesh work from that of a typical 'polystelic' fern.

Meanwhile the leaf-traces, as has been said, increase in size, and at the same time the dichotomy above referred to extends farther and farther towards their bases till it becomes apparent almost as soon as they leave the central strand, or as we prefer to term it, siphonostele. The roots frequently originate directly from the siphonostele, though oftenest not from the margin of a gap, but rather from a broader part of the vascular tissue; they may, however, also spring directly from a leaf-trace, and in older stems they become gradually more intimately related to the latter, though a few may still spring from the axile strand itself. The latter series pursue a sinuous course through the parenchymatous ground-tissue of the stem, finally passing out through a foliar gap into the outer cortex.

The skeletal tissue now rapidly assumes a more complex character, and begins to exhibit the features appertaining to the adult form, after which the increasing thickness of the stem only produces further complication on the lines thus early inaugurated.

The traces of all but the earlier formed leaves become double from their point of exit from the siphonostele, and above each pair there is a huge foliar gap. The commissural strands which traverse the axile parenchyma of the siphonostele become more obvious, though they still are very slender as compared with the strands of which the cylinder still is made up after the exit of the traces. The latter become irregularly disposed and appear at this stage to arise from the edges of the gap, an appearance due to the deep dichotomy. They also have begun to divide up farther before entering the petiole.

Finally, the siphonostele opens out to a considerable width (Fig. 6), whilst the axile commissures assume an ever-growing importance forming a sort of sympodial column. In fact, these large commissural strands may easily be misinterpreted as representing the original stele. It is this strand which seems to be marked *a* in Kühn's[1] figures. The leaf-traces also become more complex, and anastomoses take place at irregular intervals with the strands which can still be recognized as the relics of the original siphonostele, as well as with one another. Irregularities also begin to become apparent as to the relative heights at which the two members of the leaf-traces become freed from the plexus of tissue, and a stage is thus reached at which the vascular skeleton appears to consist of a stout axile strand surrounded by upwardly diverging zones of steles which ultimately pass out above to the leaves. The complexity and obscurity is primarily due to the commissural strands which connect up the margins of the siphonostelic foliar gaps, and the whole arrangement is to be correlated with the presence of the bulky parenchyma of the stem.

In the much older stems, such as that described by Mettenius, the principal leaf-traces can still be recognized, in the light of what has been said, as being represented by the two stout lateral strands of the plexus which travels out to the petiole (Mettenius, loc. cit., Taf. III, Figs. 1, 2, the strands lettered *a*, *b*). The smaller strands which arise between these merely form an extension of that tendency to the formation of supernumerary strands which early finds its expression in the formation of the commissures already referred to in connexion with the vascular system of the stem.

The vascular skeleton of *Marattia* (Figs. 7, 20) is simpler than that of *Angiopteris*, at any rate in young plants of equal size. The protostele opens out to form a siphonostele in a similar manner in both, but the earlier leaves are not so crowded in *Marattia* as in the other genus. Nevertheless the foliar gaps are relatively larger, and hence in transverse section the polystelic arrangement of vascular tissue appears more striking. The foliar gaps are also much wider than in *Angiopteris* and hence the siphonostele condition is perhaps not so obvious, as the impression is gained of anastomoses rather than of lack of disunion, when observed in transverse sections.

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[1] Loc. cit., Taf. xviii and xix. Figs. 22–24.

Sooner or later, however, commissures of an attenuated form appear in this plant also, and cross the intervening parenchyma (Fig. 7) exactly as in *Angiopteris*. We unfortunately had no plants old enough to enable us to follow out fully the later developments. The roots come off, so far as we have seen, from the outer surface of the siphonostele, and are even less regularly related to the leaves than is the case in *Angiopteris*. The leaf-traces are at first single, but those subsequently formed fork once whilst still in the stem cortex, and the dichotomy, as in *Angiopteris*, extends farther backward in the successively produced leaves, till it is obvious at their first origin at the base of the foliar gap.

The most striking feature of difference between *Angiopteris* and *Marattia* at this stage lies in the large diameter of the siphonostele, and the very large foliar gaps which are very characteristic of the latter genus.

Kaulfussia. The vascular skeleton has been excellently elucidated by Kühn[1], and our investigations largely confirm his results. Unfortunately we were unable to secure any young plants of this genus, so we are not in a position to trace the ontogenetic evolution of the vascular strands. As might have been anticipated from its markedly dorsiventral habit and comparatively thin rhizome, the vascular system of *Kaulfussia* is much simpler than that of the other two genera, but it also exhibits features of interest which serve to illustrate some points in the anatomy of the preceding ferns. The vascular strands in the mature stem consist of an outer network from which the leaf-traces are given off on the upper side, and the greater number of the roots on the lower. This network encloses a parenchyma in which is embedded an axile vascular strand which pursues an undulating course, bending first to the upper and then to the lower face of the reticulated cylinder, with which it is alternately connected in the way described by Kühn. We regard this as certainly representing the commissural strand which occupies an exactly analogous position in both *Angiopteris* and *Marattia*, whilst

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[1] Loc. cit.

we look on the peripheral mesh work as the representative of the siphonostelic cylinder in them.

The foliar gaps are large, and the leaf-trace strands plainly correspond exactly in their origin with those of the two genera already described. The two strong lateral steles, which in our specimens leave the outer edges of the lower margin of each gap, clearly represent the original forking trace which we may confidently expect the young sporophyte will be found to possess. Lying between these, and originating exactly as in *Angiopteris*, are a number of subsidiary strands, which anastomose both with each other and with the strong principal lateral forks of the original dichotomising petiolar steles.

Turning to the lower surface of the stem, we find diamond-shaped gaps resembling foliar gaps, but in accordance with the dorsiventral habit, no leaf-traces take their origin from them. This occurrence of gaps on the lower surface is of interest as perhaps indicating that the marked dorsiventrality which *Kaulfussia* now exhibits, may have been acquired from a radially formed ancestor, the interior anatomical characters corresponding to such a disposition having been retained.

Both *Marattia* and *Angiopteris* also exhibit a tendency to dorsiventrality, but it is not very marked in young plants. Thus in this group, we find the skeletal framework clearly showing the original type from which they have been derived, although in external conformation the departure from the radial character has in *Kaulfussia* become very complete. An interesting parallel may be drawn between the Marattiaceae and the Ophioglossaceae, in which much the same range of variety can be traced. In *Helminthostachys*, however, the dorsiventrality which is quite as pronounced as in *Kaulfussia*, has also affected its internal structure, and to a more profound extent. There are no gaps at all in the lower surface of its siphonostele, and the roots are restricted to the sides and lower surface of the vascular cylinder.

In *Kaulfussia*, however, the commissural strand, as in the other genera of Marattiaceae, also may give rise to roots, which burrow through the parenchyma of the stem and pass out commonly through one of the diamond-shaped orifices on the lower surface of the siphonostele. But the great majority of the roots originate from the latter itself.

Attention has been directed by several writers to the similarity between the root-traversed cortex of Marattiaceae and the structure, apparently similar, of the fossil plants included in the genus *Psaronius*. In these plants the roots also seem to have passed through a parenchymatous tissue, and this fact has been utilized to strengthen the evidence based on other considerations of a possible affinity between *Psaronius* and Marattiaceae. Mettenius[1] also briefly alludes to the comparison between the vascular systems in the two groups, but concludes that the resemblance in that respect is but slight. And on further comparing the fine series of illustrations which accompany Zeiller's[2] splendid monograph, we find ourselves inclined to draw the same conclusion, in which we have been further strengthened by a study of preparations of *Psaronius Renaulti*, Will., and *Ps. asterolithus*, for which we are indebted to the kindness of Dr. Scott and Professor Oliver.

In the first place, without attaching too much weight to the abundance of the sclerenchyma in *Psaronius*, and its absence from the stems of Marattiaceae[3], the distribution of this tissue in the fossil stems is somewhat remarkable both as regards its position and its relations to the leaf-traces. The region traversed by the roots is very sharply delimited from the central tissues by a strongly defined ring of sclerenchyma, which is only broken here and there, at points where leaf-traces are in the act of passing out of the central region[4]. At these places the roots are absent, and it might be perhaps argued that the peripheral sclerenchyma, within the root-zone, really represented the

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[1] Mettenius, loc. cit., p. 517 (footnote).

[2] R. Zeiller, Bassin houiller et permien d'Autun et d'Épinac, fasc. ii, Flore fossile, 1890.

[3] Cf. R. Kühn, Ueb. d. anatomischen Bau von *Danaea*, Flora, 1890.

[4] Cf. especially Zeiller, loc. cit., Pl. XVIII, Fig. 2; XIX, Figs. 1, 2, 3; XX, Fig. 4.

periphery of the stem, the petioles of the leaf dying back to this region. Zeiller not only does not figure any leaf-traces as passing out through the root-zone, but in the text he expressly emphasizes their non-existence in this region. He explains their absence by supposing that, as in *Caulopteris endorhiza*, the original cortex was very thin, but that the parenchyma increased in amount behind the apex of the stem where the roots pass down through it. The external surface of the stem, together with the leaf-scars, is supposed to have become detached, leaving the root-traversed cortex exposed. But we find it difficult to accept this explanation without some reservation. It is not easy to see, even assuming the growth in thickness of the cortical parenchyma, how the vascular strands which originally passed through and across it, can have become so ruptured or have suffered such entire obliteration as to leave no trace of their existence, if the tissue in question is thus correctly interpreted. *Psaronius*, however, resembles *Angiopteris* in possessing, besides those roots related to the leaf-traces, others that may arise from within the central plexus of vascular strands. We have observed several instances in which they could be traced running across the cauline sclerenchyma in their outward course to join the peripheral zone of sheathing roots.

Turning to the parenchymatous tissue itself, in its relations with the roots, one is at once struck by a point of difference between *Psaronius* and Marattiaceae in an important particular. In the latter plants, the peripheral parenchyma of the root is sharply defined from the stem cortex, owing to the discontinuity of the tissues in development. The root is obviously an intrusive organ in the Marattiacean cortex. But in *Psaronius,* in the best preserved sections that we have seen, the outer cortex surrounding the zone of small-celled sclerenchyma, and forming a peripheral ring in the roots, passes almost insensibly into the parenchymatous tissue between them. Furthermore the cells of the latter are very irregular in character, often producing the effect of elongated cells 'combed' in various directions.

Is it possible that these cells of the supposed cortex belong to the periphery of the roots themselves, and are really of the nature of hairy outgrowths which have become woven into a pseudo-parenchymatous tissue? Whilst retaining an open mind on this question we are inclined to see in the suggestion a solution of some difficulties, which, in the face of the evidence we have been able to collect, appear to us to render the commonly accepted interpretation somewhat inconclusive. Such a weaving of hairy tissue does actually occur to a limited extent in some tree ferns of the present day; and if the roots really did enclose the stem, instead of traversing its tissues, the mechanical advantage of such an arrangement would be obvious, and at the same time the elaborate sclerenchymatous system which appears as a mechanical anomaly in the centre of a stem at once becomes intelligible, if the outer sclerenchymatous band really marked the external limits of the young stem.

We do not raise the question as to the affinity, or the reverse, of *Psaronius* with the Marattiaceae generally, but only desire to point out some of the difficulties at present in the way of accepting the equivalent character of the root-zone in the two cases as having been satisfactorily demonstrated.

INTERNAL STRUCTURE OF THE YOUNG SPOROPHYTE OF ANGIOPTERIS EVECTA.

The stem terminates below in a primary root containing a diarch vascular strand or stele (Fig. 8). The phloem is not always clearly marked from the pericycle, although with care the distinction can commonly be made out. The whole stele is surrounded by an extremely well-marked endodermis. Sometimes the protoxylem does not directly abut upon the endodermis, but may be separated from it by a layer of parenchymatous (pericyclic) cells, and the same feature may also recur in connexion with the structure of the few first-formed lateral roots, in which also a diarch or tetrarch character is retained. In the greater number of roots, however, the protoxylem clearly extends outwards as far as the endodermis, and even in the case of those which exhibit the exceptional features just alluded to, it commonly happens that it does not affect all the xylem rays of the root.

The transition from the root to stem is accompanied by a rearrangement of the vascular constituents of the stele. The diarch xylem-plate loses its definite outline, owing to a considerable increase in the number of its tracheids that appear on the sides of the plate (Figs. 9, 10), which thus causes the wood to become roughly circular in transverse section; at the same time the protoxylem loses its individuality and thus the diarch character becomes entirely lost or obscured. The phloem also extends over the whole periphery of the wood, and in this region it consists chiefly of parenchyma, the small cells of which are very clearly defined by reason of their striking protoplasmic contents and large nuclei. Sieve-tubes may be detected here and there, but they are not numerous, and they are very different from the large and well characterized sieve-tubes in the later-formed parts of the stems of older plants. They appear in these young stems as elements with thick and densely staining walls, and possess but little contents, and are thus clearly distinguishable from the adjacent phloem parenchyma. The sieves on their walls are very plain when examined in longitudinal sections. Callus, however, so far as we have been able to discover, is absent from the sieves.

When young plantlets are examined, the tissue lying just outside the xylem is seen to be in a state of division and new elements are in this way produced, which may retain their parenchymatous character, and thus more widely sever the protophloem from the wood, or some of the cells may undergo further change and become converted into tracheids which thus reinforce the primary wood of the stele. It is easy to find in suitable material all stages in a process which represents the commencement of a secondary thickening in these plants. In older specimens this phenomenon assumes a more striking aspect, as we shall describe later on.

Outside the phloem is a well-marked tissue bounded externally by a characteristic endodermis. The extra-phloic (pericyclic) parenchyma is cut off from a primary layer which also gives rise to the endodermis, as is so common in ferns. The parenchymatous layers internal to the actual endodermis become more numerous and easier to trace in older plants, and the common origin of the respective tissues is exceedingly clear.

The leaf-traces which pass out from this region of the stem are very simple, forming single strands, and their exit from the axile stele does not occasion the formation of foliar gaps in the ordinary sense of the expression. What happens is simply that a sector of the stele bends outwards towards the leaf, and then the loss of the tissues thus detached from the stele is at once made good above the exit of the trace.

But sooner or later the xylem ceases to form a solid axile rod. One or two parenchymatous cells appear in the centre, and form the commencement of a pith (Figs. 11, 12). The time at which this pith first appears varies greatly. It may be present in a rudimentary form when the first leaf-traces are formed, but more commonly it does not occur until after several of these have been given off; when it has once been differentiated it increases rapidly in importance, and then the subsequently produced leaf-traces begin to become associated with foliar gaps, inasmuch as the entire thickness of the now cylindrical vascular strand becomes involved in the formation of the leaf-trace. This occurrence of foliar gaps commonly begins in connexion with the sixth or seventh leaf-trace. But there is as yet no permanent disturbance of the 'monostelic' arrangement, for the gaps continue to be repaired as fast as they occur, and no phloem or endodermis is to be discovered within the cylinder of xylem. As the leaf-traces, however, become more numerous and the foliar gaps larger, the cylindrical vascular strand loses its first character. Traces succeed each other rapidly, and before the gaps left by older ones have quite closed. In this way the annular appearance, as seen in transverse section, disappears, and several isolated strands apparently replace the cylindrical strand below. Furthermore, the peripheral phloem, instead of remaining as a strictly external ring surrounding the cylindrical xylem, is seen to differentiate in an intravasating manner through a gap, and thus to 'dip down,' so to speak, into the pith. Then as the gaps close up above, this phloem, which has thus become 'invaginated' into the centre is found to have disposed itself as a mantle lining the internal surface of the wood (Fig. 23). The endodermis does not necessarily take any share in the process at least in these early stages, and thus the new phloem internally borders directly on the pith-parenchyma. It is only in rather exceptionally favourable instances that this pseudo-solenostelic condition can be clearly made out in *Angiopteris,* owing to the fractionation of the vascular cylinder in connexion with the increasingly crowded state of the foliar gaps. In *Marattia*, where the gaps are not so numerous, the character is more easily observed. The phloem on the inner and outer sides of the xylem is constantly continuous through the foliar gaps, and hence the appearance, as presented in sections, is given of a change from a 'monostelic' to a repeatedly branching 'polystelic' or 'dialystelic' condition. And owing to the reparation of the foliar gaps above the exit of the traces, 'gamostely' (or solenostely) is the rule, save for the absence of the internal endodermis. As the fractionation of the vascular cylinder progresses, however, the inner phloem also may come to be lined by an endodermis, and the arrangement thus brought about coincides with that stelar arrangement termed by Jeffrey[1] amphiphloic siphonostely, if the pith be regarded as excluded from the stele. We shall, however, discuss this point of view in detail further on.

It may be especially remarked here that the *external* endodermis is always present in all the plants of *Angiopteris*, *Marattia*, and *Kaulfussia* that we have examined. It is easy to demonstrate its presence by treating sections with sulphuric

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[1] E. C. Jeffrey, The development, structure, and affinities of the genus *Equisetum*. Mem. of the Bost. Soc. of Nat. Hist., v.

acid, and although in *Angiopteris* it might escape detection if only superficially looked for, we are at a complete loss to account for these statements, constantly repeated, as to its absence in the other two genera. *Kaulfussia* indeed is even a somewhat favourable object on which to demonstrate its occurrence (Fig. 16), as it can readily be rendered visible by careful staining as well as by the use of sulphuric acid. The existence of an endodermis which is thus proved to be present in the Marattiaceae is a matter of some interest, as its supposed absence has been looked upon as an important differentiating character between this group and the Ophioglossaceae. But after what has been said it is clear that no such line of argument can any longer be sustained.

As has now been pointed out, the vascular tissue early loses its primitive simplicity: not only does the central strand ultimately become dialystelic (siphonostelic), but the leaf-trace strands become more complex, first by becoming forked, from the point of their origin, and in still more advanced stems by further forming an increasingly elaborate network of anastomoses by which the series of zones distinguished by Mettenius are produced. Meanwhile the commissural strands previously alluded to are formed across the central (pith) parenchyma that is still enclosed within the original fractionating siphonostelic cylinder. These commissures at their first appearance are probably secondary in origin but they rapidly acquire a considerable degree of importance in relation to the peripheral vascular cylinder. The earliest formed commissures may consist chiefly or even entirely of phloem, starting as a local hypertrophy of this tissue on the inner surface of the xylem. They become detached from it higher up; and cross over to the opposite side of the siphonostele. Here they become reinforced by xylem elements, and a leaf-trace is commonly given off at the place where they join up with the tissues of the cylinder. It is, however, not very unusual to find some of these rudimentary commissural strands ending blindly in the central parenchyma, a fact which supports the view as to their secondary origin in such cases. As the stem grows and becomes larger, and the vascular system more complicated, the commissural strands gain in size, and completely resemble in structure that of the larger strands of the siphonostele forming the margins of the foliar gaps.

Allusion has several times been made to the addition of fresh elements to the tracheidal mass of the stele. A careful comparison with corresponding parts of the lower region of the stem in sporophytes of different ages suffices to awaken the suspicion that a secondary addition occurs in consequence of merismatic activity in the parenchyma outside the xylem [1]. That such is the fact is easily proved, for the new tracheids not only by their position are easily referable to their initial cells from which they respectively originated (Figs. 26, 28), but the various stages of their development may be traced with a certainty. The cells which undergo cambial division are commonly situated next the existing xylem, and they may occur singly or in groups. We have not observed any instances in which the whole parenchyma surrounding the xylem was at one time merismatic, but in favourable instances as many as six or eight such cells may be detected. The secondary wood thus formed is unimportant in amount, seldom exceeding three cells in depth, but the existence of secondary thickening in the Marattiaceae adds yet another example to those groups of Cryptogams in which it has been recognized, and shows that its presence is even less limited than has been supposed. Traces of it may still be found in larger stems, but in them it is of more isolated occurrence as compared with the younger plantlets. It is easily seen in *Marattia* (Fig. 22), but we have not been able to observe it in *Kaulfussia*.

In addition to this secondary formation of tissue within the stele, there is in *Angiopteris* considerable and very regular tangential division (Fig. 23) in the endodermal layer of the stem. In this way a number of radially arranged layers of cells are formed which may be as many as five to six in number. Commonly the outermost cell-row of this tissue assumes

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[1] T. G. Hill, Annals of Botany, xvi, p. 173.

(though faintly) the characters of an endodermis. It may perhaps be urged that this is merely the tangential division of tissue which has never yet become adult, but the extreme lateness of its occurrence is opposed to such an interpretation. It was thought that the anomalous position of the sieve-tubes, which, in *Angiopteris* as well as in *Marattia*, lie outside the protophloem, might be related to this activity, but we failed to find conclusive evidence that such was the case.

In *Marattia*, where the same thickening of the parenchyma bordering on the stele takes place, though to a much more limited extent, only very few layers are formed. The endodermis here is usually formed from the innermost layer if there is any secondary formation at all. This endodermis is a very well marked tissue, and is interrupted here and there by curious cells resembling the 'passage-cells' met with in the roots of many plants. Commonly these passage-cells undergo several tangential divisions, but the depth of the whole number of cells thus produced does not greatly exceed that of the adjacent endodermal cells.

Passing to the apical region of the stem, in which the stelar tissues are in process of differentiation, it is observed that the xylem of the leaf-traces is endarch in position, whilst that of the larger strands of the stem is inclined to assume a mesarch character. This practically confirms Mettenius's statement[1] as to the position of the spirally marked elements in cases in which they can be distinguished.

After examining a number of young plants we have come to the conclusion that the young stem possesses a single apical cell of a large size and of prismatic form, though somewhat irregular in transverse section. It sometimes has a more or less triangular form when seen from above, and it then presents a four-sided appearance. The place of origin of the leaves is clearly marked by the large apical cells which characterize their early condition.

The tannin cells which are so abundant in the leaves and roots are comparatively rare in the stem, except in connexion

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[1] Mettenius, loc. cit., p. 516.

with the bases of these organs. In the latter they form a circle around the stele, and the cells containing the secretion are apparent at a very early age. The presence of the tannin seems to be associated with a suppression of cell divisions, for the individual cells grow to a great length as the organ as a whole increases in size. They often form chains of cells which are continuous for a considerable distance, and in some cases at least we have found evidence that the cross walls separating two adjacent cells may break down[1].

The mucilage ducts, which are, unlike the tannin cells, chiefly confined to the stems in young plants, commonly make their first appearance within the pith, or horse-shoe shaped area of parenchyma which is formed when the continuity of the vascular cylinder is interrupted owing to the departure of the leaf-trace. At first, in the parenchyma exposed by the foliar gap, a mucilage duct is formed, and it dies away above, when the level is reached at which the gap is closed. Frequently, however, it branches below this, and one of the two limbs accompanies the leaf-trace for a short distance before ending blindly. The subsequently formed ducts may traverse a longer interval before ending blindly, but all of them, so far as the study of young sporophytes serves to illustrate them, are isolated and of no great length; they all divide before ending blindly, one of the arms passing out with the leaf-trace strand. They all arise lysigenously, as was stated by Kühn, at any rate in the young plants; we were not able to find any instances which admitted of explanation as having arisen schizogenously. Brebner[2] has described a schizogenous origin for those studied by him in species of *Marattia* and *Angiopteris*, and Lutz[3] states that their origin may be either schizogenous or lysigenous. The only instances we saw which could give rise to the appearance of schizogeny always proved to belong to the extreme upper ends of the lysigenous ducts. It would thus appear that at any rate the lysigenous origin is characteristic of the stems of the young plants, and therefore

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[1] Cf. Farmer, loc. cit.

[2] Journ. Linn. Soc., xxx.

[3] Journ. de Botanique, xii, p. 135.

should be regarded as the primitive type, the alternative form being, perhaps, confined to older ones. The general cortical parenchyma of the stem calls for no special mention, but it may be stated that the cells contain well-marked leucoplasts, and that their relation to starch formation can be very easily traced.

Roots. It has already been stated that the primary root is diarch. The first few lateral roots are somewhat variable in their structure, and often retain a diarch character. Then others appear which are triarch or tetrarch, and the latter are especially frequent. It is only by slow degrees that the more complex roots with their numerous rays of xylem and phloem put in an appearance. The roots arise, as has been already said, without any very definite relation to the leaves, a character which recalls the Ophioglossaceae. They also vary considerably both in old and young plants as to their attachment. Sometimes they unite with the more central strands, though far more commonly with those peripherally situated. The striking relation obtaining in *Kaulfussia* has already been described above.

They originate in the very young region of the stem, before it is possible to distinguish clearly the nature of the tissue from which they spring, though in all probability it should be referred to the endodermis. There appears to be a single initial cell in the first instance, of a prismatic six-sided form, and segments are cut off parallel to the elongated sides, and also from the distal end, the latter giving rise to the root-cap.

If transverse sections be examined which happen to pass through the root near its junction with the vascular tissue of the stem it will be often noticed that although as regards the radial arrangement of its xylem and phloem it conforms to the normal type of tissue arrangement, nevertheless it may exhibit an anomaly which recalls that already described for the primary and first-formed lateral roots, namely, that the protoxylem of many or even all the rays do not abut immediately upon the endodermis (which is sharply marked from the first) but are separated from it by one or more layers of pericyclic parenchyma. Possibly this unusual character should be correlated with the fact that the roots of these plants traverse a bulky mass of cortex before passing out to discharge their functions with which the normal structure is so obviously connected.

The cortical parenchyma of the roots whilst still enclosed in the stem-tissues frequently presents a curious appearance. The cells are elongated and their walls exhibit very regularly alternating transverse bands of thickening, the bars being separated by wider bands of unthickened wall substance. The whole somewhat recalls the scalariform markings of the tracheids, except that the bars are rather distant and the wide unthickened pits are not bordered.

Having thus considered the development and distribution of the vascular strands in the preceding stems, it still remains to attempt to correlate the structure thus elucidated more generally with the corresponding parts of other plants, and to ascertain what general conclusions, if any, can be arrived at as the result of our investigation. And at the outset of such an endeavour we are confronted by difficulties of various kinds. The most serious ones are occasioned by the divergent views which are entertained as to the 'typically' (or 'morphologically') distinct regions of the tissues themselves, but which nevertheless form the subject-matter out of which comparative estimates are derived. Moreover, we still possess surprisingly little accurate information as to the ontogenetic evolution of the variously complex tissue-arrangements which have so often within recent years formed the subject of anatomical memoirs. The unwieldy terminology that tends to further obscure the true relations of the vascular tissues of different plants to each other is also in part due to the fact, only just beginning to become appreciated, that certain complex types may originate in different ways from the non-differentiated embryonic tissue. We are threatened with the substitution of an elaborate but purely formal description of these various types, based on a totally inadequate knowledge as to their actual genesis, in the place of a rigorous appreciation of the really essential characters corresponding to real entities, the development of which can be definitely traced, and which, stripped of subordinate details, admit of consistent comparison both with one another at the various stages of ontogeny, and also with those structures which are homologous with them in other plants.

In dealing with the attempts to frame a morphological account of the tissues it is well to recognize at once both the possibilities and the limitations which necessarily attend any efforts made in this direction. The value, morphologically speaking, of a *tissue* appears to us to rest on a different footing from that of an external *member* such as a leaf; and for this reason; that the morphological nature of the latter is, in the vast majority of instances, already determined from its first appearance as a cellular outgrowth, and is entirely unaffected by the particular course of further development which it may undergo, and equally so by the nature of the differentiation which the cells and tissues composing it may exhibit.

But in estimating the morphological nature of a *tissue*, or even of a tissue region, we are on much less assured ground. Our criteria only become applicable as the adult condition is reached, or when, at any rate, cellular differentiation has so far progressed that we are able to recognize the characters which will stamp the tissue at its maturity.

Even the older attempts to found a morphology of the internal regions, which explicitly started from germinal layers, or what were believed to be such, left much to be desired; and the efforts which have been made since that time to combine more or less hypothetical embryonic limits with observed ontogenetic differentiation can hardly be regarded as entirely successful. The stele, at least in the stem, admittedly corresponds for the most part with actual tissues in course of differentiation, but woven into it are other conceptions such as phloeoterma and the like, which are of a more purely subjective nature.

It is worth while dwelling for a moment on the criterion (endodermis) which is employed to limit the stele from the rest of the tissues that lie outside of it, and are regarded as forming no integral part of it.

The endodermis is a tissue, on the importance of which great stress is often laid, perhaps on account of its obvious characters (when present) and perhaps also because we possess so very little knowledge as to its physiological significance. And yet this same endodermis is almost whimsical in the vagaries it exhibits both in respect of its non-appearance in places where it (theoretically) should be present, as well as in its frequent occurrence in anomalous situations.

Strasburger indeed, with the acuteness that always marks his treatment of intricate problems, clearly recognized the difficulty, and he frankly abandoned the endodermis as a delimiting zone of prime morphological importance. He, as is well known, proposed the term Phloeoterma to signify the band of tissue immediately lining the stele, and peripherally separating it from the cortex; and the existence of this phloeoterma is to be conceded, even when it cannot be objectively distinguished by special markings on its cell walls. But the special advantages of the term would really appear to be involved in a tacit assumption of its coincidence, or analogy, with the older form of demarcation as laid down by Hanstein. The latter writer, at least by implication, went farther back than the differentiating tissues to the meristems from which they took their origin. So long as 'monostely' alone is concerned the phloeoterma may serve, but in cases of polystely and schizostely, where it might be of critical value, it seems to possess but little advantage over the endodermis itself. For to put one of several aspects of the case, why should the entire limiting layer of vascular strands containing $1 + n$ bundles be regarded as a phloeoterma, whereas if there be but 1 bundle in the strand, part must be regarded as phloeoterma and the rest as endodermis? What is the special value of the addition of n bundles, that it should so alter the conception as to the 'morphological' nature of the sheath? But the confusion becomes incomparably more profound when the vascular continuity of the main cylinder or strand becomes interrupted as the result of the exit from it of the leaf-traces. Taking a 'medullated monostele' as the simplest case, the xylem at this period forms a cylinder of wood enclosing a pith or axile core of parenchyma, and is itself ensheathed in a continuous ring of phloem outside of which the endodermis is situated. For a time the gaps due to the exit of the vascular elements of the leaf-trace continue to be repaired, but sooner or later the reparation becomes insufficiently rapid, and a differentiation of phloem may proceed to extend round the edges of the gap and coat the inner face of the xylem. This may be, and usually is, accompanied by a similar differentiation of endodermis. Henceforth, the central parenchyma is no longer regarded as belonging to the stele, although it may continue to occupy the same position in the vascular cylinder taken as a whole, but is considered as now belonging to the cortex of the stem. Essentially it is the 'extension' on the part of the phloem and endodermis, but especially the latter, which has made the difference. The various forms of polystely, dialystely, schizostely, with their correlatives gamostely and gamodesmy, merely form variants of the process depending respectively on the degree of union or separation of the vascular constituents.

It may happen, however, that the development proceeds on somewhat different lines, and that within the vascular cylinder phloem or endodermis, or both, may be differentiated within the xylem from the whole or the peripheral portion of the axile parenchyma. In this way are produced the various phases of siphonostely[1] and solenostely[2], which, however, become indistinguishable from the other above-mentioned types of stelar arrangement, as soon as the continuity of the tissues has been broken by the foliar gaps.

Jeffrey's conception of the siphonostele[3] was designed to

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[1] In the sense of the term as employed by Jeffrey.

[2] Cf. Gwynne-Vaughan, Observations on the Anatomy of Solenostelic Ferns. Annals of Botany, xv, p. 73.

[3] E. C. Jeffrey, The development, structure, and affinities of the genus *Equisetum*. Mem. of the Boston Soc. of Nat. Hist., v, p. 160.

embrace those cases in which the vascular tissues had passed out of the protostelic condition (in which a solid core of xylem occupies the axis of the stele), but he retained the inner endodermis as an essential constituent delimiting the inner region of the stele from the axile parenchyma, which he rightly, as we think, regards as not belonging to it.

We regard this as a step in the right direction, but in our opinion Jeffrey has not gone far enough. The great advantage which the idea of the siphonostele possesses over that of the monostele for us, lies in the emphasis which it throws on the unity of the *vascular tissue as a whole* as opposed to the circumjacent ground-parenchyma, instead of merely laying stress on one particular arrangement or collocation of tissues which may or may not be preserved in its integrity according to the nature, firstly, of the foliar gap development, and secondly, of the internal differentiations which may occur in connexion with them. We prefer, as a preliminary step, to dissociate the stele altogether from the endodermis which is certainly not always present. For us it is a matter of absolutely subordinate importance whether there is an internal endodermis or not; and, so far as we know, there is no inherent or *a priori* need of postulating its theoretical existence when it cannot be objectively demonstrated.

The inherent weakness of the position which relies on the existence of an internal endodermis, as forming an essential zone of demarcation of the stelar tissue from the medullary parenchyma, is rendered manifest by many test cases in which it may or may not be present. Thus in the young rhizome of *Helminthostachys zeylanica*[1] it does not occur, whilst it appears fitfully and irregularly within the steles of older plants.

Again, the case of the genus *Botrychium* is of interest in this connexion. Van Tieghem[2] regarded the stem of *B. lunaria* (together with the other members of the Ophioglos-

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[1] Farmer and Freeman, On the Structure and Affinities of *Helminthostachys zeylanica*. Annals of Botany, xiii. Cf. also W. H. Lang, Prothalli of *Ophioglossum pendulum* and *Helminthostachys zeylanica*. Annals of Botany, xvi, p. 43.

[2] Van Tieghem, Remarques sur la structure de la tige des Ophioglossées. Journ. de Botanique, t. iv.

saceae investigated by him) as monostelic up to the formation of the first leaf. Above this an internal endodermis appears, and the arrangement becomes in consequence astelic, and, from the mode of grouping of the individual bundles, gamodesmic. But in *B. virginianum*, according to Jeffrey[1], the medulla is not separated from the xylem by an internal endodermis, and thus, to use the terminology of Van Tieghem, there is a perpetuation of the monostelic condition. That is, in closely related forms there exists a fundamental difference in the 'morphological structure' of their stems, as decided by the criterion of the endodermis.

Perhaps, however, the best examples of its irregular distribution are afforded by the Osmundaceae which have recently been investigated by Faull[2]. The stems of these Ferns are siphonostelic, the vascular tissue being arranged in a cylindrical fashion round an axile pith. But it is only in one species, *O. cinnamomea*, that this pith is delimited by an endodermis from the vascular strand. It is on this ground that the Osmundaceae are held to be siphonostelic, and the absence of the endodermal criterion is looked on as a consequence of degeneration, a view which seeks support in the occasional presence of internal phloem (also confined to this species) which is, however, restricted to the regions where the stem is forking. We question the legitimacy of the argument, and dissent from the conclusions as to degeneration. But we entirely agree with the author in the appropriateness of the term siphonostele as applicable to the vascular tissues of the stems of all these plants, though our reasons, as will have become apparent above, are not quite identical with his own.

By thus emphasizing the *vascular tissues* as the feature of paramount importance, the pith is reduced to a subordinate position, similar to that which it occupied in the systems of De Bary and Sachs. But we become the gainers at least

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[1] E. C. Jeffrey, The Gametophyte of *Botrychium virginianum*. Trans. of the Canadian Institute, v, pp. 283-4.

[2] Faull, The Anatomy of the Osmundaceae. Botanical Gazette, xxxii.

in this, that we are thereby emancipated from the highly artificial considerations such as begin by regarding the pith as an integral part of the unit (the monostele), and then proceed to disregard or deny its further existence as soon as the peripheral mantle of phloem, pericycle, or endodermis shall have extended around the inner face of the xylem. Such a point of view seems to us to originate in and depend upon a one-sided and abstract contemplation of isolated transverse sections, and to omit all reference to the mutual relations of the tissues to each other, as continuous and concrete realities in the body of the plant. By concentrating attention on the vascular strand as the thing of real importance, whether it be present in the form of a solid rod (protostele) or as a hollow cylinder (siphonostele), one is equally concerned with a definite unit, and the various transitions to polystely, &c., become clearly referable to a single plan, and their several relations become at once obvious. It is the inclusion of the pith as an integral part (which has to be subsequently discarded) together with a strained and artificial criterion as to the boundary of the stele, that seem to us the fatally weak points in the whole stelar theory, and which have resulted in unnatural interpretations being given in not a few instances of structures that do not conform to the more ordinary types of stem structure.

It may, perhaps, be objected that inasmuch as all gradations may be traced between a xylem parenchyma that is intermingled with tracheids, and a true pith such as forms the core of a 'medullated monostele,' this in itself constitutes a sufficient reason for not dissociating it from the vascular tissues in defining our conception of the stele. Similar objections could probably be urged against most morphological distinctions, and certainly against all which are affected by tissue differentiation. The whole matter is really a question of consistency and convenience. If the inclusion of the pith in the stele is, however, no longer conducive to a clear comprehension of the latter in its comparative relationships, and still more if it can be shown rather to obscure them, then it is best to enforce the distinction. In any event, to render its inclusion or exclusion contingent on the differentiation of a zone (endodermis) notoriously uncertain, and inconstant even in nearly related forms, appears to us as a gratuitous introduction of a confusing element into a subject already sufficiently provided with artificial difficulties.

It would appear to be probable that no right understanding of a difficult vascular structure is possible apart from a study of its ontogenetic development. Only in this way can the complex arrangements, such as may occur for example in the stems of many lianes, be understood and referred to the relatively simple condition typical of the great majority of dicotyledons.

But although we are unable to accept, at least in their entirety, the views held in many quarters as to the morphological relations assumed to subsist between the various tissues, we are far from underrating the value of evidence derived from a study of comparative anatomy in dealing with questions of affinities. On the contrary, we are completely in accord with those who regard such evidence, when properly sifted and checked, as of great value; and it is largely on this very account that we have felt bound to state our grounds for diverging from the opinions entertained by many others as to the importance of the quasi-morphological relationships of the various tissue-systems to one another. But, as with all characters, the value of those which can only be distinguished by the aid of a microscope requires to be appreciated with caution and applied with care. Perhaps, indeed, anatomical characters need this even more than most others, on account of the relative ease with which so many of them are apparently susceptible to alteration or suppression.

To return to the structure of the Marattiaceae, we may summarize our results as follows. The stem of *Angiopteris*, and that of *Marattia* is in close agreement with it in all essential respects, contains in the young plant a single solid protostele. In the centre of the xylem, certain cell-rows cease to differentiate as tracheids, but proceed to give rise to a parenchymatous pith which we regard as distinct from the now tubular stele. The latter forms at this stage a hollow cylinder or siphonostele, although in using the latter word we do not, as already explained, attach to it precisely the same meaning as Jeffrey did when he originally defined it. Nevertheless our own view forms so simple an extension of that put forward by the Canadian botanist, that we have not hesitated to retain his terminology in preference to coining a new word.

The siphonostele thus formed becomes more or less broken up, giving rise to those kinds of vascular arrangements which have been elsewhere designated as 'polystelic' or 'dialystelic,' as well as to the concomitant appearances of 'gamostely' or 'solenostely' as the foliar gaps are intermittently repaired.

The earliest important change in the arrangements of the siphonostelar tissues results from a differentiation, in a more or less continuous sheet, of phloem on the internal face of the xylem. We have not, as already stated, succeeded in making out a good case for the occurrence of a regular internal endodermis, except as a late and purely secondary occurrence, and it is in this respect that our plant in its earlier stages departs, objectively, from the siphonostelic condition as defined by Jeffrey. Such a departure is not very uncommon amongst the Ferns. We have alluded to the case of the Osmundas, and *Schizaea*[1] supplies a similar example. The tubular vascular strand is not delimited from the pith by any special layer, nor is there any internal phloem. On the other hand, the young plantlet of *Aneimia phyllitidis*[2] only resembles *Angiopteris* in the protostelic stage. Its subsequent condition is solenostelic, or it might also be cited as an example of amphiphloic siphonostely in Jeffrey's sense. Internal phloem and endodermis are, however, developed in this plant directly, in contradistinction to what obtains in *Angiopteris*, as a differentiation of intraxylar tissue without reference, in the first instance, to the external corresponding tissues of the

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[1] L. A. Boodle, On the Anatomy of the Schizaeaceae. Annals of Botany, xv, p. 373.

[2] Boodle, loc. cit.

foliar gaps. It is only subsequently that the inner and outer phloem and endodermis become united by way of the leaf gaps. In *Angiopteris*, as has already been pointed out, the internal phloem clearly arises in relation to, and in consequence of, the occurrence of the leaf gaps. Again, in *Platyzoma microphyllum*[1] there is no internal phloem, but a well-marked endodermis, whilst in *Helminthostachys* there is only an irregular internal endodermis in the older stems, the young plants being quite destitute of any tissue, apart from pith-parenchyma within the xylem. The latter point is singular, since, according to Poirault[2], precisely the reverse obtains in *Botrychium*. But it is of interest to note that, in spite of these very diverse modes of development and of completeness, the siphonosteles all exhibit, as seen in transverse sections, the 'polystelic' or 'dialystelic' condition in consequence of the enlargement and frequency of the foliar gaps.

The examples thus quoted might be greatly extended and amplified; they may serve to show how readily the vascular system of the Ferns may be treated from a comparative standpoint, if the salient and more permanent features are clearly divested of variable details of subordinate importance; and in this connexion the principal characters and mode of fractionation of the vascular strands and the primary relation of the process of the leaf gaps is clearly of first-rate importance. Cases of apparent exceptions, e. g. *Kaulfussia*, in respect of the ventral gaps in the siphonostele, are readily brought into line with the rest. But the degree of importance of this or that tissue in the composite strands themselves is shown by comparative anatomy to be a feature of minor significance, inasmuch as considerable variations may exist not only in related forms, but also in the body of one and the same individual.

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[1] Boodle, On the Anatomy of the Gleicheniaceae. Annals of Botany, xv, p. 735.

[2] Poirault, Rech. anat. sur les Cryptogames vasculaires. Ann. Sci. Nat. (Bot.), sér. 7, t. xviii.

EXPLANATION OF FIGURES IN PLATES XVI, XVII, XVIII.

Illustrating Professor Farmer and Mr. Hill's paper on the arrangement and structure of the vascular strands in *Angiopteris evecta, &c.*

Abbreviations.

a. apical cell; *cb.* cambium; *com.* commissure; *c.t.* (Fig. 22) crushed tissue; *end.* endodermis; *f.g.* foliar gap; *l.t.* leaf-trace; *p.* parenchyma; *ph.* phloem; *p.r.* primary root; *p.x.* protoxylem; *rt.* root; *r.a.* apical cells of root; *st.* stele; *s.t.* sieve-tube; *t.2.* secondary tracheids; *t.s.* tannin sac; *x.* xylem; *x.p.* xylem parenchyma.

Fig. 1. Young stele of *Angiopteris evecta*, side view (× about 50).

Fig. 2. Older stele, two foliar gaps are seen near the apex.

Fig. 3. Portion of stele of older plant showing the foliar gaps.

Figs. 4, 5. Two different views of the stele of a still older plant showing the transition from the preceding simple, to a more complicated, structure. (The numbers of the roots and leaf-traces refer to the same individual members in the two figures.)

Fig. 6. Stelar system from a much older plant. (The natural proportion between the length and breadth is here somewhat exaggerated, in order to render the parts more distinct.)

Fig. 7. Upper portion of a siphonostele of *Marattia fraxinea* viewed obliquely from above; × 12 (cf. Figs. 20 and 21).

Fig. 8. Transverse section of the primary diarch root of *Angiopteris.*

Fig. 9. Section from the same root in the transitional region between root and stem.

Fig. 10. Section from the same still higher up showing formation of intraxylar parenchyma.

Figs. 11–13. *Angiopteris.* Transitional region from another series showing formation of a pith (× 170).

Fig. 14. Longitudinal section or apex of stem of *Angiopteris* showing apical cell.

Fig. 15. Transverse section of apex of stem of *Angiopteris.*

Fig. 16. *Kaulfussia aesculifolia.* Transverse section of stele showing endodermis.

Fig. 17. *Angiopteris.* Transverse section of stem showing the exit of a leaf-trace, *lt.*, and the fusion of a root stele, *rt.*, with the central strand.

Fig. 18. *Angiopteris.* The origin of a root in the apical region of the stem. *x.a.* Root apex.

Fig. 19. *Angiopteris.* Central strand, root, and leaf-trace, with sieve-tubes within the stele.

Fig. 20 (cf. Fig. 7). *Marattia.* Stelar system as seen obliquely from above.

Fig. 21. The same viewed from the side.

Fig. 22. *Marattia.* Transverse section of stele in the stem, showing merismatic tissue. Endodermis well marked.

Fig. 23. *Angiopteris.* Transverse section of the stem with secondary tracheids and an internal phloem.

Fig. 24. *Angiopteris.* Leaf-trace.

Fig. 25. Same with increased development of xylem (× 290).

Figs. 26, 28. *Angiopteris.* Transverse section of stem, showing secondary formation of tissues.

Fig. 27. *Angiopteris.* Division in extra-stelar tissue. Longitudinal section of the stem.

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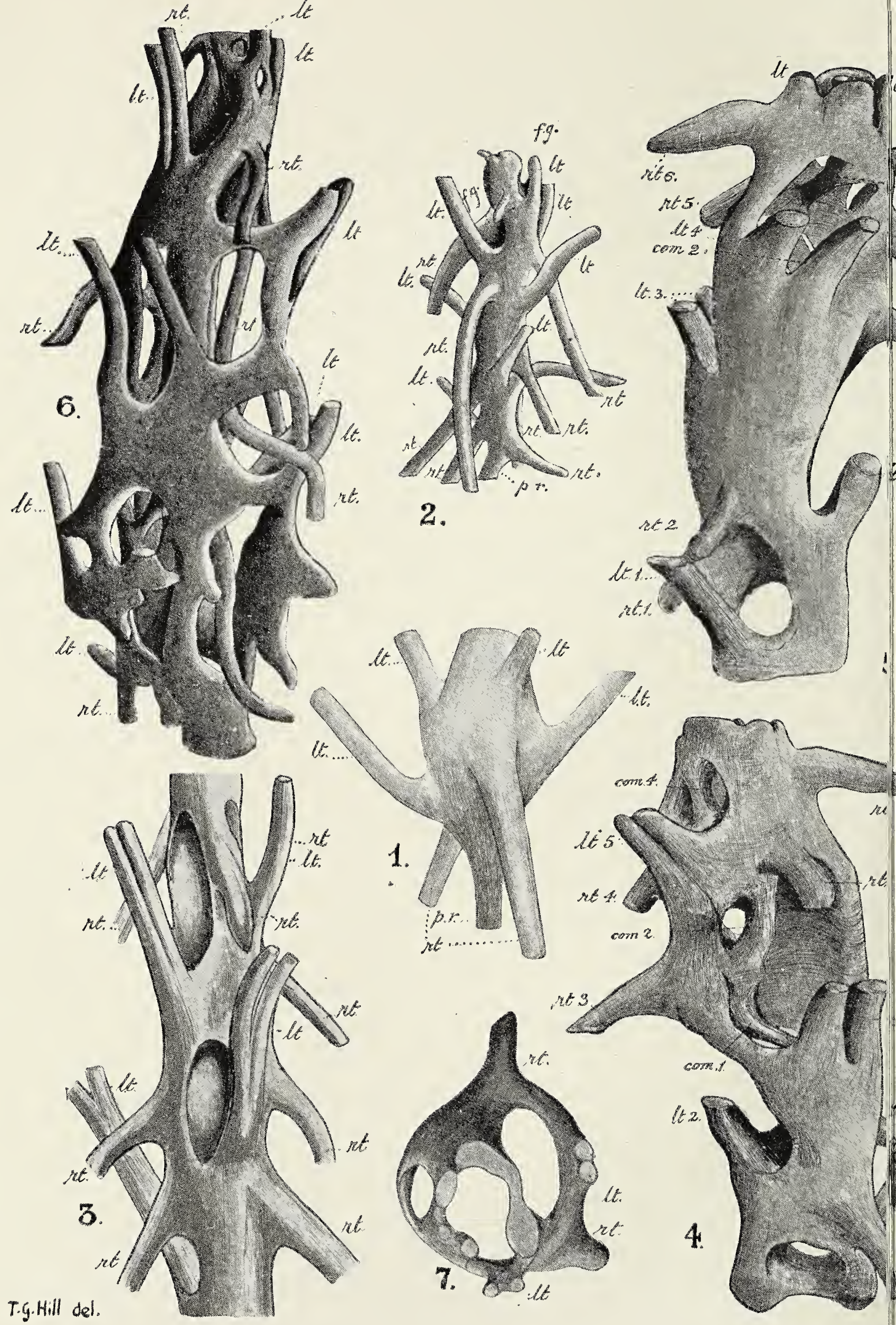

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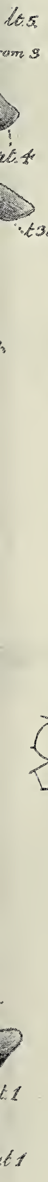
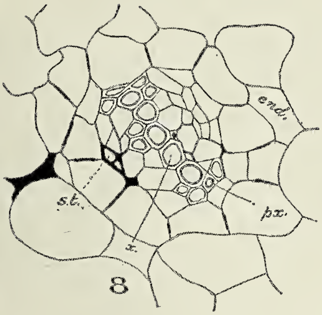
FARMER AND HILL.—AN





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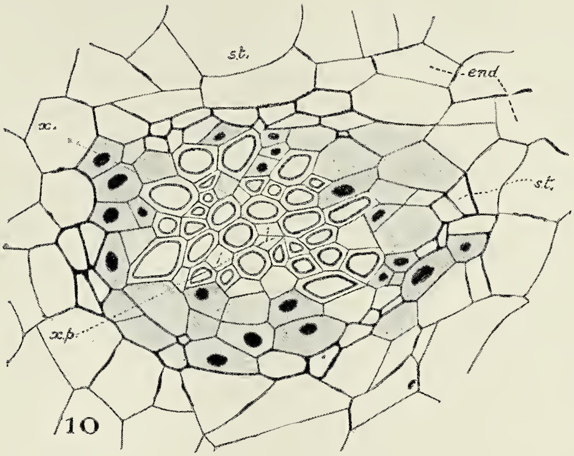

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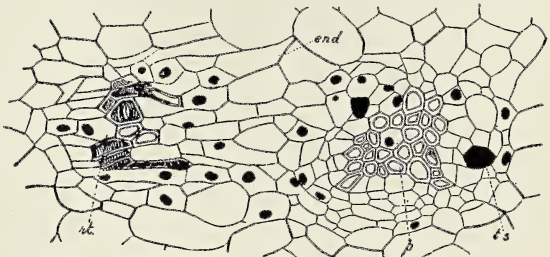

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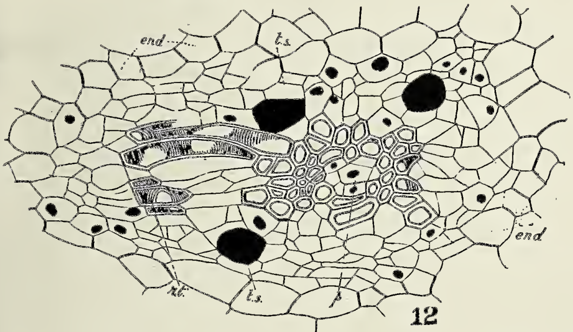

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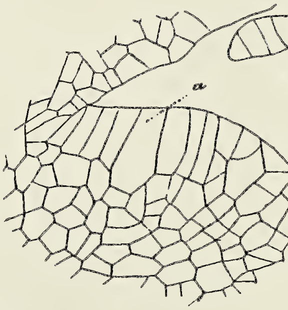

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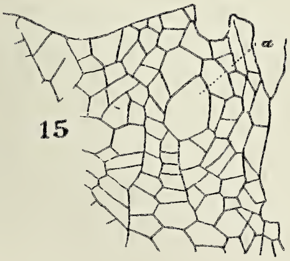

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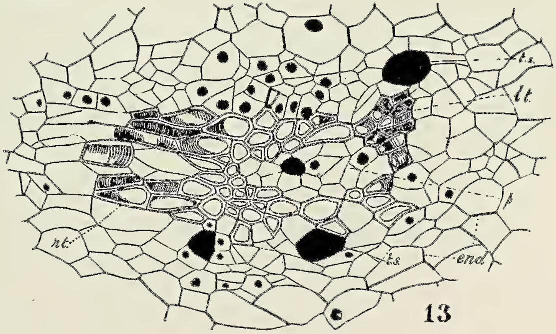

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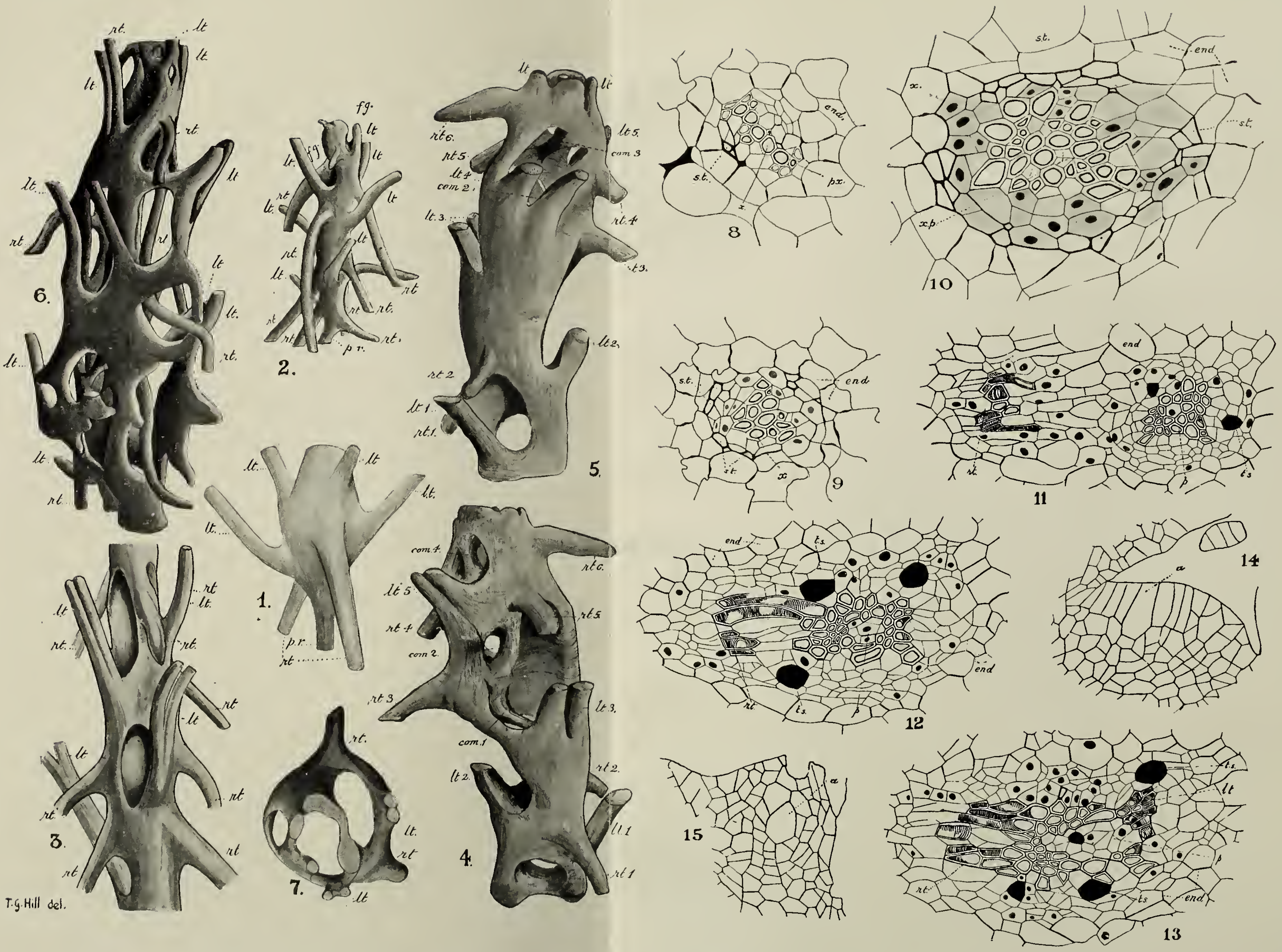

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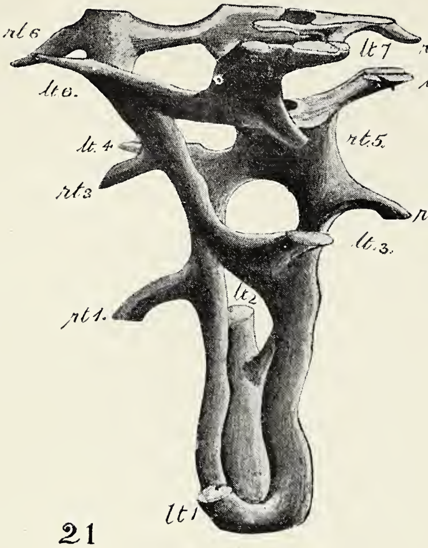

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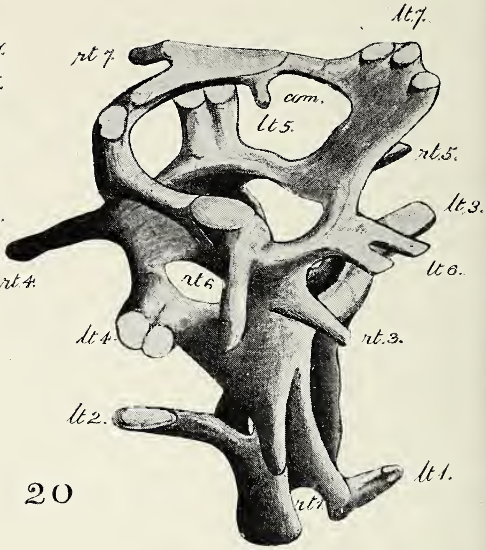

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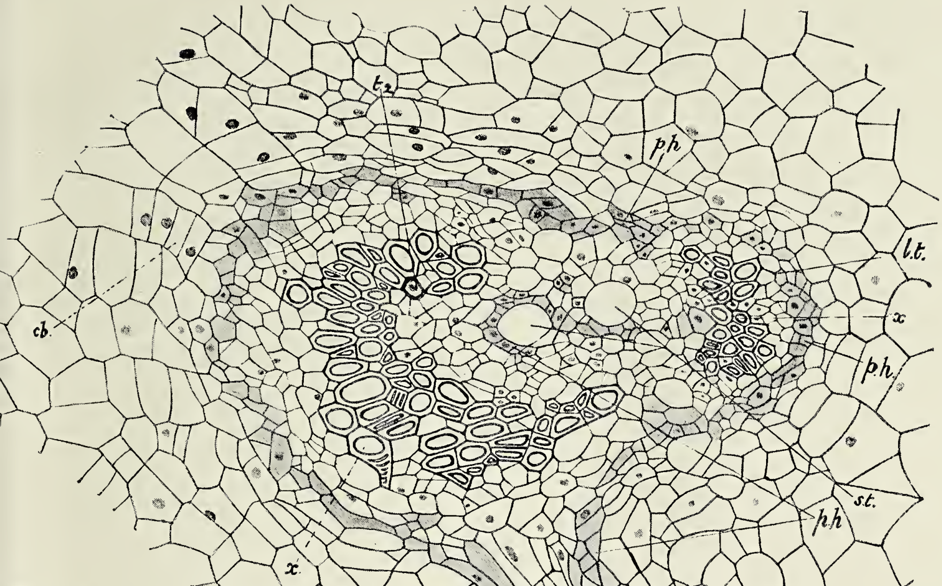

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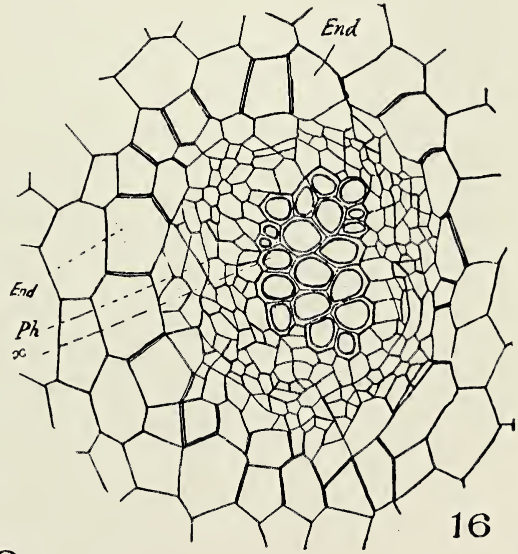

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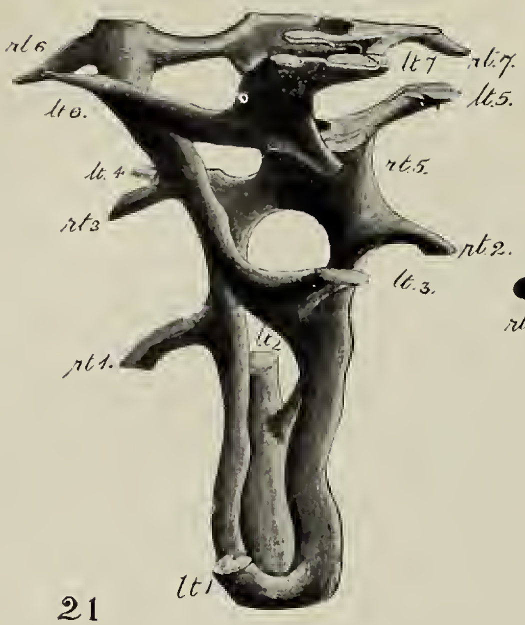

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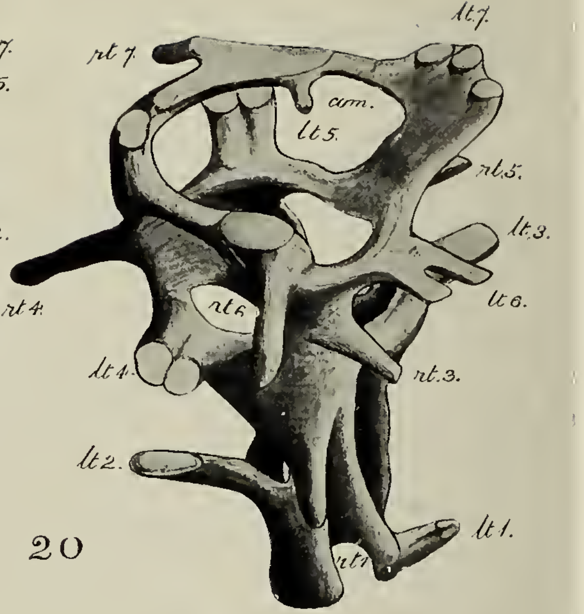

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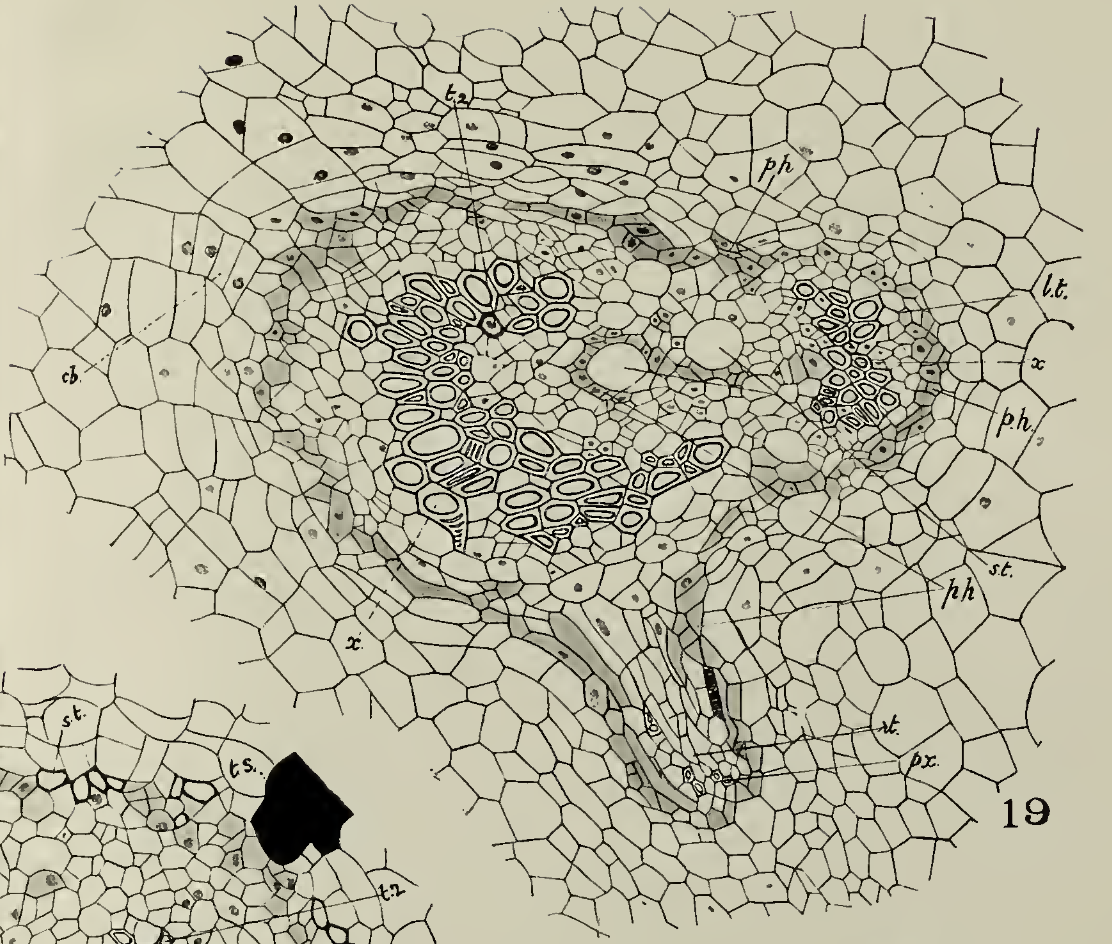

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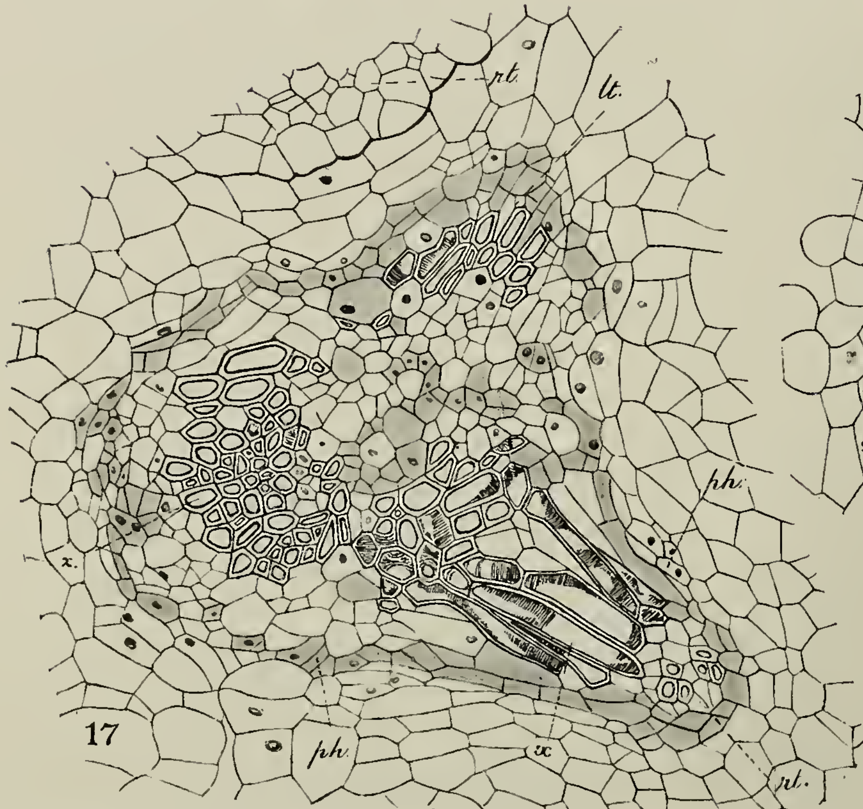

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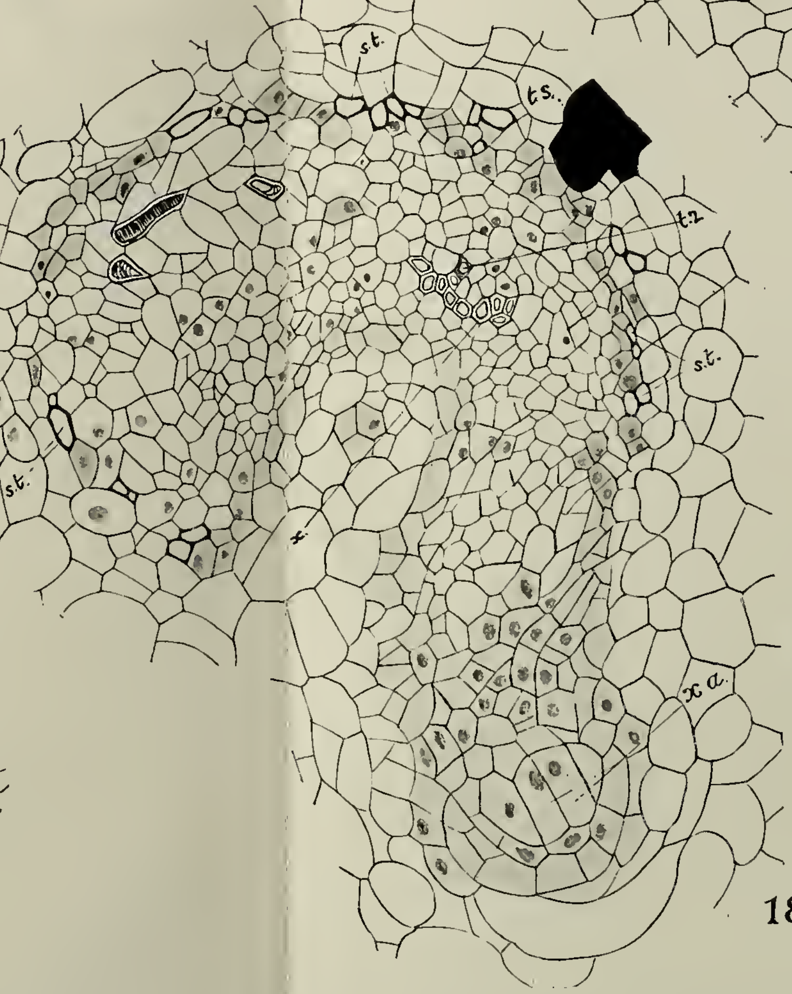

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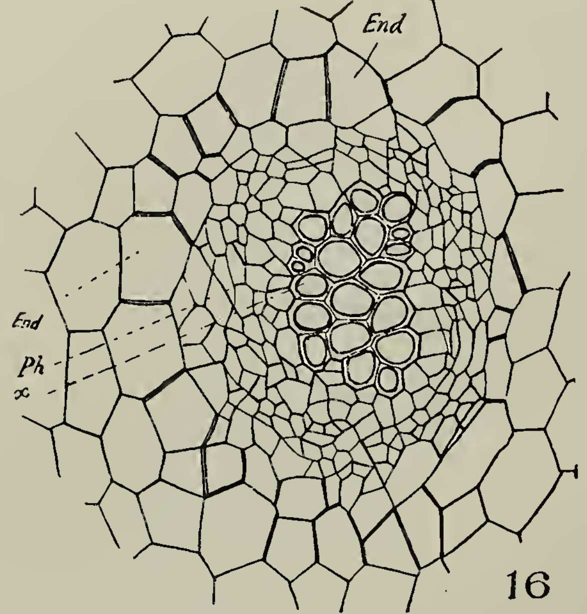

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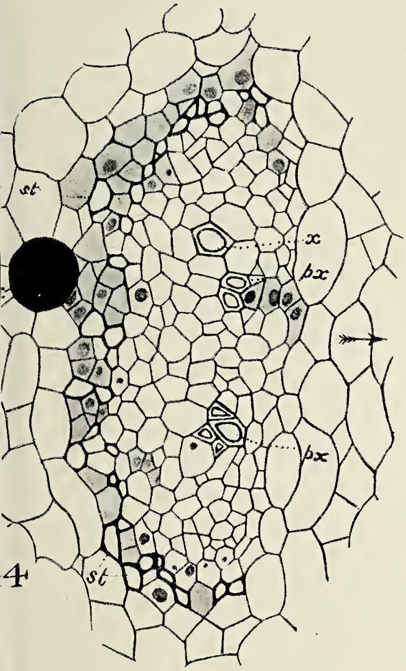

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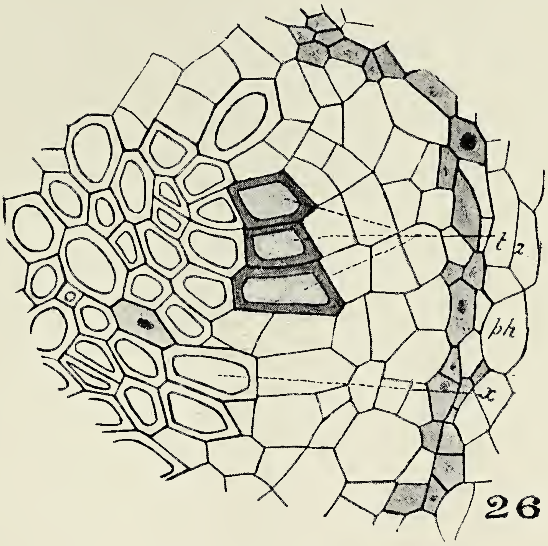

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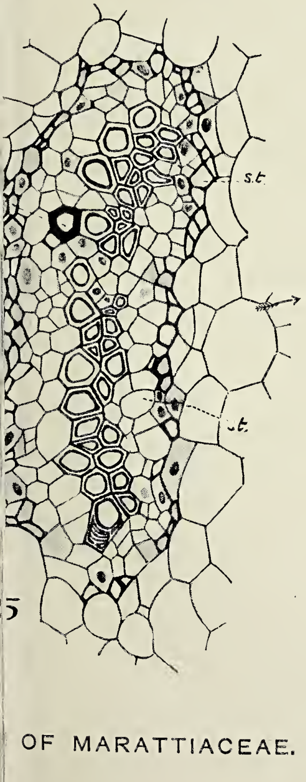

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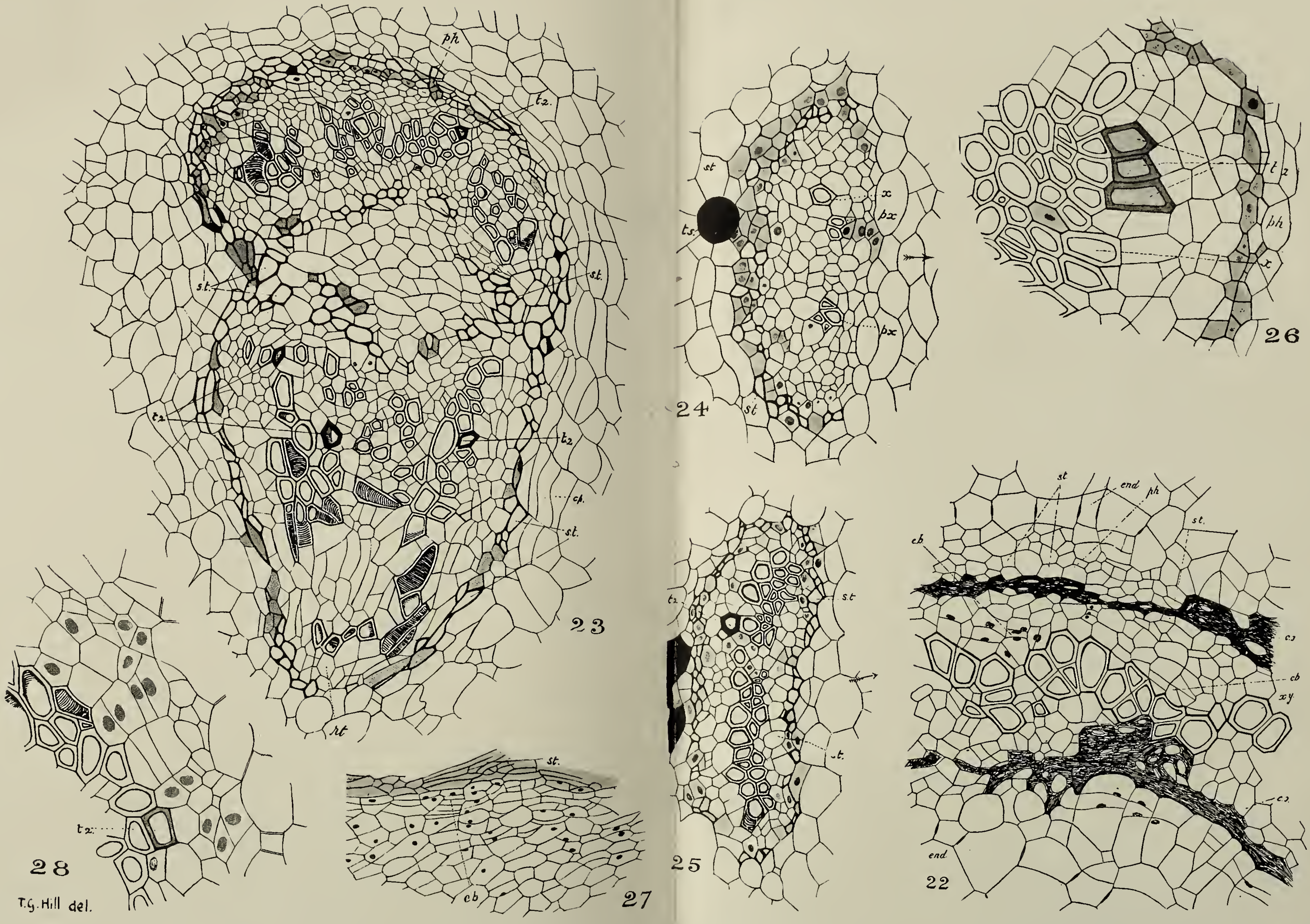

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FARMER AND HILL.—ANATOMY OF MARATTIACEAE.

NOTES.

ALGOLOGICAL NOTES.—

I. OBSERVATIONS ON SPECIES OF APHANOCHAETE, Braun.—Last autumn, whilst examining a mass of Algae, collected in a ditch on Sheen Common, near Richmond, I found a large quantity of an epiphytic species, growing on *Cladophora*[1] (*fracta*, Kütz). A closer examination showed it to belong to the genus *Aphanochaete*, A. Br. Each individual consists of a short filament, of usually only 2–4 cells, although longer filaments of 6–10 cells are not rarely met with (see Fig. 22, 1). Branching of the filaments is exceedingly rare, but the short 2–3 celled individuals may be so closely collected together, that a sort of cushion is formed, which quite obscures the *Cladophora* at that point. The cells of the filaments are more or less spherical in outline, containing a single large pyrenoid (Fig. 22, 6 and 7), and usually filled with large numbers of starch-grains. These latter so obscured the chloroplast, that I was unable to determine its exact structure. There seemed, however, to be only one present, more or less parietal in position, and differentiated so as to appear as a number of grains lining the wall of the cell. Each cell bears a variable number (2–5) of hairs, which sometimes attain great length, quite thirty times that of the cell from which they arise. These hairs are shut off by a transverse wall from the cell below, and their basal portion is more or less swollen to form a kind of bulb. Above this the diameter and therewith the lumen of the hair gradually decreases in magnitude, the apex being often so fine, that it requires careful focussing to see it properly. Certain highly refracting portions in the course of the hair look very much like transverse walls, and make it appear multicellular (Fig. 22, 7).

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[1] Intermingled with the *Cladophora* was a species of *Spirogyra*, and although at some points the former was crowded with the epiphyte, I never saw a single individual on the *Spirogyra*. As far as I am aware no species of *Aphanochaete* has as yet been observed on *Spirogyra*, although frequently on the allied genera, *Mougeotia* and *Sirogonium*.

[Annals of Botany, Vol. XVI. No. LXII. June, 1902.]

Although I have observed this Alga at intervals for a period of over six months, I am as yet unable to give any details as to the method of reproduction. Cells were frequently observed, in which the contents had divided into two masses along a plane parallel to that of the ordinary vegetative division of the cells; each portion contained a pyrenoid. In other cases cells were found, in which the contents were still undivided, but contained two pyrenoids. These are probably stages in the formation of zoospores. (Cf. Braun, Rejuvenescence; Huber in Bull. Soc. Bot. France, XLI.)

These points agree to some extent with the description and figures Hansgirg[1] has given of his *Herposteiron polychaete*, and I believe that the Alga I have just described is possibly identical with this species. Especially Hansgirg's Fig. 5 has a very similar appearance to my Fig. 1. Hansgirg however says (loc. cit.): 'Die Fäden von *Herposteiron polychaete* Hansg. sind mehr oder weniger reichlich verzweigt, die Verzweigungen auf der Unterlage . . . kriechend, seltener treten auch einzelne aufrechte . . . Aestchen auf.' Such upright branches he shows in Fig. 1, and I must say, that I have only very rarely observed them in the Alga in question, and they were even then not nearly so well developed as Hansgirg's figures show. It was probably the occurrence of these upright filaments that led Hansgirg to regard this species as being only a stage in the development of some *Stigeoclonium* or *Chaetophora*, and indeed his Figs. 1–3 look rather like young *Stigeoclonium* plants. Although I have had my Alga under cultivation in various conditions for over six months, I have seen nothing to warrant the assumption that it is a stage of evolution of some higher form. Finally, the hairs which Hansgirg figures on his plant have such very definite transverse walls, that they could scarcely be due to a false articulation, as in the case of the species I have examined. They very much resemble the hairs of *Stigeoclonium*.

Hansgirg[2], in 1888, gave a new scheme for the classification of the species of the two genera *Herposteiron* and *Aphanochaete*. The latter

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[1] Flora, 1888, p. 214, and Plate XII, Figs. 1–5. Klebahn (Zur Kritik einiger Algengattungen, Pringsheim's Jahrb. f. wissenschaftl. Bot., vol. 25, 1893, p. 295) has no right to state that Hansgirg's diagnosis of *H. polychaete* lacks an illustration, as the figures were published in a later number of the same volume.

[2] Ueber die Gattungen *Herposteiron*, Näg., und *Aphanochaete*, Berth. non A. Br., Flora, 1888, p. 211.

genus was established by Braun[1] in 1851. Later, Berthold[2] described a species under the same name as Braun's (*Aphanochaete repens*) considering that there was not sufficient reliable evidence for a specific separation. He found that his plant differed from that of Braun in possessing zoospores, which were enclosed in pairs in a delicate membrane at the time of liberation, and provided with four instead of two cilia. The hairs also were not articulated, and were swollen distinctly at the base. Rabenhorst[3] had cast considerable doubt on Braun's observations by the figures, which he gives of *Aphanochaete repens*, Br., in which he figures zoospores with four cilia, at first enclosed in pairs in a membrane. As Rabenhorst[4] mentions only having seen the authentic dried specimens, it was difficult to understand how he came to figure zoospores, differing so markedly from those described by Braun. This matter has been partly cleared up by Klebahn[5], who publishes a note found amongst Braun's manuscripts after his death; this shows that Braun had once more observed the formation of zoospores, and had come to the conclusion that there were four instead of two cilia. Although he mentions the occurrence of the zoospores in pairs, he did not observe the membrane described by Berthold in his species. Undoubtedly, however, Rabenhorst had seen this note of Braun's, and had taken his figures from those appended to the note. All species of *Aphanochaete* at present known possess zoospores with four cilia.

Although, as we see, there was thus little reason for separating Berthold's species from Braun's, Hansgirg[6] established for the former a new genus *Aphanochaete*, Berth. non A. Br., at the same time merging the *Aphanochaete* of Braun into the genus *Herposteiron* of Nägeli, the distinctions drawn between this latter genus and *Aphanochaete*, Berth., being that the former had multicellular hairs, which were destitute of a sheath, whereas the latter had unicellular hairs provided with a delicate sheath at the base. In the genus *Herposteiron*, Näg. (=*Aphanochaete*, Br. non Berth.) were placed three species: (1) *repens* (A. Br.) Wittr. (*Aphan. repens*, A. Br. non Berth.), (2) *con-*

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[1] Betrachtungen über die Erscheinung der Verjüngung in der Natur, 1849–1850, p. 196, foot-note. English Transl. by Henfrey, 1853, p. 184, foot-note.

[2] Untersuchungen über die Verzweigung einiger Süsswasseralgen (Nov. Act. Ac. Leop. Carol. XL, 1878), pp. 214 and 215.

[3] Flora Europaea Algarum, III, p. 304.

[4] Loc. cit., p. 391.

[5] Pringsheim's Jahrbuch, vol. 25, 1893, p. 288.

[6] Flora, 1888, p. 216.

fervicola, Näg., (3) *polychaete*, Hansg. The genus *Aphanochaete*, Berth. non A. Br., included: (1) *repens*, Berth. non Br., (2) *globosa*, Nordst. (*Herp. globosa*, Nordst.), (3) *vermiculoides*, Wolle, (4) *polytricha*, Nordst.

Although De Toni [1] and Wille [2], to some extent, adopted this system of Hansgirg's, it was soon to be attacked by Möbius and Huber. The former [3] points out on p. 85 that Rabenhorst's Fig. 114 *a* (loc. cit.) of *Aphanochaete repens*, Braun, although agreeing in other respects with Braun's description, seems to indicate that the hairs are not truly septate, but only contain a number of masses at definite distances from one another. Further on (p. 97) he describes the development and structure of the hairs in a species, which he takes to be *Herposteiron confervicola* (A. Br.) Hansg.[4] He describes the development of a thin sheath round the base of the hair, and denies the presence of any articulations in the hairs of this species. According to Hansgirg, however, the presence of a sheath would preclude the possibility of the hair being articulated, for the species Möbius examined must then belong to the genus *Aphanochaete*, Berth., and not to *Herposteiron* at all.

Huber [5] examined the original specimens of *Herposteiron confervicolum*, Näg., *H. repens* (Br.) Wittr., and of *Aphanochaete*, Berth. He found that in all three the hairs were simple and unicellular, and showed that what Braun had taken for transverse walls in his *Aphanochaete repens* were really only 'bouchons d'une matière réfringente qui fait apparaître le poil comme indistinctement articulé' (loc. cit., p. 327). I have been able to show the same for the species from Sheen Common, which I think may probably be identical with *Herposteiron polychaete*, Hansg. If the young hairs, which appear

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[1] Sylloge Algarum, 1889, p. 179.

[2] Natürl. Pflanzenfam. I. 2, pp. 94, 95. Quite recently West (Algal Flora of Yorkshire, 1901) also adopts this system.

[3] Morphologie der haarartigen Organe bei den Algen. Biologisches Centralbl., 1892, vol. xii, pp. 85, 97.

[4] Hansgirg later (Flora, 1888, p. 505) united *Aphanochaete repens*, Br. = *Herposteiron repens* (Br.) Wittr. with *Herposteiron confervicola* Näg. I do not quite understand what Möbius means by the two authors' names he places after his species (cf. also Klebahn, loc. cit., p. 292). Möbius also examined *Aphanochaete globosa*, Nordst. (p. 104); in which he found a distinct sheath, as has been observed by other investigators.

[5] Observations sur la valeur morphologique et histologique des poils et des soies dans les *Chaetophorées*. Journal de Botanique, 1892, p. 325.

quite distinctly articulated (cf. Fig. 22, 7), are treated with chlor-zinc-iodide, we find that, whereas the external wall of the hair takes on a distinct violet tinge, the transverse portions round themselves off, becoming slightly yellow. Congo-red stains the walls of the cells a light red colour; the walls of the hairs take on a similar, but much fainter tinge, and no transverse portions in the course of the hair are stained, thus proving that there are no transverse cellulose-walls. The false septa show up well in the stained hair, but do not seem to take on any colour themselves. They are seen to be small, highly refracting bodies of various size and shape, and at high focus appear to have a slight yellow tinge.

The first indication of a developing hair is to be seen when the cell elongates slightly in the direction of the future hair. At the same time the (somewhat bluntly) pointed apex of the cell becomes colourless (Fig. 22, 5), the green contents collecting in the hinder part of the cell. The colourless tip is full of protoplasm, which no doubt plays an important part in the elongation of the hair, which now takes place (Fig. 22, 6). I was not able to observe the division of a nucleus and the transfer of the one half into the young hair, as described by Huber[1] for *Aphanochaete repens*, Braun. After the first rudiment of the hair is formed, elongation goes on more and more rapidly, and the growing colourless apex becomes more slender. When the hair has reached from 2–3 times the length of the cell, the bulbous base commences to form, and the hair is cut off by a thin transverse wall from the cell below it; this wall may be formed sooner or later in different cases, however. Before the formation of this wall the protoplasm extends irregularly into the hair for some little way, but afterwards only a small quantity remains in the young hair. This is chiefly aggregated at its apex, which at this stage has the appearance of being quite solid; there is only a distinct lumen in the bulbous base. When this base is once formed, elongation proceeds very rapidly, and at the end of about twenty-four hours the hair is 6–10 times as long as the cell it has developed from[2] (Fig. 22, 7). During this later elongation the protoplasm, which was before aggregated in the apex, becomes split up into a number of separate portions, some

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[1] Loc. cit., p. 326, Fig. 2 *a*, and *b*.

[2] It will be observed, that this account does not agree in all respects with Huber's; we have, however, undoubtedly examined different species, and the differences are not very important.

of which form transverse plugs in the lumen of the hair, and come to look like walls. Later still, the highly refracting bodies[1] appear in the protoplasm, and in the adult hair it is they that look like transverse partitions.

Similarly, I have examined the hairs on a specimen of *Aphanochaete repens*, Br.[2], contained in the British Museum. Here the masses were very distinct inside the hairs, and did not at all have the appearance of transverse walls. Specimens from various localities in the Royal Botanic Gardens at Kew have also induced me to accept Huber's explanation, and led me to the assumption that septate hairs do not occur at all in either *Aphanochaete* or *Herposteiron.*

In a young *Stigeoclonium* the hairs develop in exactly the same way as in *Aphanochaete.* The zoospores on coming to rest have an elongated, elliptical shape, bearing a great resemblance to some species of *Characium.* At the one end a hair very soon begins to form, this end becoming colourless, and gradually growing out to form the hair. This rapidly lengthens, and becomes segmented, so as to form a long multicellular structure. Soon after this is well developed, the young plant becomes two-celled by the formation of a transverse wall. No branching takes place until it is several cells in length (cf. Fig. 22, 3);—generally 2–3 lower ones filled with chlorophyll, succeeded by one or two with sparing contents, these leading off to the absolutely colourless cells of the hair-tip. The lowest cell then first puts out a lateral process, which rapidly increases in size, and soon the second cell shows signs of branching, this branch being developed either on the same or on the opposite side (Fig. 22, 4).

After what has been said above, there is thus no longer any reason for believing that multicellular hairs occur at all in either *Herposteiron,* Näg., or *Aphanochaete,* Berth. Further, it seems very probable that Hansgirg's observations[3] on the occurrence of a sheath in *Aphano-*

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[1] The development of the hair would seem to indicate that these are derived from the protoplasmic plugs referred to in the text; and the yellow colour taken on with chlor-zinc-iodide shows them to be proteid in their nature. I tried the Xanthoprotein-reaction on them with little success; there was a trace of colouration, but generally the acid was too much for the delicate hairs. These bodies are insoluble in alcohol and xylol, so that they do not consist of any fatty substance. They remain dark in polarised light.

[2] Phycotheca Boreali-Americana, No. 762.—Collins, Holden and Setchell.

[3] Flora, 1888, p. 214.

chaete repens, Berth., are erroneous[1], and that this latter species belongs to the same genus as the three species of *Herposteiron* mentioned on p. 373. I am entirely of Klebahn's opinion[2], that these four species should be included in the genus *Aphanochaete*, Braun, which has priority over the *Herposteiron* of Nägeli; and that this latter genus, together with *Aphanochaete*, Berth., which was never established by the author, whose name is appended to it[3], be dropped altogether. *Herposteiron globosa*, Nordst., has been included by Klebahn partly in his genus *Chaetosphaeridium*, and partly in *Dicoleon*, Kleb.; *Herposteiron polytricha*, Nordst., is put by him in a new genus *Conochaete*. There seem ample reasons for these separations.

A few more words may be said on the species from Sheen Common. As I have mentioned above, it is certainly not a stage in the development of a *Stigeoclonium*, as *Herposteiron polychaete*, Hansg., may be. It, however, evidently does not agree in several respects with the specimens of *A. repens*, Braun, that I have seen; for these latter specimens have all only one hair to each cell[4], and these hairs have a broader base than in my species. Other differences are to be found in the average number of cells in each individual, and in the branching of the filaments in *A. repens*, Braun. There is scarcely sufficient evidence to warrant my establishing a new species, and for the present I place it in *Herposteiron polychaete*, Hansg., which must now go under the name *A. polychaete* (Hansg.) Fritsch. I think it very probable that this is really the species I have examined.

I add a scheme of the classification of the species discussed above[5], according with the views expressed in this note:—

Genus *Aphanochaete*, Braun (1849).

1. *A. repens*, Br., Verjüngung, 1849–50, p. 196, foot-note (= *A. repens*, Berth.[6]).

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[1] Cf. Klebahn, Pringsheim's Jahrbuch, vol. xxv, 1893, p. 290; cf. also Huber in Journal de Botanique, 1892, p. 337.

[2] Klebahn, loc. cit., p. 294; his remarks do not include *Herposteiron polychaete*, Hansg.

[3] Klebahn, loc. cit., p. 290.

[4] According to Huber, Journal de Botanique, 1892, p. 327, *A. repens* sometimes bears two or more hairs on each cell, but as far as I have seen this does not occur nearly as frequently as in the species I have examined.

[5] No count is taken here of species published after Hansgirg's paper in the Flora of 1888.

[6] There is no reason now for believing that *A. repens*, Berth., differs in any

2. *A. confervicola* (Näg.) Rabh.=*Herposteiron confervicola*, Näg., in Kützing, Species algarum, 1849, p. 424.

3. *A. polychaete* (Hansg.) Fritsch=*Herposteiron polychaete*, Hansg., Prodromus der Algenflora von Böhmen, p. 258.

Genus *Chaetosphaeridium*, Kleb. (1891).

1. *Ch. globosum* (Nordst.) Kleb. = *Herposteiron* (*Aphanochaete*) *globosa*, Nordst.
2. *Ch. Pringsheimii*, Kleb.

Genus *Dicoleon*, Kleb. (1893).

1. *D. Nordstedtii*, Kleb.=*Aphanochaete globosa* forma *paulo maior*, Nordst.

Genus *Conochaete*, Kleb. (1893).

1. *C. polytricha* (Nordst.) Kleb. ⎫ = *Aphanochaete polytricha*,
2. *C. comosa*, Kleb. ⎭ Nordst.

It seems probable that *A. vermiculoides*, Wolle, is not one of the Chaetophoraceae at all.

Before concluding, I should like to mention the frequent occurrence of cells with curious red granular contents, which are evidently in some way connected with the Alga I have been examining. I found them in great numbers in the winter months, but since then they have disappeared, and not a single one remains. The contents of an ordinary vegetative cell begin to lose their bright green colour, and this is generally followed by the escape of the contents, which however remain lying immediately outside the empty cell (Fig. 22, 1 and 2, E) and are surrounded by a distinct membrane. The contents become more and more granular (Fig. 22, 1 and 2, C), and the green matter becomes replaced by red granules. These granules increase in size, apparently at the expense of the smaller ones, until only 3–7 large ones remain in the almost empty membrane (Fig. 22, 1, R); these exhibit a slight movement, probably due to convection currents. Ultimately the membrane becomes disorganized, and the granules sink to the bottom; a considerable mass of them collected on the bottom of the vessel in which I kept the *Aphanochaete*, forming a dark

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essential particular from the same-named species of Braun (cf. Klebahn, loc. cit., pp. 293, 294). Probably also *A. repens*, Br., and *A. confervicola* (Näg.) Rabh., belong together.

red layer. Unluckily they were by mistake thrown away before I could observe them properly or follow up their future fate. I am

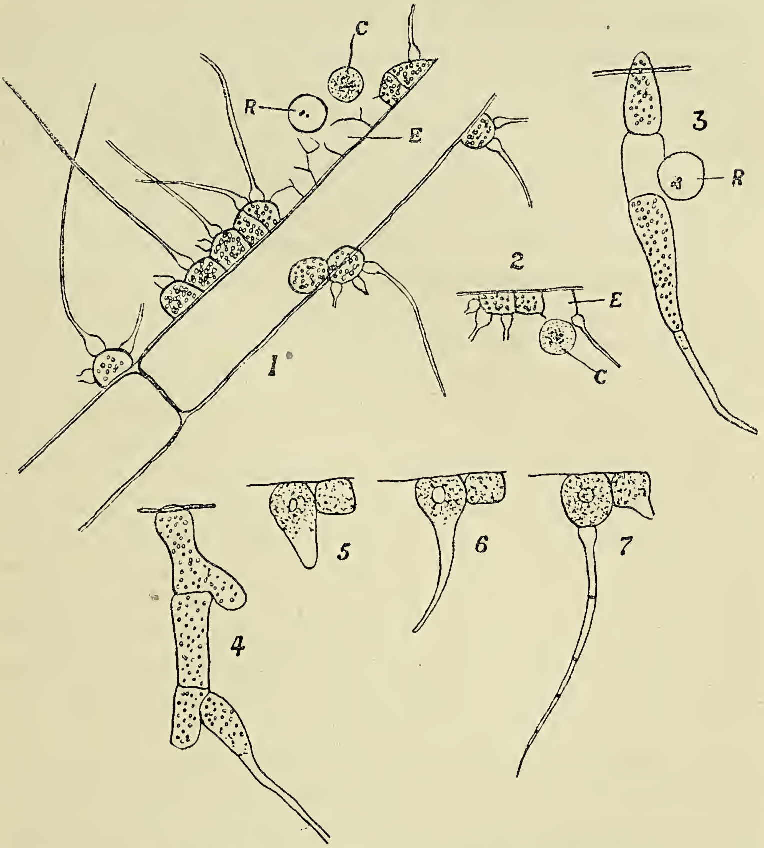

FIG. 22. 1, 2, 5, 6 and 7, *Aphanochaete polychaete* (Hansg.) Fritsch. 1. A number of individuals, epiphytic on *Cladophora fracta*; on the upper side a many-celled individual is to be seen. × 500. 2. A three-celled plant, one cell of which has liberated its contents, *C*. × 500. 5. The first stage in the development of a hair. × 600. 6. A further stage, the bulbous base beginning to form. × 600. 7. Young hair, containing a number of highly refracting masses, which look like transverse walls (but are, however, much thicker than the walls in the hair of a *Stigeoclonium*, for example); in the cell on the right the rudiments of another hair are to be seen. × 600. 3, 4. *Stigeoclonium*, sp. 3. A young unbranched plant, at *R* the contents have been emitted from one of the cells. × 450. 4. A young plant beginning to branch. × 450. (*E* = empty cell, which has set free its contents; *C* = the liberated contents, surrounded by a distinct membrane; *R* = the almost empty membrane, only containing a few big granules.) In most cases only a small portion of the hairs has been figured.

very much puzzled to explain the object of these cells. At first sight they would appear to be due to the attacks of some parasite (possibly *Chytridium*), but after a considerable amount of observation, I do not think this very probable. As far as I have been able to make out, they have also no connexion with any process of reproduction. In fact I might not have mentioned them at all here, if I had not come across exactly the same cells whilst examining some young plants of *Stigeoclonium* (Fig. 22, 3, R). They in every way resembled the cells I had found in the *Aphanochaete*, but were not present in such quantities. The fact that they occur in two different genera is interesting.

I have as yet been able to find little mention of them in the literature of the Chaetophoraceae. Somewhat similar cells have been observed in connexion with the liberation of zoospores in other genera of Chaetophoraceae. Thus, Wille[1] mentions that outside the mother-cell, from which the zoospores are derived in *Trentepohlia umbrina*, Born., a vesicle is to be found, which is considerably larger than the zoospores themselves. He goes on to say: 'Diese Blase enthielt beinahe stets einige runde Körner von der Beschaffenheit des Zellinhalts, welche Körner Molecularbewegung zeigten. . . . Nachdem sie eine Weile gelegen hatte, löste sie sich in dem umgebenden Wasser auf.' Hildebrandt[2] describes a similar structure in the case of the zoospores of a species of *Chroolepus*; here, however, a small mucilaginous sphere is emitted from the sporangium, and round this a number of red granules are aggregated. At present I can say no more on this subject, but hope to return to it at a future date.

II. THE GERMINATION OF THE ZOOSPORES IN OEDOGONIUM.—Several authors (Wille[3], Cleve[4], and Poulsen[5]) have already described the germination of the zoospores in *Oedogonium*. Unluckily in all these cases the species which was used was not

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[1] Ueber die Schwärmzellen u. deren Copulation bei *Trentepohlia*, Mart., Pringsheim's Jahrb., vol. xviii, 1887, pp. 427, 428. Pl. XVI, Fig. 1, *v*.

[2] Ueber eine *Chroolepus* mit Zoosporenbildung. Botanische Zeitung, 1861, pp. 82, 83; Pl. III, Fig. 9.

[3] Algologische Mittheilungen.—V. Ueber das Keimen der Schwärmsporen bei *Oedogonium*. Pringsheim's Jahrb. f. wissenschaftl. Bot., vol. xviii, 1887, p. 454.

[4] Iakttagelser öfver den hvilande *Oedogonium*-sporens utveckling. Öfvers. af K. Vet.-Akad. Förh., 1863, p. 247.

[5] Om sværmsporens spiring hos en art af slægten *Oedogonium*. Botanisk Tidsskrift, 3rd ser., vol. ii, 1877–79, p. 1.

certainly determined. There seems reason to believe that various characters in *Oedogonium*, which have received different interpretations by different authors, are really distinct, according to the species examined. This certainly appears to be the case with regard to the first division of the young plant.

I have examined the germination of the zoospores in *Oed. capillare*, Kütz., a species in which the end cell of the filaments bears a distinct tip[1]. During its active movement the zoospore has a nearly spherical form, but on the cessation of activity it acquires an oblong elongated shape (Fig. 23, *a*). Immediately after coming to rest, a strip of thick, whitish membrane begins to make its appearance at the end opposite to that which bore the cilia. This becomes gradually more and more distinct, whilst at the same time a delicate membrane is formed round the rest of the zoospore (Fig. 23, *a*). Soon after the thick portion of the membrane (which marks the anterior end of the new individual), undergoes, as it appears, mucilaginous degeneration, for shortly a clear space containing mucilage is to be found at this point, bounded towards the exterior by the thin membrane, which surrounds the whole zoospore. Thereupon this colourless portion grows out to form a short *hollow* tip[2] (Fig. 23, *b*). When this has reached a slight development, we see a similar strip of thickened membrane formed at the opposite, posterior end of the embryo (Fig. 23, *b*). Just as at the anterior end this is disorganized, leaving a well-marked clear space behind (Fig. 23, *c*), which grows out to form the root of the new individual (Fig. 23, *d*). In the case described, the root after growing for some time divided at the apex into two rootlets, which continued to grow separately and apically. I was unable to figure the whole course of the development in a single individual, so that the stages in Fig. 23, *a–d*, are from different plants.

It is noteworthy that the tip practically always commences its development before the root. It is not uncommon to find a young plant with an almost fully-developed tip, whereas the root is scarcely developed. The time in which the tip develops seems to vary very much, from 2–24 hours; probably from 3–4 hours is the normal

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[1] A number of species of *Oedogonium* are provided with a tip like that of *Oed. capillare*; thus Wolle (Freshwater Algae of the United States, 1887) figures the young plants of *Oed. autumnale* (Pl. 81, Figs. 4 and 5), which bear a very distinct tip: cf. also *Oed. crispum*, var. *rostellatum* (Pl. 74, Figs. 12 and 13).

[2] Later on this tip becomes solid (cf. Fig. 23, *f*.)

time. I occasionally observed zoospores which still exhibited a jerking movement, whose one end had already commenced to form the tip.

Cohn[1] gives figures of the development of a zoospore of *Oed. capillare*, but gives no description thereof. The figures are excellent, but do not illustrate the details of the development.

Developing zoospores of *Oed. capillare* are also figured by Kützing[2]. In Fig. 4 the germinating zoospore is shown, and this shows a well-developed root before the tip is scarcely developed. My observations in general do not agree with this, although occasionally the development of the tip commenced after that of the root. It is noteworthy that all the young plants figured by Kützing have long rhizoids, although some of them consist of as many as five cells. The fact that no disc is figured makes me rather doubtful whether he had the same species as I had[3].

Cleve[4] only observed the germination of the zoospores derived from the sexual generation. Although much smaller, their appearance is very much like that of the common zoospores. The young plants possess a tip, and figures illustrating its development to some extent are added, but no details are given in the text.

In my cultures the young plants rarely divided to form a several-celled filament, but after some two or three days again liberated their contents as a zoospore; the upper part of the cell-wall together with the tip being pushed on one side like a hinged lid (Fig. 23, *e*). This is differentiated in the same way as in the cells of the adult plant, the contents rounding themselves off at the corners, and a distinct colourless area being developed on one side. Indications of the formation of the lid are to be found some little time before the liberation of the zoospore. A little way below the tip the membrane shows a very slight thickening on its inner side, extending right round the circumference of the wall of the young plant, and appearing as a faint line in surface-view, and as two little knobs on the inside of the wall in optical section. This is the line along which the lid is split off.

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[1] Untersuchungen über die Entwickelung der mikroskop. Algen u. Pilze. Leop.-Akad., 1854, vol. xxiv, pars I, p. 231.

[2] Phycologia generalis, 1843, p. 254, Tab. 12^{II}, Fig. 4–10.

[3] The young plants of *Oed. capillare* usually possess a well-marked basal disc; an elongated rhizoid is rare in this species.

[4] Öfvers. af K. Vet.-Akad. Förh., 1863, pp. 248, 249.

If the cultures containing such germinated zoospores were retained for some days, the successive generations of zoospores, derived from the first individual, showed a gradually decreasing scale of development. Thus the zoospores liberated from the fully-developed unicellular plants, described above, on coming to rest and germinating did not form nearly so long a root, nor was the tip fully developed before the contents of the young individual were again liberated as a zoospore. The plant, resulting on the latter's germination, was still less developed, until in the final stage the zoospore on coming to rest merely surrounded itself with a membrane, and after some hours, without further germination, the contents were again set free. Such are the last struggles for the maintenance of the species against the accumulating masses of bacteria!

Under normal conditions the zoospores of *Oed. capillare* on coming to rest formed a well-developed basal disc, and after a short time proceeded to divide and form a two-celled plant (Fig. 23, *f*). Poulsen[1] has carefully described this first division in the case of an (unluckily) unknown species. He found that this first division took place in a manner rather different from that found in the adult plant. He says (loc. cit., p. 5): 'When the club-shaped cell prepares to divide, the first preparation for the stretching (of the cell) is made by part of the cell-membrane's inner layer, which lies in the uppermost arched part (and thus has the form of a spherical cap), thickening itself, so that this layer, consisting of pure cellulose, is at least double as thick as usual at the point mentioned. However, it is thickened far more strongly at its lower end than higher up in the arch.' In the fully developed condition this is not unlike the normal cellulose-ring in appearance, 'but there is the difference, that whilst the ring's[2] . . . outline . . . makes acute angles with the cell-membrane's inner limit, there is only one of these angles present here, . . . namely, the lower one; above the ring goes slowly over into the upper, less thickened part of the cellulose layer (cf. Figs. 7, 8, 13, 12).' In the next stage of development a hemispherical slit appears in this thickened portion of the wall, and stretches down into its swollen lower margin, dividing this part of the membrane into two (secondary) layers. 'When the thickened part of the cellulose-layer has reached its ultimate development, the upper end of the wall of the cell is burst off as a little

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[1] Botanisk Tidsskrift, 3rd ser., vol. ii, 1877-79, p. 1, &c.

[2] The ring in the cell of the adult plant is meant here.

watch-glass-shaped cap (Figs. 9, 10, 11, 13, 4), which consists of cuticula and the outermost of the above-mentioned secondary layers' (p. 6). Through the aperture thus formed, the contents protrude, bounded apically by the inner (elastic) secondary membrane mentioned above. After this new membrane has been considerably stretched by the growing out of the contents, the first transverse-wall appears. The further divisions generally took place normally, but in some few cases this phenomenon appeared in a later stage, when the plant already consisted of 6–8 cells (p. 7).

Hirn[1] rather passes over this point, merely mentioning that the form of the first ring is slightly different from that of the succeeding, and that owing to its peculiar shape the cap is not infrequently cast off.

I have omitted to follow out the first division of the germinating zoospores in detail, but I have seen nothing like what Poulsen describes and figures. Certainly the first cap is not thrown off in *Oed. capillare*, or we should not find the tip present on the many-celled young plants. All species of *Oedogonium*, that in the older state bear a tip or hair apically, probably behave in the same manner. But even in other species the casting-off of the cap appears by no means to be the rule; in a small (undetermined) species from the River Severn this is not the case, nor in

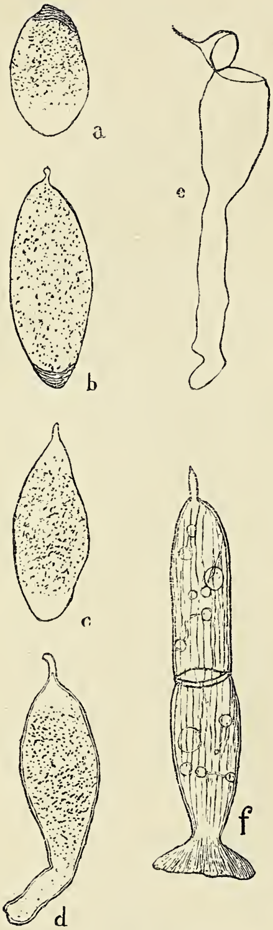

FIG. 23. *Oedogonium capillare*, Kütz. *a*, *b*, *c*, *d*. Stages in the development of the zoospores: *e*. The young, unicellular plant has liberated its contents, the upper part of the cell-wall forming a kind of lid. *f*. A young, two-celled plant with a well-developed basal disc. (All Figs. × 375.)

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[1] Monographie und Iconographie der Oedogoniaceen. Act. Soc. Scient. Fenn., tom. XXVII, 1900, p. 15. Wille (loc. cit., pp. 455–6) agrees with Poulsen's description in all essential points.

another (also undetermined) species from a tank in one of the pits at Kew. I was able to determine this point by the number of caps found on the apical cell of few-celled individuals; these were always found to be one less than the number of cells present. If the first cap had been cast off, their number must have been two less. Probably the case observed by Poulsen is not very common in *Oedogonium*, or rather, although for all I can say, the formation of the first ring may always take place in the above-described peculiar manner, the cap is certainly very often retained.

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Studies on the Gametophyte of Selaginella.

BY

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With Plate XIX.

SEVERAL years ago the writer undertook the study of the development of the female gametophyte in *Selaginella Kraussiana*, and the results were published in brief form[1]. Before their publication a paper by Heinsen[2] appeared, and since then four other contributions have been made, by Arnoldi[3], Bruchmann[4], Fitting[5], and Lyon[6]. Of these, the most important was the paper by Fitting, who corrected an error into which all previous investigators had fallen, the mistaking of the very much contracted protoplast of the young spore for the nucleus. Fitting also made a most satisfactory study of the development of the spore membranes. The most recent paper on the subject is by Miss Lyon. This is a somewhat extended study of the development of two native species, *S. apus* and *S. rupestris*. The most interesting point recorded by Miss Lyon is the retention of the macro-

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[1] Structure and Development of the Mosses and Ferns, pp. 485–504, 1895.

[2] Die Macrosporen und das weibliche Prothallium von *Selaginella*, Flora, 78, 1894.

[3] Die Entwickelung des weiblichen Vorkeims bei den heterosporen Lycopodiaceen. Bot. Zeit. 54, 1896.

[4] Untersuchungen über *Selaginella spinulosa*. Gotha, 1897.

[5] Flora, 1900.

[6] A Study of the Sporangia and Gametophytes of *Selaginella apus* and *Selaginella rupestris*. Bot. Gazette, xxxii, August–September, 1901.

[Annals of Botany, Vol. XVI. No. LXIII. September, 1902.]

spore within the sporangium until after the fertilization of the archegonia. Miss Lyon also confirms Fitting's account of the real nature of the protoplasmic vesicle of the young macrospore.

Miss Lyon, in her paper, criticizes the work of the writer on *S. Kraussiana*, and this led to a re-examination of the preparations upon which the account was based as well as the making of a number of new preparations of the same species. The result was to confirm in every detail the statements previously made, with the single exception of the point which had been corrected in Fitting's paper. Being at a loss to see how Miss Lyon could have reached such very different results, she was written to on the subject, and it turned out that she had misunderstood the writer's use of the term 'spore-cavity,' which was interpreted as synonymous with 'vacuole.' In reality her results agreed closely with those of the writer. It seemed well, however, to make a definite statement as to the real facts in the case, especially as the new preparations filled several gaps which had been left in the older series of preparations.

METHODS.

The earlier preparations were made from material fixed with 1 % chromic acid, double-stained with alum-cochineal and Bismarck-brown. In making the new preparations Flemming's weak solution was used for fixing, and the triple safranin-gentian-violet-orange stain was employed. In this way, especially in the younger stages, very beautiful differentiation of the nuclei was obtained. In the later stages, especially after the spore-cavity became completely filled up, the strongly staining coarse albuminous granules often made it difficult to clearly recognize the nuclei.

In fixing the spores and embedding them for sectioning the individual spores were removed from the sporangia and sectioned separately. Owing to the brittle exospore, some trouble was experienced in sectioning, but by using hard paraffine this was to some extent corrected.

THE SPORE-MEMBRANES.

During its earlier stages, the growth of the massive and complex membrane is almost entirely due to the activity of the tapetal cells of the sporangium. As was pointed out by the writer[1], the extremely small amount of protoplasm in the young spore could not account for the massive wall developed at a very early period. Fitting's demonstration that the small and delicate protoplasmic vesicle of the young spore is almost free from the wall emphasized this, and the writer has been able to verify his results for *S. Kraussiana*, and Miss Lyon has done the same for *S. apus* and *S. rupestris*. It is highly probable that all species agree essentially in this respect.

The process is, in brief, as follows. The young spore shows a small globular vesicle near the apex, which is very evident in the fresh spore, and has the appearance of a large nucleus, for which it was taken until Fitting pointed out its true nature. This vesicle is the protoplast of the spore, and grows much more slowly than the membrane, between which and the protoplast a large cavity is developed (Pl. XIX, Fig. 1). At an early stage, the thick membrane separates into two layers, the 'exospore' and 'mesospore' (Fitting). These are in contact at the apex of the spore, but the former enlarges more rapidly than the latter, and thus a second space is formed (Figs. 1, 2). The single small nucleus of the young spore divides at an early stage, and this division is repeated, the protoplasmic vesicle enlarging as the nuclear divisions proceed.

At this stage (Fig. 1) the exospore in section appears as a thick, strongly staining layer, with marked sharp perinium or ridges upon its outer surface. These in *S. Kraussiana* form a reticulate pattern upon the outside of the spore. The mesospore (*m*) presents much the same appearance as the exospore, but is of nearly uniform thickness. It looks as if it were formed by the splitting off of an inner layer from the exospore. Miss Lyon, in her description of the spore-coats,

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[1] l. c. p. 504.

calls this the endospore, apparently overlooking the development of the true cellulose endospore which arises later in contact with the protoplast. She also mentions a layer (mesospore) between the two thick layers (exospore and mesospore of Fitting), but no evidence of such a membrane was found in *S. Kraussiana* which agrees essentially with *S. Helvetica* as described and figured by Fitting. The principal difference lay in the mesospore being thinner than in that species, and remaining more nearly of the same thickness in the earlier and later stages; thus indicating that its increase in size in the late stages was due to actual growth, and not to mere stretching.

Between the protoplast and the mesospore and between the latter and the exospore the space is filled with what appears to be a fluid, doubtless containing plastic material derived from the tapetum. In all the preparations examined, this substance appeared perfectly homogeneous, staining pale purple or blue with gentian-violet (Fig. 2). No trace of the peculiar fibrillae figured by Miss Lyon[1] in the species studied by her, could be seen, and it would be well if a further examination could be made in these species to determine whether or not this fibrillar appearance is due to the action of reagents.

As to the nomenclature of the various spore-membranes, it might be better to use the term 'epispore' or 'perinium' for the outer, sculptured membrane, considering the 'mesospore' as the equivalent of the exospore of the lower archegoniates.

THE FEMALE GAMETOPHYTE.

The very peculiar behaviour of the early stages in the development of the gametophyte was first made clear by Fitting. He showed that the vesicle supposed to be the nucleus by all previous observers was in reality the whole protoplast, which forms a very small, extremely delicate membrane containing the single small nucleus. Heinsen gave

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[1] l. c. Figs. 42–44.

an accurate figure of this stage, but interpreted the nucleus as a nucleolus. Miss Lyon, in her work on *S. apus* and *S. rupestris*, fully confirmed Fitting's statement, and the writer has found the same condition to obtain in *S. Kraussiana.*

Fig. 1 shows a transverse section of a young spore of this species, made a short distance back of the apex. The primary nucleus was divided into four, these being much flattened. The very thin protoplasmic vesicle is still free from the mesospore. The nuclei continue to divide, but this takes place slowly, and does not keep pace with the rapid expansion of the protoplasmic vesicle, which soon becomes closely applied to the inner surface of the mesospore. The vesicle is so thin as to be scarcely discernible, except where it has become detached from the mesospore. The latter increases rapidly in size, the protoplasmic vesicle keeping pace with it, and finally the mesospore again comes into close contact with the exospore. The protoplasm is still reduced to an exceedingly thin film which may be very easily overlooked, and the nuclei are small and widely scattered. Neither at this stage, nor in any subsequent ones, are the nuclei in *S. Kraussiana* confined to the apical region of the spore, as Miss Lyon states is the case in the species examined by her.

The protoplasmic layer now begins to thicken rapidly, and the nuclei increase in number, and also become larger and lose their flattened form (Fig. 4). For some reason, possibly because the fixing process was slow, no karyokinetic figures were encountered in the earlier stages, but there is no reason for supposing that the division is amitotic, as Heinsen[1] suggests.

The structure of the nucleus is somewhat peculiar. Its contour is clearly marked and there is present a central nucleolus-like body which stains very strongly, but the rest of the nuclear cavity appears quite destitute of anything which could be interpreted as a nuclear filament or chromatin. In later stages (Fig. 14), the central mass sometimes appears

[1] l. c. p. 478.

to be composed of crowded granules, and it seems probable that the apparent nucleolus is really composed of chromatin; the structure being, perhaps, comparable to that of the nucleus of *Spirogyra* and some other Algae.

The protoplasmic layer thickens more rapidly at the apical region, where the nuclei are also more numerous (Figs. 6, 8). Instead of the nuclei at the apex being in six or seven layers as described by Miss Lyon for the species examined by her [1], in *S. Kraussiana* they are mainly restricted to a single layer, although there may be an occasional nucleus below this (Fig. 8). In regard to the first cell-formation, *S. Kraussiana* seems to differ widely from either *S. apus* or *S. rupestris*. There is no trace of the preliminary blocking out of protoplasmic areas by protoplasmic fibrillae, but the first divisions are effected at once by cell-walls (Figs. 8, 9). These form simultaneously between the nuclei in the central part of the apical region, precisely as in ordinary endosperm-formation. The central cells (areoles) thus formed are regularly hexagonal in form, and usually contain but a single nucleus. Toward the margin of the prothallial disc they are larger and more irregular, and may contain two or more nuclei. Whether the formation of these walls is immediately preceded by nuclear division could not be determined. Faint indications of connecting fibres between the nuclei could be seen in some cases, but these were not very evident, and in the few cases where the young walls were found all of the nuclei were in the resting stage.

The areoles thus formed are open below (Fig. 8), but between this stage and that where the prothallial disc was complete no stages could be found, and the exact method by which the subsequent cell-formation takes place must be left for future investigation. Presumably the next nuclear divisions are in a radial direction, and are accompanied by the formation of cells-walls which result in the development of the definite cellular disc, or primary prothallium which is found at the apex of the ripe spore (Fig. 10). This disc consists of

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[1] l. c. p. 182.

a single superficial layer of small cells, beneath which, in the central portion, may usually be found two others. At the margins the disc is reduced to a single layer. As the spore ripens, the walls of the lower cells become much thickened and form the diaphragm (*d*), separating the prothallia disc from the thick layer of protoplasm which lines the spore cavity (Fig. 11).

The protoplasmic layer thickens until the vacuole, which at first occupies very much the larger part of the spore cavity, becomes very much reduced in size (Fig. 10), but at the time that the spore is ripe it is still evident. Neither at this time nor at an earlier stage was there found in the microtome sections any trace of oil or any solid matter. If oil is present in the living spore, it was entirely dissolved out in the process of embedding. Some time after germination begins the vacuole closes completely, and in a few preparations, before this was completed, the vacuole showed a spongy-looking mass filling it.

In the later stages the nuclei lying in the cytoplasm immediately below the diaphragm (Fig. 12) are much smaller than those in the basal part of the spore (Fig. 13), and much more numerous. The cytoplasm below the diaphragm is more finely granular than at the base of the spore; and everything indicates that it is more active, which is what might be expected, as it is here that the secondary cell-formation begins after the fertilization of the archegonium.

In the later stages of germination the development of coarse masses of proteid materials which stain deeply makes the study of the nuclei difficult, and they are by no means easy to demonstrate at this time.

Comparing Miss Lyon's account of the gametophyte of *S. apus* with that of *S. Kraussiana*, the first difference is the much greater development of the primary prothallium of the former, which consists of six to seven layers of cells instead of the three usually occurring in *S. Kraussiana*. To judge from the figures, there are two types of prothallium in *S. apus*, one in which there is a sharp demarcation of the base of the primary prothallium, and one where apparently there is no interruption in its development. It is not quite clear from Miss Lyon's account what is the history of the part of the spore-cavity below the prothallium. She states that the vacuole becomes filled with an emulsion and later with a semi-solid mass of granular matter, and that neither in the central nor basal part of the spore-cavity are nuclei present at any period of its development. It is impossible to determine from her figures whether any protoplasm is present in the lower part of the spore, as everything below the apical mass of cells is represented as absolutely similar ; it being impossible to say where the protoplasm (if any) ends, and the vacuole begins. Fig. 57 of her paper shows the whole spore-cavity to be ultimately filled with cellular tissue, which implies the presence of nuclei, thus contradicting the assertion that at no period are nuclei found in the central or basal part of the gametophyte. This raises the question, whether proper standing will not reveal the presence of nuclei in the basal part of the spore-cavity before the cell-formation begins.

THE MALE GAMETOPHYTE.

Miss Lyon's account of the development of the male gametophyte and antheridium differs widely from that of previous investigators, especially Belajeff[1]. It cannot be said, however, that either her account or figures are quite convincing. From an examination of sections of the earlier stages in *S. Kraussiana* there seemed little reason to doubt that the masses surrounding the groups of sperm-cells are, as they have every appearance of being and were interpreted by Belajeff, cells, and not mere structureless masses of food-stuff developed in vacuoles. Owing to the dense granules, which stain strongly and resemble nuclei, the presence of the latter, as in the later stages of the female gametophyte, is difficult to demonstrate, but in several instances what seemed to be undoubted nuclei were seen. The formation of the

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[1] Antheridien und Spermatozoiden der heterosporen Lycopodiaceen. Bot. Zeit. 43, 1885.

groups of sperm-cells by a process of free cell-formation, like that of ascospores, is, to say the least, improbable, and must be positively demonstrated before it can be accepted.

THE OLDER GAMETOPHYTE.

The later stages of the gametophyte, the structure, and development of the archegonium were not further investigated, as these have been sufficiently described and figured by the writer before.

SUMMARY.

1. Fitting's account of the development of the spore-membranes and the character of the protoplast in the young spore was confirmed.

2. Except for the mistake of interpreting the young protoplast as the nucleus of the young spore, the account previously published by the writer was found correct in every particular.

3. The nuclei in *Selaginella Kraussiana* are uniformly distributed through the cytoplasm of the young spore; later they are more numerous in the apical region, where the cytoplasmic layer is also thicker.

4. No preliminary blocking out of nucleated areas takes place, but cell-walls are formed at once. The primary cells ('areoles') are at first open below.

5. A definite cellular body (primary prothallium) is formed at the apex of the spore. This is a disc, usually composed of three layers of cells in its central part. The inner walls of the lower layer of cells become thickened, and form a diaphragm separating the primary prothallium from the undivided spore-cavity below.

6. The cytoplasm of the spore-cavity increases rapidly in amount, so that the central vacuole becomes much reduced in size, but it is still evident when the spores are shed. Ultimately it becomes completely obliterated. Except in the very latest stages it is quite free from granular contents, appearing entirely empty in microtome sections.

7. The nuclei in the cytoplasm just below the diaphragm are smaller and more numerous than those in the basal part of the spore. The central body is probably not a nucleolus, but a mass of chromatin.

8. The masses surrounding the complex of sperm-cells in the germinated microspores are probably true cells.

EXPLANATION OF FIGURES IN PLATE XIX.

Illustrating Professor Campbell's paper on the Gametophyte of *Selaginella.*

All figures refer to *Selaginella Kraussiana*, A. Br. All camera drawings from microtome sections. Figs. 1, 2, Leitz, oc. 1, ob. 7; Fig. 10, Leitz, oc. 3, ob. 3; the others Leitz oil im. $\frac{1}{16}$ oc. 1. *Ex.* exospore; *m.* mesospore; *pr.* protoplast; *n.* nuclei; *v.* vacuole; *d.* diaphragm.

Fig. 1. Transverse section of young macrospore; the protoplasmic vesicle, *pr*, still free from the mesospore, *m*. Two of the four nuclei of the spore are shown in the section.

Fig. 2. Nearly median longitudinal section of an older spore, the protoplasmic vesicle in close contact with the mesospore.

Fig. 3. *a*, part of a similar section more highly magnified. *b*, a single nucleus seen from above.

Fig. 4. An older stage; the cytoplasmic layer has thickened and the nuclei are no longer flattened.

Fig. 5. Surface view of a portion of the cytoplasmic layer with the nuclei.

Fig. 6. Nearly median section through the apex of the spore shortly before the first cell-formation, showing the thickened cytoplasmic layer and nuclei.

Fig. 7. Section of the cytoplasmic layer of the same spore, near the base.

Fig. 8. Beginning of cell-formation at the apex of the spore. The areoles are still open below.

Fig. 9. Transverse section through the young prothallium, showing the regular form of the central cells.

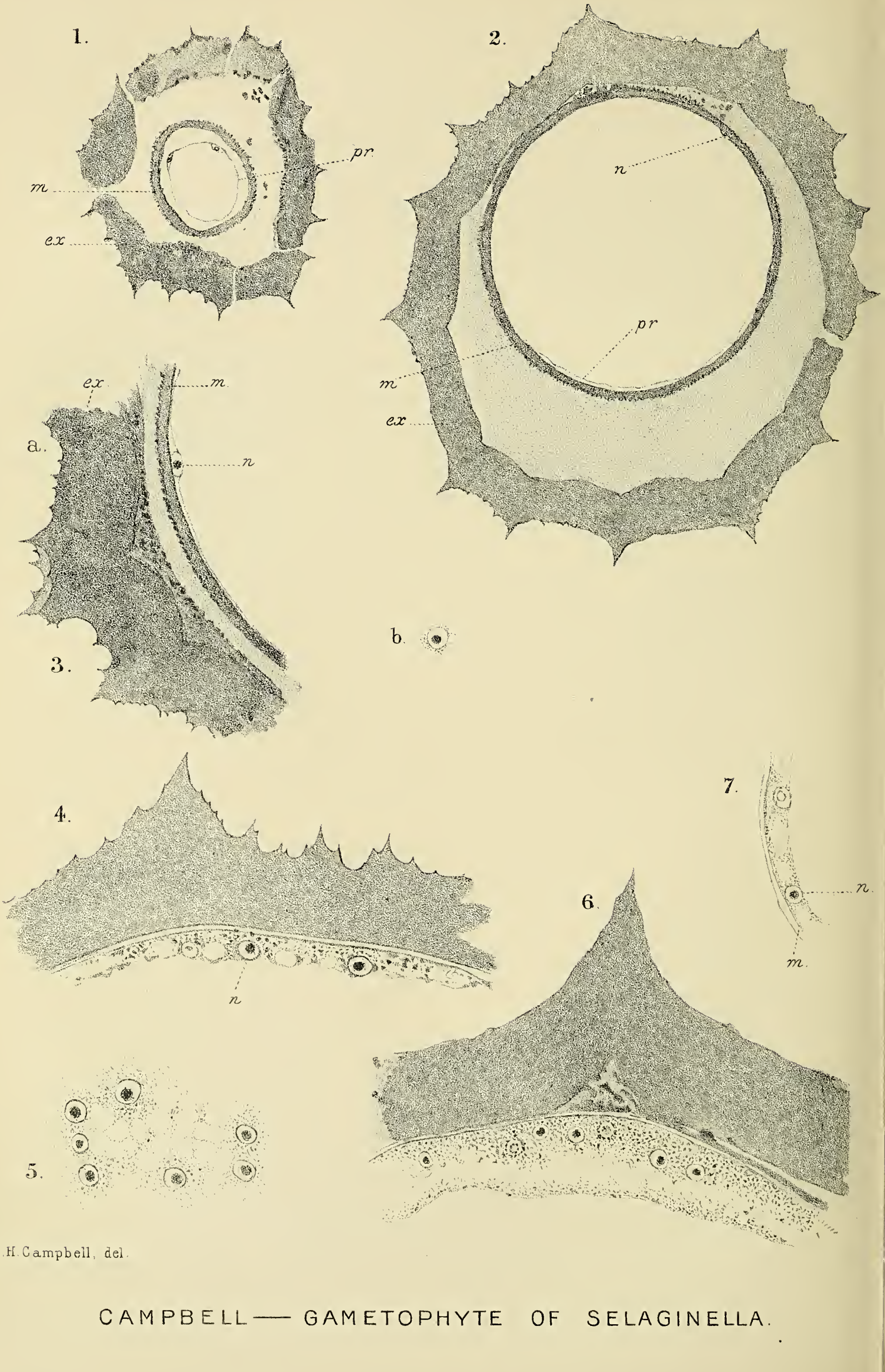
Fig. 10. Nearly median longitudinal section of a ripe spore; the primary gametophyte, *g*, separated from the cytoplasm of the spore-cavity by a diaphragm; many nuclei are scattered through the cytoplasm and the vacuole is still present. The outer spore membranes are not shown.

Fig. 11. Median section of the central part of the prothallium, showing the diaphragm separating it from the spore-cavity.

Fig. 12. Cytoplasm and nuclei from the upper part of the spore-cavity.

Fig. 13. Part of the basal cytoplasm and nuclei from the same spore.

Fig. 14. A single nucleus showing the nucleolus-like central chromatin mass, composed, apparently, of several crowded granules.



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CAMPBELL — GAMETOPHYTE OF SELAGINELLA.

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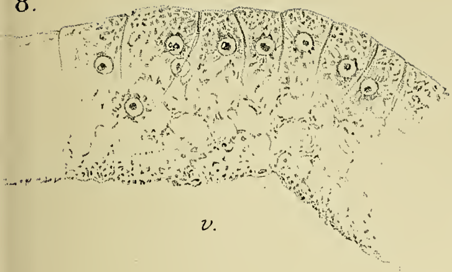

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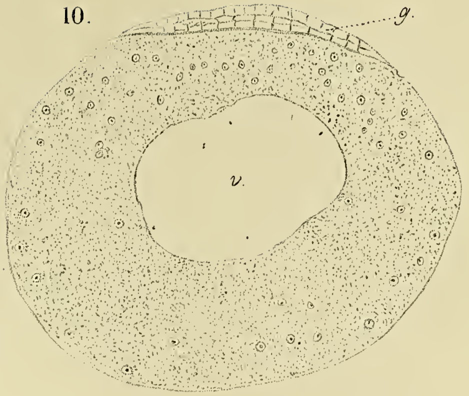

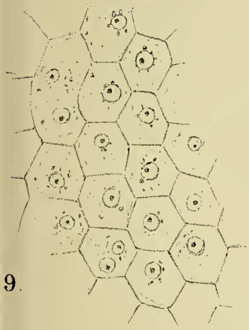

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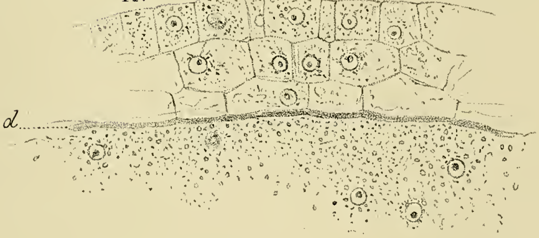

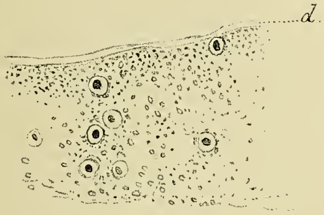

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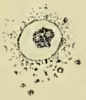

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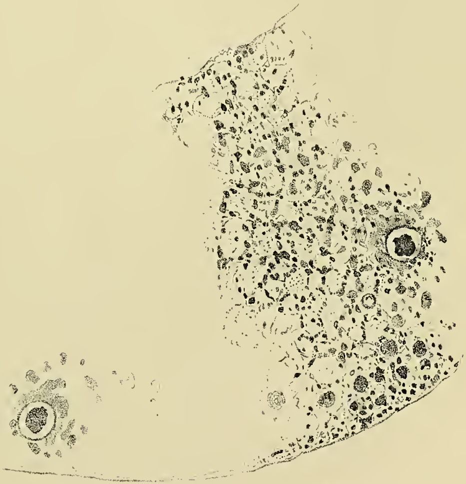

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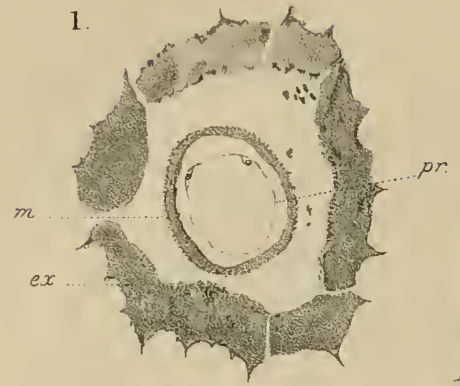

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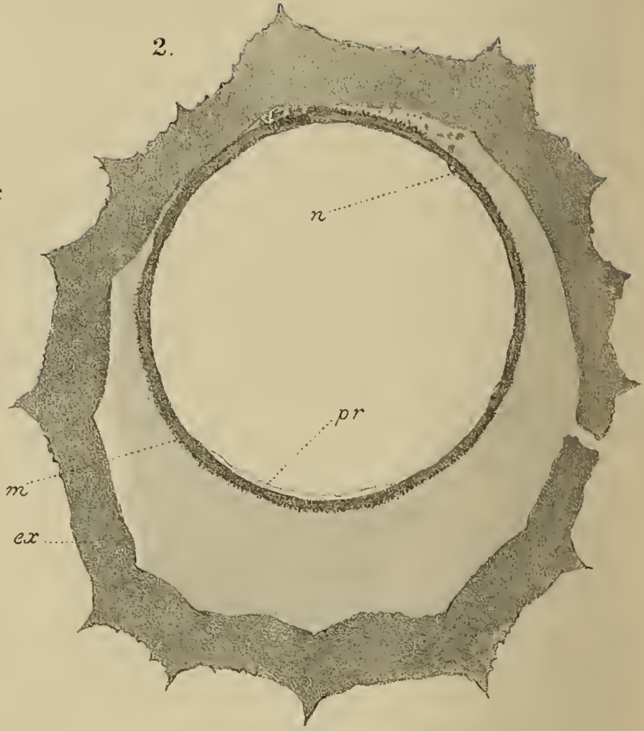

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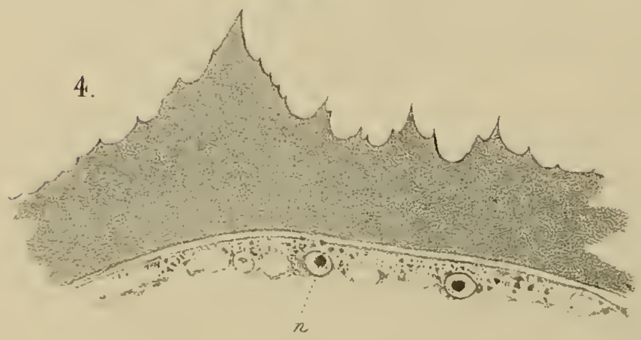

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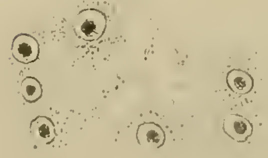

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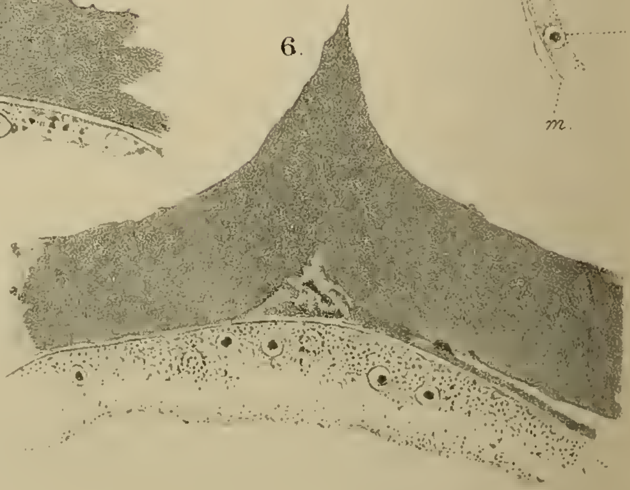

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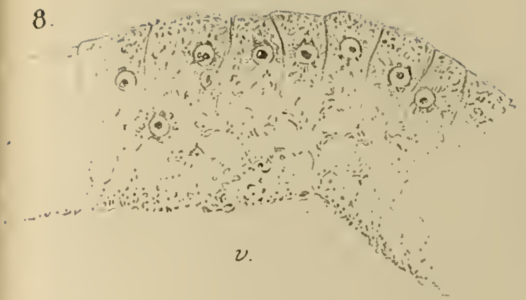

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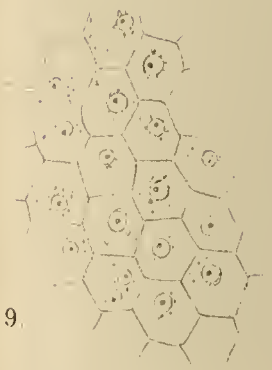

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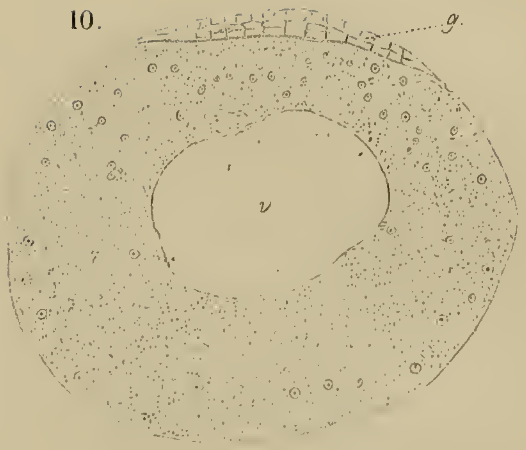

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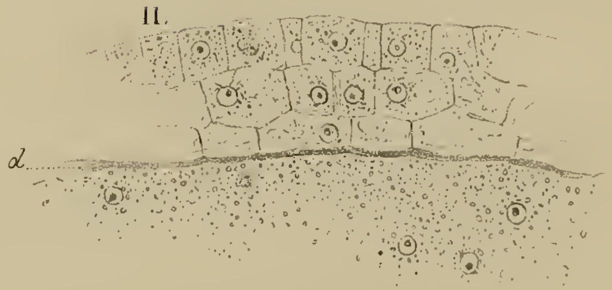

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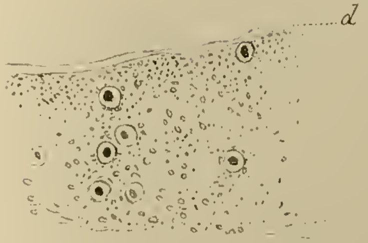

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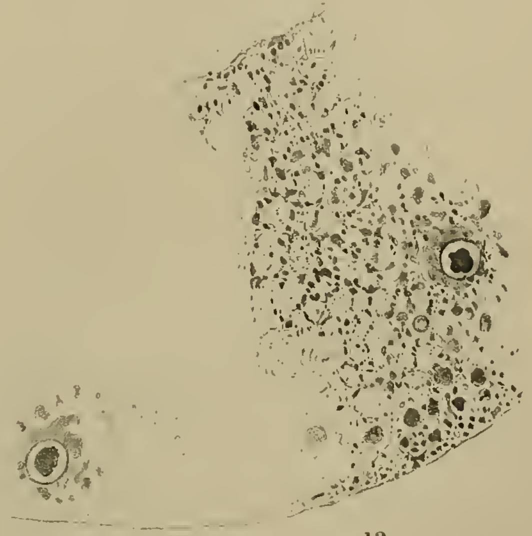

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CAMPBELL — GAMETOPHYTE OF SELAGINELLA.

The Sensory Zone of Roots.

BY

FREDERICK C. NEWCOMBE,

University of Michigan.

With a Figure in the Text.

I. INTRODUCTION.

IN a recent paper[1], evidence was offered to show that the stimulus giving the response known as *rheotropism* is perceived by the apical millimetre of *Zea Mays*, L., and of *Raphanus sativus*, L. There was evidence to show also that, in the root of the latter plant, the stimulus was perceived throughout the elongating zone, and still more posteriorly, to a distance even 15 mm. back of the apex, this being at least 10 mm. beyond the limit of the elongating zone.

This discovery was of such interest that it seemed advisable to extend the research to other plants, to ascertain whether the phenomena, observed in *Raphanus*, might be found to be general. The results obtained in such an investigation are reported in the present paper.

By way of retrospect, it may be said that the various tropisms of roots so far determined have their sensory seat either in the apex or in the elongating zone. Confined to the apex in front of the elongating zone is the sensory tissue controlling the responses known as geotropism[2], and trauma-

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[1] Newcombe, The Rheotropism of Roots. Bot. Gazette, xxxiii, 1902, p. 177.

[2] Czapek, Jahrb. f. wiss. Botanik, xxvii, p. 255; xxxv, p. 317.

[Annals of Botany, Vol. XVI. No. LXIII. September, 1902.]

tropism [1], and probably heliotropism [2] and hydrotropism [3]. Thermotropism [4], aerotropism [5], galvanotropism [6] and rheotropism [7], are responses known to be due to the sensitiveness of the elongating zone, but in these cases the root-apex is not known to be insensitive. Thigmotropism [8], as such, has as yet no place among phenomena of irritability in any but aerial roots, for Wiesner [9] and Spalding [10] have shown the thigmotropism of Darwin to be traumatropism, and I shall shortly offer evidence to show the same thing regarding Sachs' thigmotropism.

The foregoing statement is enough to indicate that in roots no sensory area has been found posterior to the elongating zone. The following pages will show that several plants possess sensitive areas removed by a considerable distance from the elongating zone. Evidence will also be offered to show that the rheotropic sensitiveness of the root-apex of *Brassica alba* is to be assumed as well as that of *Raphanus sativus* and *Zea Mays*.

II. THE RHEOTROPIC SENSITIVENESS OF THE APEX OF THE ROOT.

In the paper [11] already referred to, experiments were detailed in which the rheotropic sensitiveness of the apical millimetre of the roots of *Helianthus annuus*, L., and *Brassica alba*, Boiss., was made probable by the application of fine

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[1] Wiesner, Sitzb. d. k. Akad. d. Wissensch. Wien, Bd. lxxxix, I. Abth., 1884. Also Spalding, Ann. of Bot., viii, 1894, p. 423.

[2] Kohl, Die Mechanik der Reizkrümmungen, p. 26.

[3] Molisch, Sitzb. d. k. Akad. d. Wissensch. (math.-nat. Cl.), Wien, Bd. lxxxviii, I. Abth., 1883, p. 897. Also Pfeffer, cited by Czapek in Jahrb. f. wiss. Bot., xxxv, p. 316.

[4] Wortmann, Bot. Zeit., xliii, p. 232.

[5] Molisch, Sitzb. d. k. Akad. d. Wissensch. (math.-nat. Cl.), Wien, Bd. xc, I. Abth., 1884, p. 175.

[6] Brunchorst, Ber. d. D. Bot. Gesellsch., ii, 1884, p. 204.

[7] Juel, Jahrb. f. wiss. Bot., xxxiv, 1900, p. 518.

[8] Darwin, Power of Movement in Plants, p. 129. Also Sachs, Arbeit. d. Bot. Inst. Würzb., i, p. 437.

[9] Wiesner, loc. cit.

[10] Spalding, loc. cit.

[11] Newcombe, Bot. Gaz., xxxiii, 1902, p. 177.

jets of water to one side of the tip. Four seedlings of *Helianthus* were used, and all four roots responded with positive curves; while fourteen seedlings of *Brassica* were used, of which six roots gave positive curves, two gave negative curves, and six remained neutral. This evidence was not conclusive.

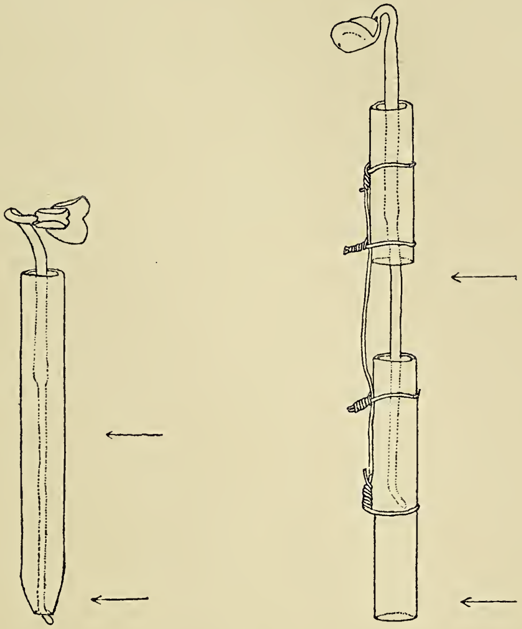

FIG. 24 (I). Illustration of a preparation to determine the sensitiveness of the apex of the root. The glass-tube with its seedling was fastened to a bar of wood. The packing of cotton is not represented. The arrows indicate the direction of the current of water.

(II). Illustration of a preparation to determine the extent of the sensory zone. In this preparation 15 mm. of the apex of the root is covered, the lowest circle of wire serving to mark the height at which the root-tip is to be kept during the experiment.

Better results were obtained by another method. This consisted in the employment of glass-tubes to shield all of the root, except the apex, from the action of a stream of water in which the lower part of the seedlings was immersed. Thin-walled glass-tubes with an inner diameter of 3 mm. were cut to suitable lengths, the roots and hypocotyls of the seedlings passed into these, and wet cotton was used as packing to fix the seedling in the tube. The preparation is illustrated in Fig. 24 (I).

The seedlings with encasing tubes were secured to a bar of white pine 20 cm. in length, the bar was adjusted parallel with the diameter and just above the water of a glass basin 22 cm. in width. The roots and glass-tubes project into the water. The seedlings were now adjusted to the proper exposure of apex by moving them up or down the tubes, and the basin of water was set revolving. Such a preparation as this needs almost constant watching, for the growth of the roots necessitates the raising of the seedlings in the tubes at intervals of fifteen to thirty minutes.

Tested by this method, *Zea Mays* (popcorn), when only 1 mm. to 2 mm. was exposed to the action of the stream, gave nine positive curves out of a total of twenty-one roots, the twelve remaining neutral. The period of the experiment was only four hours in one case and eight hours in the other, thus accounting for the small number of curves. Since there were no negative curves, however, the positive ones may be counted as irritable responses. In a later experiment with the same species, ten roots were in the water-stream for seven hours with never more than 1·5 mm. exposed beyond the glass-tubes. Six positive curves resulted, and four roots remained straight.

Raphanus sativus tested by the foregoing method, with not more than 2 mm. of apex exposed, the duration of the experiment being six hours, gave positive responses in all of the thirteen roots used. In a second similar experiment lasting for eight hours, with never more than 1·5 mm. being exposed, nineteen roots became positive and one remained neutral. In a third experiment lasting nine hours, in which nineteen seedlings were used, with never more than 1 mm. of the root-apex exposed, eleven roots became positive, while the other eight remained neutral.

Since the publication of the foregoing results a third species has been tested as were the two others, this being *Brassica* *alba,* Boiss. Only eight seedlings were used; the temperature of the water was 24°C.; the velocity of the water-steam ranged from 200 cm. per minute for the roots nearest the centre to 700 cm. for those most distant; the duration of the test was six hours, and there was never more than 1 mm. of apex exposed. Seven roots showed strong positive curves, and the eighth was neutral.

From the foregoing results there can be no doubt that the apex of these roots is rheotropically sensitive.

III. SENSITIVENESS OF THE POST-ELONGATING ZONE.

It has already been shown[1] that the root of the seedling of *Raphanus sativus* is sensitive to a rheotropic stimulus from its apical millimetre back to at least the fifteenth millimetre. Since the method in that study is the same as that used in the more recent testing of other species, it may be briefly summarized as follows:—Glass-tubing of 3 mm. internal calibre was cut into appropriate lengths, varying from 1 to 3 cm., and paired tubes were made by joining two pieces together by fine annealed iron wire, as shown in Fig. 24 (II). These tubes were washed in water for twenty-four or more hours before using. When the seedlings had attained a proper size, usually 3 to 5 cm. in length, the paired tube was filled with water, and the root of a seedling was passed in, the seedling being secured in the tube by packing wet cotton around the upper part of the root, or the lower end of the hypocotyl, as this was held in the upper section of the paired tube. A flattened needle with its point broken off did very good service in packing the cotton around the seedling. As each seedling was secured in a tube, the preparation was set vertically upright in a dish of water. When ten such seedlings were ready, a bar of wood about 1 cm. square and 20 cm. long was clamped in a vice at one end, and the glass-tubes with the contained seedlings were fastened to the bar. In fastening the preparations to the bar of wood, one side of the bar was first covered with wet blotting paper, the tubes were

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

laid against this, one by one, and secured in place by a strip of cloth and rubber bands. While these tubes and seedlings were being fastened to the bar, they were kept constantly in the vertical position, and hence throughout the whole preparation there was no chance for a geotropic stimulation. As these tubes were arranged on the bar, none of them came nearer than 2·5 to 3 cm. from the middle, and the extreme ones were about 9·5 cm. from the middle. The interval between two neighbouring tubes was about 1·5 cm. As the seedlings were secured in the paired tubes, they were adjusted so that any length of apex desired was enclosed by the lower piece of the paired tube. Thus when the bar of wood with its load was suspended over a revolving basin of water, with the glass-tubes projecting into the water, the only part of the root exposed to the water-stream was the portion, usually 5 to 10 mm. in length, between the two pieces of the paired-tube.

As stated elsewhere[1], it was with great surprise that I observed the roots of *Raphanus sativus*, L., making positive curves within glass-tubes when the part that was stimulated was 10 mm. distant from the apex, especially as observation with the horizontal microscope had shown that the elongating zone, when the roots are kept in water, is confined to the first 5 mm. of the apex. The roots of *Raphanus sativus*, when 10 mm. of the apex were enclosed in the tubes, showed thirty-four positive curves in a total of forty-eight seedlings; and when a length of 15 mm. of the apex was shielded, ten positive curves in a total of 23 seedlings. When, however, a length of 20 mm. of the apex was shielded from the water-stream, in a total of nineteen roots, only seven curved positively, while four became negative, and eight remained neutral.

Since this record was made for *Raphanus sativus* (early long scarlet), five other tests have been made with the same variety, and in the same manner as before. The total result obtained in all the experiments with this plant may be presented in the form of the following table :—

TABLE I. *Raphanus sativus* with root-tips shielded from

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

the water-stream by glass-tubes. Temperature of the water =23° to 24°; duration of experiments=from 9 to 12 hours; velocities=from 200 cm. to 700 cm. per minute.

No. Seedlings.	*Extent of Apex shielded.*	*Positive Curves.*	*Neutral Roots.*	*Negative Curves.*
48	10 mm.	34 = 71%	11	3
50	15 mm.	28 = 56%	18	4
33	20 mm.	14 = 42%	14	4

The results recorded in this table would seem to show that the root of *Raphanus sativus* is sensitive to the water-stream at least 20 mm. back from the apex. It is true that the number of positive responses is not large, but it is large enough to indicate clearly that some directive influence was at work, especially as there were but four negative curves. The roots of *Raphanus* do not distort in water, nor do they nutate through any considerable angle. The angles attained in all the curves counted as rheotropic were never below 10°, and were often 30° to 45°. A majority were above 15°.

The foregoing table also shows that the sensitiveness of the roots decreases with the distance from the elongating zone, though, when the stimulus is applied 10 mm. from the apex, nearly as many positive curves appear as when the whole root is exposed to the water-stream. My former paper[1] shows that this plant, when the whole root receives the stimulus, gives 87 per cent. of positive responses; when the apex to a distance of 10 mm. is shielded, positive curves equal to 71 per cent. appear.

A second plant whose irritability back of the elongating zone was tested is *Brassica alba*, Boiss. This plant was known to be highly sensitive to the action of a stream of water[1], and for this reason was selected for experiment. The preparation was made and the experiments carried out in the same way as for *Raphanus*, the plants being shielded

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

from the light also at all times, except for the few minutes when observations were being made.

TABLE II. *Brassica alba* with root-tips shielded from water-stream by glass-tubes. Temperature of the water = 22° to 24°; duration of experiments = from 7·5 to 11·75 hours; velocities = from 200 cm. to 700 cm. per minute.

No. Seedlings.	*Extent of Apex shielded.*	*Positive Curves.*	*Neutral Roots.*	*Negative Curves.*
16	10 mm.	12 = 75%	4	0
33	15 mm.	28 = 85%	4	1
18	20 mm.	9 = 50%	9	0
22	25 mm.	11 = 50%	9	2

This summary, if it teaches what it seems to, is remarkable in showing that this plant is sensitive rheotropically at a place at least 25 mm. distant from the apex of the root. One must not, however, put too much faith in summaries. Let us examine the individual experiments to see whether they tend toward a constant result: there were three sets of seedlings prepared and carried through the experiment with 25 mm. of the apex shielded. One with ten seedlings gave seven positive curves, one with nine seedlings gave four positive curves, and one with three gave one positive curve. None of the curves counted were less than 10°, and the average was 22°. Inasmuch as the roots did not become contorted, and there were only two negative bends, I see no escape from the conclusion that the most of these positive curves were caused by the water-stream. Should we consider the experiments in which 20 mm. of the apex were covered by the tube, we should find the same relations. When, however, we consider the cases in which only 15 mm. of the apex were shielded by the tube, even the most sceptical must admit the evidence. The total of thirty-three seedlings used were distributed in six experiments, and in every experiment two-thirds or more of the roots responded with positive curves.

These curves varied between 10° and 90°, the most of them being between 15° and 30°.

To determine the extent of the elongating zone of *Brassica alba*, the roots of four plants were marked with India ink, and immediately measured with a horizontal microscope. Subsequent examination showed that three of these plants had elongated only in the first 5 mm., while the fourth had made a slight growth in the sixth millimetre also. These roots were kept in water both before and after the preparation for measurement.

Fagopyrum esculentum, Moench., when its naked roots are immersed in flowing water of suitable velocity[1], has shown a positive response in 92 per cent. of the total number of roots used. It is therefore highly sensitive rheotropically. But unlike *Raphanus sativus* and *Brassica alba*, it has the disadvantage of growing with a considerable number of contortions in water. It has been selected for experiment in the study of the extent of the sensitive area in roots, but it gives, as one would expect, a larger number of negative bends, these negative bends being considered not as rheotropic responses, but rather as the result of the objectional environment of water, whatever that may be. The tabular summary of the behaviour of *Fagopyrum*, when treated as the two preceding plants were, appears as follows:—

TABLE III. *Fagopyrum esculentum* with root-tips shielded from water-stream by glass-tubes. Temperature of the water = 23° to 24°; duration of experiments = 10 to 11 hours; velocities = from 200 to 700 cm. per minute.

No. Seedlings.	*Extent of Apex shielded.*	*Positive Curves.*	*Neutral Roots.*	*Negative Curves.*
38	10 mm.	29 = 76%	3	6
41	15 mm.	24 = 59%	10	7
36	20 mm.	17 = 47%	5	14
5	25 mm.	0 = 0%	4	1

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

Compared with the tables for *Raphanus* and *Brassica*, this one for *Fagopyrum* shows a proportionally much larger number of negative curves and a smaller number of neutral roots, indicating that we cannot for *Fagopyrum* reckon all the positive curves as due to the water-stream. If we subtract from the positive curves in each group, the number of negative curves in the same group, we ought to obtain approximately the true number of rheotropic responses. This statement, of course, assumes that there is no such response as negative rheotropism, a belief in which I have been confirmed by all my work on rheotropism.

The individual experiments in the group with 10 mm. of the root covered, and also those with 15 mm. covered, are uniform in showing in all cases a majority of all roots with positive curves. The five experiments in the group with 20 mm. of the apex covered varied considerably in the results shown, three having a majority of positive curves, one a majority of negative curves, and two having an equal number of positive and negative curves. The apparent tendency toward positive curving is here so slight that no claim can be made for sensitiveness at a distance of 20 mm. from the apex.

The explanation of the relatively much larger number of negative roots when 20 mm. of the apex are covered than when 10 mm. or 15 mm. are covered, is found probably in the weaker effect of the stimulus of the water-stream when applied at 20 mm. from the apex. As a result of the lesser effect of this stimulus, the direction of growth of the root is left more under the control of the stimulus which leads to distorted growth. It has been shown elsewhere[1] that, in rheotropic experiments with the naked roots of this plant in water, the initial distortion curves are converted into positive rheotropic curves, or rather that the various directions taken initially, due to distortion, are later brought into a common direction which is parallel with the current of the water.

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

Helianthus annuus, L., like *Fagopyrum esculentum*, does not produce all its roots straight in water. It is a plant giving 70 per cent. of positive rheotropic curvatures when the naked roots are acted on by a stream of water, but the angles attained average less than 45°. This behaviour places this plant among those with a good degree of sensitiveness to a stream of water, but considerably below the grade of *Raphanus* and *Brassica*. The following table will show that, like *Fagopyrum*, this plant gives a considerable number of negative bends, which are to be interpreted as merely the result of the environment of water.

TABLE IV. *Helianthus annuus* with root-tips shielded from the water-stream by glass-tubes. Temperature of the water = 24°; duration of the experiments = 11 hours; velocities = from 200 cm. to 700 cm. per minute.

No. Seedlings.	*Extent of Apex shielded.*	*Positive Curves.*	*Neutral Roots.*	*Negative Curves.*
30	10 mm.	22 = 73%	6	2
46	15 mm.	23 = 50%	14	9
29	20 mm.	11 = 38%	14	4
32	25 mm.	11 = 34%	15	6

The results of individual experiments carried through on various days agree very closely with the proportions shown in the totals of the table. For those roots with 10 mm. shielded, two experiments were made with fifteen seedlings in each. Each experiment gave eleven positive curves, while one experiment gave two negative curves and two neutral roots, and the other gave no negative curves, but four neutral roots. The experiments with 15 mm. of the root covered numbered four. The first one of these four sets of roots had eight individuals, and gave three positive curves, three negative, and two neutral roots; the second had fourteen individuals, and gave seven positive curves, two negative, and five neutral roots; the third set had twelve individuals, and gave seven positive curves, one negative, and four neutral roots; the fourth set had twelve individuals, and gave six positive curves, three negative, and three neutral roots.

In a plant like *Helianthus annuus*, not growing well in water, it is not at all surprising that occasionally a set of seedlings will vary somewhat, as did the first set noted above, from the general behaviour. The result of the four experiments seems to me to teach unmistakably that the root of this plant is sensitive to a water-stream at the distance of 15 mm. from the apex. The negative curves appearing in these experiments would nearly all be turned into positive curves were the roots not covered by the tubes. This is shown in my paper on 'Rheotropism,' and is to be explained probably by supposing that the rheotropism of the roots overcomes in most cases the initial tendency to contorted growth. When the roots are partially shielded by tubes, the rheotropic stimulus affects the plant to a much less degree, and the tendency to contorted growth manifests itself much more strongly.

If we assume a sensitiveness of the root of *Helianthus* at a distance of 15 mm. from the apex, the recorded results will hardly warrant such an assumption for the part of the root 20 mm. distant from the apex. For if we take the four negative curves as due to contortion and assume an equal number of contortions among the positive roots, we shall have left but seven positive roots in a total of twenty-nine, a proportion almost too small to serve as a basis for any conclusion. We cannot assume that the root of *Helianthus* is insensitive 20 mm. distant from the apex, but rather that the method employed gives no sufficient evidence for a judgement either way.

Five roots of *Helianthus annuus* were marked and observed with the horizontal microscope for the extent of the elongating zone, the roots being kept in water, and light excluded. Of these, four roots showed growth in the first 7 mm. only, while the fifth root showed growth in the first 5 mm. only. It must be therefore that the root of this plant is sensitive to the rheotropic stimulus at least 8 mm. back of the limit of the elongating zone.

Zea Mays, L. (the variety commonly called *white popcorn*), unlike its near relatives, the *sweet* and the *field corn*, produces mostly straight roots in water, and shows a good degree of rheotropic sensitiveness. In seventy-nine seedlings whose naked roots were subjected to a stream of water, 72 per cent. showed positive curves. This plant was selected therefore as promising results by the employment of glass-tubes. In the experiments with 15 mm. of the apex of the root shielded from the water-stream, so many roots responded, that it was thought unnecessary to experiment with but 10 mm. of the apex covered.

The roots of this plant are so large, that larger glass-tubes were used, viz. tubes of 4 mm. internal diameter.

TABLE V. *Zea Mays* (white popcorn) with root-tips shielded from the water-stream by glass-tubes. Temperature of the water = 24° ; duration of the experiments = 10 hours to 12 hours ; velocities = from 200 cm. to 700 cm. per minute.

No. Seedlings.	*Extent of Apex shielded.*	*Positive Curves.*	*Neutral Roots.*	*Negative Curves.*
30	15 mm.	23 = 76%	5	2
30	20 mm.	21 = 70%	8	1
30	25 mm.	11 = 37%	13	6

These ninety seedlings were used in nine sets, each set having ten seedlings. The results for the various sets were remarkably consistent, and each group of ten showed about the same proportionate number of curves and neutral roots as shown by the total of its class in the table.

Measured with the horizontal microscope as they were growing in water, one seedling of *Zea* (popcorn) showed the elongating zone of its root to be confined to the first 8 mm., three showed growth in the first 9 mm., and a fifth showed growth in the first 10 mm. 10 mm. may be assumed as the limit of elongation for most individuals of this variety. At the distance of 20 mm. from the apex, the sensitiveness of the roots is so great as to bring approximately the same percentage of curves as is produced when the whole root is subjected to the water-stream. It is probable, though not certain, that the roots are sensitive 25 mm. from the apex.

In the effort to extend the study of the phenomena here treated over as wide a range as possible, an attempt was made to add a representative of the *Leguminosae* to the number of those included in the experiments. So far as tested, only two species of this family could be thought of with any hope of success, these two being *Pisum sativum*, L., and *Vicia sativa*, L. In my tests [1], I had found *Pisum* somewhat more sensitive than *Vicia.* Both plants give a rather high proportion of crooked roots in water, and both have been shown to respond rather slowly to a rheotropic stimulus. Individual roots in both species, when the whole root received the stimulus [2], have been seen to respond within two hours after the application of the stimulus, but the majority of roots in both species show no curves till after the lapse of six to eight hours.

Pisum sativum was selected for experiment, and over one hundred seedlings tested by shielding various lengths of root from the water-stream. The roots curved, but in all directions, and the curves were evidently due to the objectionable environment of water, and not to the water-stream. A control was set up in still water, without using the glass-tubes, and the curves came in the same way. Ten seedlings with naked roots were tested for rheotropism, but gave no rheotropic curves, only distortion curves, during twelve hours. The attempt to use this plant with the glass-tubes was thereupon abandoned.

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

[2] Juel, Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. f. wiss. Botanik, xxxiv, p. 507. Newcombe, loc. cit.

IV. SUMMARY AND CONCLUSION.

As far as we know, there is no reason in the nature of the case why the sensitiveness of roots to stimuli should be confined to the region capable of elongation. A grass-stem receives and responds to the gravitation stimulus when under ordinary conditions its growth has ceased[1]; the cotyledon of *Panicum*[2] is sensitive to light after growth has ceased; and the leaves of *Mimosa* and of numerous other plants continue to receive and respond to stimuli long after growth has ended. The region of roots shown in the foregoing pages to be sensitive to stimuli, though no longer capable of elongation, may still grow in diameter. And it may be said here that the assumption of the limitation of sensitiveness of roots for certain stimuli to certain regions is not in all cases justified. Czapek[3] appears to have tenable ground for limiting the perception of gravitation to the root-apex. But that moisture stimulates only the apex, cannot be maintained until the elongating zone and the part back of it are tested in the neutralization of gravitation. So also with thermotropism, aerotropism, and the like; for aught we know, the stimuli for these responses may be received beyond as well as in the elongating zone.

In carrying out the experiments detailed in the foregoing pages, there are various difficulties involved and various objections which may be raised. These will now be briefly considered. In the first place, I may admit that the employment of glass-tubes is but an imperfect method; the tubes necessarily obstruct the flow of water. If, however, fibres of cotton are attached to the glass-tubes, they are seen to trail constantly in the direction at right angles to the diameter of the revolving basin of water, showing that a current approximately constant in direction is maintained. The current, after being disturbed by the tubes and seedlings in one-half of the diameter, is recomposed by its undisturbed progress through the following

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[1] De Vries, Ueber die Aufrichtung des gelagerten Getreides. Landw. Jahrbücher, ix, 1880, p. 473.

[2] Rothert, Ueber Heliotropismus. Cohn's Beitr. z. Biol., vii, p. 176.

[3] Czapek, Jahrb. f. wiss. Botanik, xxvii, p. 255; ibid. xxxv, p. 317.

half-circle before it reaches the row of seedlings in the other half of the diameter. The speed of revolution (this being twelve times to the minute) is rapid enough to overcome in large measure the tendency to eddies and cross-currents. The constancy of response by the roots indicates a constancy in direction of water-stream.

A second criticism that might be advanced against the method here employed may be found in the assumed possibility of a current through the tubes, even if a very slow one, thus bringing the current against the elongating zone. This notion is worth considering, for it has been shown that a velocity of only one centimetre, or less, per minute is sufficient to call forth a rheotropic response in *Raphanus sativus*[1], and a velocity of 2 cm. per minute will call forth a response in the roots of *Zea Mays*[2], *Vicia sativa*[2], and *Brassica alba*[1]. There are three reasons why this possible explanation of the cause of the curves will not suffice. (1) The glass-tubes with the seedlings were kept as nearly vertical as the eye could detect. If the glass-tubes were vertical in the water, no current could pass through the tubes, though there might be a little movement of the water a slight distance within the opening of each end of the tube. In all my experiments the lower end of the root was kept three or more millimetres (usually 10 to 12 mm.) above the lower end of the tube. It seems impossible to assume that any movement of water in a constant direction could have taken place within the tube at such a distance from its opening. (2) If the tubes were in some cases slightly inclined from the vertical direction, thereby causing possibly a very slow stream through the tubes, only those streams which flowed from above downward through the tubes could have caused the curves of the roots; for a stream flowing from below upward through the tube would keep the root from bending, the tendency of the rheotropic response being to turn the root-tip toward and parallel with the current of water. It

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

[2] Juel, Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. f. wiss. Botanik, xxxiv, 1900, p. 515.

is, however, out of any possibility that so many tubes should have been inclined in a direction favourable to a downward flow of a stream, and that, owing to this flow, so many roots should have been bent in a constant direction as to give the percentages of responses shown in the tables. (3) To guard against the possibility of a flow of water in the tubes, several experiments were carried through in which the lower ends of the tubes were closed by a firm plug of cotton. In these cases the curves came just as promptly and as numerously as when the tubes were left open.

There was no possibility of mistaking geotropic or heliotropic curves for rheotropic; for, as stated elsewhere, during the preparation the seedlings were kept in the vertical direction, and all the experiments were carried on in the dark-room. Moreover, the preparations often stood at rest for hours after setting up before the revolution of the basins of water was begun, thus affording time for overcoming the effect of any preceding geotropic or heliotropic stimulus. Besides all this, the initial bends in my experiments never came in less than two hours, and, in the majority of roots, not till five or more hours after the beginning of the revolution. Such a latent period as this is not at all unusual for rheotropism, as shown by the work of Berg[1], Juel[2], and myself[3].

It might be thought that the contact of the root with the glass-tube would cause a curvature. To this it may be said that no response to contact has been demonstrated for roots. Moreover, experiments set up to test the effect of contact between roots and glass-tubes have shown no curves resulting.

From all the considerations presented in the foregoing pages, the rheotropic sensitiveness of the root at a considerable distance from the limit of the elongating zone may, I believe, be accepted as demonstrated. Juel[4] had obtained curves in two roots of *Vicia sativa* covered with collodion caps for a distance of 7 to 8 mm. from the apex. This number was

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[1] Berg, Studien über Rheotropismus. Lunds Univ. Årsskrift, xxxv, II, No. 6.

[2] Juel, Jahrb. f. wiss. Botanik, xxxiv, 507.

[3] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

[4] Juel, loc. cit., p. 519.

too small to serve as a demonstration, and it is probable that the caps did not cover the whole of the elongating zone. In the present paper not only was the whole of the elongating zone covered, but several millimetres beyond. It may with safety be said that the root of *Zea Mays* (popcorn) is sensitive at a place 10 mm. back of the limit of the elongating zone; that of *Fagopyrum esculentum*, 9 mm., or more, from the elongating zone; that of *Helianthus annuus*, 8 mm., or more, from the elongating zone; and those of *Brassica alba* and *Raphanus sativus*, certainly 10 mm. and probably 15 mm. to 20 mm. from the elongating zone.

As to the velocity of the water-stream causing these curves, it should be noted that it was not so great as given in the tables, since there no account was taken of the resistance offered by the glass-tubes and the roots. Elsewhere[1] it has been shown that velocities of current between 100 cm. and 500 cm. per minute bring good rheotropic responses in the uncovered roots of eighteen species of plants tested. It may well be believed that in spite of the obstruction offered by the glass-tubes and the roots, the velocities of flow fell within the limits for good responses.

The results here given should not be taken as showing the limit of the sensory tissue. With better means, not only might the limit of sensitiveness be extended, but a greater percentage of curvatures might be obtained. In my work on rheotropism[2] it was found that many individuals of many species did not show a response for twelve to twenty hours after the application of the stimulus of the water-stream. It is however, when glass-tubes are used, not advisable to continue an experiment more than about twelve hours. A longer period brings distortion to several of the roots. These distortions are apparently due to want of exchange of water in the tubes surrounding the roots, the excreta from the roots accumulating in the imprisoned water. It is probably not due to a lack of oxygen; for the roots still

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[1] Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

[2] Ibid.

continue to grow, and a lack of oxygen does not cause distortion so far as my observation goes.

A final reference may be made to the significance and nature of rheotropism. Of biological significance, it is difficult to perceive any. The nature of the stimulus remains as obscure as ever. Of course there is pressure against the roots by the stream of water. But thigmotropism has not been and probably cannot be demonstrated in ordinary roots by ordinary means. If rheotropism is not thigmotropism, we do not know what the nature of the stimulus is; but until thigmotropism has been demonstrated in roots, no claim can be made for the identity of these two responses.

Contributions towards a Knowledge of the Anatomy of the Genus Selaginella.

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With Plates XX and XXI.

PART IV. THE ROOT.

THE most important contribution to our knowledge of the anatomy of the root-system of *Selaginella* is that contained in Nägeli and Leitgeb's well-known monograph (2). Hofmeister, it is true, makes a brief reference to the subject (1), but confines his remarks to certain general points with regard to the origin and branching of the roots. He speaks of adventitious roots arising at the forkings of the stem in such species as *S. denticulata*, *helvetica*, *Martensii*, &c., either generally throughout its length or on the basal region of the stem only. The root, Hofmeister says, arises in the axil of the ventral leaf situated at the forking of the shoot axis, and from the outer side of the cross-band which unites the vascular systems of the two branches (e. g. in *S. denticulata*). The roots branch freely, the first forking being in the plane of the leaf in whose axil the root arises, and the second branching being at right angles to the first. Hofmeister also draws attention to the swelling

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that occurs at the end of the aërial portion previous to the first bifurcation. He gives no detailed account, however, of the anatomy of the root.

Nägeli and Leitgeb's researches lay the foundation of our knowledge of the anatomy of the roots, and as their observations and conclusions have been called in question by more recent investigators, it may be advisable to summarize their results at somewhat greater length. Their observations were apparently made on four species, viz. *S. Kraussiana*, *S. Martensii*, *S. cuspidata*, *and S. laevigata.* They commence by calling in question the accuracy of applying the term 'root' to the organs arising at the branchings of the stem, and point out that a root-cap is absent from the apices of such organs. They further express the belief that these bodies are in reality cauline in their homology, giving them the name of 'rhizophores' (*Wurzelträger*). Despite the fact that several authorities have brought forward evidence and arguments against this view, the name is still commonly employed in textbooks, &c., to designate the unbranched aërial portion of the root in such species as possess such organs. In the present paper the rhizophore is designated as the 'aërial part of the root,' and that portion which is embedded in the soil as the 'subterranean part.' The rhizophores, according to Nägeli and Leitgeb, originate on the upper side of the stem, near the base of the weaker branch, arching round towards the ground on that side. Following the system of bifurcation of the stem they arch alternately to right and to left, and occur at all the points of branching of the stem. In *S. Kraussiana* two rhizophores are occasionally given off, the accessory rhizophore arising close to the normal one from the upper side of the stem, but at a little distance from the branch, and bending round the stem on the other side. No root-cap is apparently developed at this stage. The rhizophore is at first circular in section, but later becomes elliptical, the long axis of the ellipse being parallel with the long axis of the stem. The apex of the rhizophore is occupied by a two-sided apical cell, giving off segments on the backwardly directed faces. Divisions of the apical cell cease when the rhizophore is about 1 mm. long, and by rapid divisions of the segments the apex swells and differentiation takes place within, so as to give rise to the true roots which at this stage do not exhibit further development. The cells of the swollen apex have their walls thickened, and they are filled with watery contents. Intercalary growth now becomes energetic, so as to bring the apex of the rhizophore into contact with the soil. The cells of the apex become disorganized, and the apices of the true roots enter the soil covered at first by a homogeneous slime derived from the disorganized apical cells.

In section the rhizophore exhibits a clearly marked cortex, whose cells are sclerotic save in the innermost layer, and a central vascular system. The first vascular elements arise centrally in *S. Kraussiana*; scalariform elements develop round these, and are surrounded in turn by three to five layers of small cells. The vascular cylinder of the rhizophore arises from the vascular strand of the stem of the same side at or near the conjunctive strand. The markedly centrifugal development of the vascular system in the rhizophore of *S. Kraussiana* is, according to Nägeli and Leitgeb, a unique feature.

In *S. Martensii* one rhizophore (the lower one) is alone developed, although occasionally the upper one is also. The latter is always represented by a swelling. The vascular bundles of the rhizophores unite in the stem and run parallel with its long axis to the point of bifurcation of the stem, and there unite with the cylinders of the branches. The air-space of the stem-cylinder is continued up through the rhizophore for a short distance. Nägeli and Leitgeb believe that the rhizophores are independent in origin. In the case of the true root the development of the protoxylem is lateral. Where the root branches the protoxylems face each other, hence the bundles undergo torsion to the extent of 90 degrees. Branching of the vascular cylinder takes place before the forking of the root itself, hence the end of the unbranched rhizophore contains two vascular cords. These authors compare the two cords with opposing protoxylems with the centroxylic condition of the rhizophore in *S. Kraussiana.* The planes of branching are always at right angles in *S. Martensii.* The root-cap is small, and is ultimately thrown off.

In *S. cuspidata*, Lk., and *S. laevigata*, Spr., there are no rhizophores, and the roots arise directly from the bifurcations of the stem. They differ from rhizophores in not arising at every bifurcation. The vascular system is a monarch strand with one lateral protoxylem. Pfeffer, in his paper on the development of the embryo of *Selaginella*, draws attention to the occasional development of the upper rhizophore into a leafy branch in *S. inaequalifolia* (3). Van Tieghem (4) describes the vascular bundle of the rhizophore as triangular in section, and so orientated that the protoxylem faces the ground if the stem be placed in an erect position. He also draws attention to the change in orientation of the bundles at the forkings. The so-called rhizophore Van Tieghem considers as a case of exaggerated intercalary growth of the aërial part of the root, and dissents from the view held by Nägeli and Leitgeb as to the cauline value of the organ. Russow (5) says that the so-called rhizophores and roots agree in anatomical structure, and holds the same view as Van Tieghem as to their morphological value. Division of the monarch bundle takes place in the aërial part before any appearance of external division. The xylem first of all broadens, and division takes place in the protoxylem first. The xylems suffer torsion through 90 degrees at the forkings both of the aërial and subterranean parts. In this relation it is interesting to note that Scott and Hill (10), in their paper on the anatomy of *Isoetes Hystrix*, remark that 'as the two strands (at the root-fork) separate from each other, they turn through an angle of 90 degrees so as to direct their protoxylems towards each other.'

Dangeard (6) describes and figures the central protoxylem of the rhizophore of *S. Kraussiana*, and says that a similar centroxylic condition occurs between the spore and the first two leaves, but he does not figure it. He gives no details of the anatomy of the root in any of the species which he discusses, but gives a short general summary, which, however, adds nothing to what had been previously known.

In a paper on *S. lepidophylla*, Wojinowić (8) says that there are no rhizophores in that species, that the roots arise directly from the stem, and without any relation to the branching of the axis. The root in this species shows in transverse section an epidermis with two or three layers of thin-walled hypodermis, followed by five or six layers of sclerenchyma, an endodermis, pericycle and normal-monarch vascular strand.

Bruchmann (9), in his monograph on *S. spinosa*, adds no new points beyond drawing attention to the occurrence of symbiotic fungal hyphae in the roots. He adds that this species and *S. Lyallii* are destitute of root-hairs.

In passing, it may be pointed out that Bruchmann, in describing the curious centroxylic condition of the vascular system in the creeping part of the stem, remarks: 'wie es bisher noch von keinem Stengel der Gattung *Selaginella* bekannt war.' Bruchmann's paper was published in 1897, but I may perhaps be permitted to point out that I described and figured that condition in this species in 1894 (11).

In the accounts of the root-system in the genus *Selaginella* given in the textbooks, it is customary to distinguish the unbranched aërial portion of the root as a 'rhizophore,' and to retain the term 'root' for that part which is underground and bears a root-cap and root-hairs. It would seem advisable at the outset to determine whether that nomenclature, and the views on which it is founded, can be maintained.

The chief arguments advanced in its favour are those of Nägeli and Leitgeb, who claim that the aërial part of the root is of cauline value on the ground that it has no root-cap, that it is occasionally transformed into a leafy branch, and that it arises exogenously whilst the true roots are developed from it later endogenously. This view is combated by Van Tieghem (4) and Russow (5).

In studying the comparative morphology of the root it is instructive to note that a complete series of transitions may be obtained in the different species, with *S. spinosa* at one end of the series and a typical 'rhizophore' bearing type such as *S. Martensii* or *S. Galeottei* at the other. In *S. spinosa* it will be seen that the roots arise directly from the base of the stem which is itself exceedingly delicate. Indeed the root-system in this species is out of all proportion to the comparatively massive and much branched aërial portion, and points to the important part which the lower prostrate branches play in absorption. *S. spinosa* is, indeed, largely saprophytic in habit. This characteristic is emphasized by the frequent occurrence of symbiotic fungal hyphae in the cortical cells of the root, as observed and figured by Bruchmann. On two or three occasions I have seen evidence of the presence of these symbiotic hyphae in the creeping part of the stem also. In *S. oregana* the roots spring not only from the base of the stem but also from the lower region generally, where the shoots are in contact with the tree on which this species is epiphytic. This basal origin of roots and absence of so-called rhizophores is characteristic of types where there is a short rhizomic part with numerous erect axes, e. g. *S. grandis*, *S. erythropus*, *S. Vogelii*, *S. Karsteniana*, *S. haematodes*, &c., and of those species which show a dense tuft of aërial erect axes arising from a short rhizomic basis, e. g. *S. involvens*, *S. pilifera*, &c. In *S. Braunii* and *S. Lyallii* the basal part of the stem is longer and more in the nature of a rhizome, and the roots arise from the under side of the rhizome, branching at once in the soil.

In forms like *S. Kraussiana*, *S. serpens*, *S. delicatissima*, &c., the stem is procumbent, grows parallel with the ground and a short distance from it. In these cases the aërial portions of the root are necessarily longer, and it is to this aërial part that the term 'rhizophore' is applied. In *S. Galeottei*, *S. caulescens*, *S. Martensii*, &c., the stem is at first procumbent and then becomes semi-erect. The roots have correspondingly short aërial regions below, but these become longer as the stems become more and more erect. From the point of view, therefore, of general external morphology there does not seem any stronger reason for distinguishing the aërial part of the root by a special name and ascribing to it stem-characteristics than there exists for differentiating the aërial part of the root of a *Pandanus* or a *Rhizophora* from that which is subterranean or subaquatic.

As a rule the root is intimately related to the branching of the stem, and normally one root arises from the stem at each fork. There is frequently an abortive root on the upper side of the stem, which scarcely appears above the surface, or is represented by a minute papilla, as in *S. Martensii*, *S. Willdenowii*, &c. Occasionally both roots are developed, e. g. *S. caulescens*. In *S. inaequalifolia*, as Pfeffer points out, the upper, usually abortive, root develops into a leafy shoot, and on that ground an argument is based for the cauline value of the aërial portion of the root. On the other hand, roots, as is well known, not infrequently bear both leaves and leaf-buds; and further, as Jones has pointed out in the allied genus *Lycopodium* (11), the differentiation between root and stem is far less marked in the vascular cryptogams than in higher plants, and consequently the organ in question may, without undue violence to morphological conceptions, be conceived as having a preponderance of cauline or radical characteristics according to circumstances. Pfeffer also draws attention to the neutral nature of the aërial part of the root. Another explanation is, however, possible, suggested by the condition of the roots in *S. Lobbii*. Normally, in this species, there is one aërial root developed at each forking of the stem, and that the lower one. The upper root is represented as usual by a papilla. Frequently, at all events in the material I possess, the upper root-papilla is replaced by a leafy branch; but at a short distance from its point of origin there is given off an aërial root which behaves exactly in the same manner as the lower aërial root. The question thus arises whether the leafy shoot of *S. inaequalifolia* and other species which possess this abnormality is not a genuine shoot, proliferating at the normal bifurcation, which is not robust enough to bear a root on its own account. In *S. Lobbii* the dorsal papilla may, apparently, either develop into a third proliferous shoot giving rise to a root, or the root may arise from the papilla directly, the intermediate shoot being suppressed.

Another argument advanced by those who uphold the stem-nature of the aërial root is that it is exogenous in origin and bears no root-cap. I have not as yet proceeded far enough with my own investigations into the origin of members in the genus to offer an independent opinion, but it has been shown by Van Tieghem (12) that no great weight can be laid on this argument, since neither in regard to exogenous origin nor absence of root-cap is *Selaginella* exceptional. Anatomically, it will be seen from the present paper that the aërial and subterranean parts of the root exhibit practically identical features. On all these grounds, therefore, I follow Van Tieghem in considering the root of *Selaginella* as in some cases subterranean only, in other cases partly subterranean and partly aërial, developed at the base of the stem only, and without relation to the branching of the stem, or at the bifurcations of the stem, sometimes singly and either from the dorsal or the ventral side, or both from the dorsal and ventral sides.

Anatomically the root in *Selaginella* shows comparatively little variation, being, in the great majority of cases, composed of a more or less sclerotic cortex covered externally by two or more layers of thin-walled cells, the most external of which is piliferous. These superficial layers are absent from the aërial parts of the root. The vascular cylinder is enclosed by a usually well-marked endodermis and a two- or three-layered pericycle, and consists of one xylem and one phloem bundle. It will be most convenient to study the structure of the root in one species somewhat in detail, and thereafter add such further notes as may be necessary in explanation of the variations in anatomical structure seen in other species.

S. atroviridis, Spr., was found a convenient type for examination, as being fairly robust and possessing the morphological characters most commonly met with in the genus.

The roots arise singly at each forking of the stem, and are partly aërial, party subterranean. The root is at its origin about equal in thickness to the weaker branch, and at once bends downwards and backwards. On the upper side of the stem there also arises at each forking a papilla which represents an abortive root. The branching of the root is dichotomous, the first forking being in a plane at right angles to the long axis of the stem, the next at right angles to the first and so on for several divisions, until external conditions interfere with the regularity of the branching (Pl. XX, Fig. 2). The vascular cords of the root are inserted on those of the larger branch, apically to the point of origin of the minor branch (Fig. 1). The vascular cord of the dorsal abortive root arises behind the point of origin of that of the functional root, its xylem ending halfway through the cortex of the branch. The lacuna surrounding the vascular system of the stem is continued up the vascular cords of the roots, both dorsal and ventral, for a short distance. A transverse section of the root in its unbranched portion shows a crescentic vascular cord with the protoxylem in the concavity. The protoxylem is broken up into patches in the larger bundles and distributed round the concave side (Fig. 4). The outer cortex is strongly lignified, but becomes less so inwards, again becoming lignified as the endodermis is approached. In the younger roots the endodermis shows the usual radial markings, but as age advances the cuticularization becomes complete. The pericycle is from two to four layers thick. There is one row of sieve-tubes (or, more rarely, two) round the convex side of the cord ending at the tips of the horns of the xylem. Three to four layers of phloem-parenchyma completely envelop the xylem. In young roots the crescentic form of the xylem is not so well marked, and the horns approximate so that the protoxylem becomes almost enclosed.

The convex side of the bundle faces the apex of the stem, and the branching of the vascular cord of the root takes place before external branching. At the forking of the root the vascular bundles of the branch-roots undergo a change in orientation, so that the concave faces of the branch-bundles oppose each other. This alteration of the axis of the bundles has already been pointed out by several observers and seems to be a general rule for the genus. Unicellular root-hairs occur right up to the caps of the young roots.

Although there are some slight individual differences in the structure of the cortex, the development of the endodermis and in the amount of extension of the protoxylem, the structure just described for *S. atroviridis* holds good for the great majority of the species I have examined. There are, however, a few points of interest which may now be alluded to.

Approaching quite closely to the type are the roots of *S. plumosa*, Bak., *S. Martensii*, Spr., *S. Douglasii*, Spr., *S. serpens*, Spr., *S. apus*, Spr., *S. convoluta*, Spr., *S. albonitens*, Spr., *S. flabellata*, Spr., *S. producta*, Bak., *S. bisulcata*, Spr., *S. concinna*, Spr., *S. uncinata*, Spr., *S. molliceps*, Spr., *S. Vogelii*, Spr., *S. patula*, Spr., *S. haematodes*, Spr., *S. Karsteniana*, A. Br., *S. grandis*, Moore, *S. erythropus*, Spr., *S. Braunii*, Bak., *S. pilifera*, A. Br., *S. viticulosa*, Klotz., and *S. caulescens*, Spr. In this last-named species the cortex is very sclerotic, and the endodermis becomes greatly thickened towards the pericycle. Both pericycle and phloem-parenchyma may become sclerotic in very old roots.

In *S. involvens*, Spr., the roots arise from the bases of the closely growing stems and enter the ground at once. Anatomically the root is peculiar as regards its cortex. Superficially there is a layer of cubical cells, each of which gives off a root-hair. This layer is followed by a layer of large cells ovoid in section and very regularly placed, and that by a small-celled cortex, small-celled outwardly but becoming larger inwards, and bounded internally by a well-marked endodermis. The vascular cord is normally monarch. *S. cuspidata*, Lk., and *S. lepidophylla*, Spr., agree in all points of structure with *S. involvens* (Pl. XX, Fig. 5). All the above-mentioned species are monostelic so far as their stem-structure is concerned. There are two other species, both belonging to the monostelic type, which exhibit a somewhat peculiar anomaly. In *S. helvetica*, Lk., the cortex is similar to that of *S. involvens*. The vascular cylinder of the stem is ribbon-shaped with two marginal protoxylems, one situated at each margin of the stele. At the point of origin of the vascular cylinder of the root the protoxylem becomes internally placed so that the stele shows on one side a perixylic, on the other a centroxylic structure (Pl. XX, Fig. 19). The same peculiarity is shown by *S. denticulata*, Lk., a species which has otherwise a normal structure.

Turning now to the homophyllous species, *S. spinosa*, P. B., *S. oregana*, Eat., and *S. rupestris*, Spr., it will be found that in the case of the two last-mentioned species the root is normally monarch, save that, as in the case of the stem, the metaxylem consists chiefly of tracheae or vessels (i. e. cell-fusions). The root is covered externally by two layers of thin-walled cells with root-hairs, followed by four to eight layers of thick-walled cells with brown tannin-like contents, two to three layers of thin-walled cells, very liable to be torn through in the process of cutting, and a prominent and completely cuticularized endodermis. The vascular system is poorly developed (Pl. XX, Fig. 6). *S. rupestris*, Spr., agrees with *S. oregana* in all respects. The centroxylic condition of the creeping part of the stem of *S. spinosa*, P. B., has already been described by the present writer (10), and later by Bruchmann (8). It is worth while pointing out, however, that the stem, for some considerable distance before the point of origin of the roots, contains two vascular cylinders, both centroxylic. The root is normally monarch, as figured and described by Bruchmann, to whose description I have nothing to add.

With regard to the bistelic species it may be said generally that the root-structure is, in most respects, similar to that already described for the monostelic species. In *S. Galeottei*, Spr., the aërial part of the root is very long, and one root arises at each fork of the stem on the upper side and bends over behind the lesser branch downwards to the soil. The vascular cylinder of the root arises just in front of the origin of the lateral branch and far behind the point of fusion of the steles of the main axis. The aërial and subterranean parts of the roots both contain normal-monarch cords. Root-hairs are abundant. *S. rubella*, Moore, agrees in all essential respects with *S. Galeottei.*

In *S. Kraussiana*, A. Br., the roots arise singly at each forking of the stem on the upper side and arch over to the side of the stronger branch. Since the branches are alternately right and left, the roots are alternately left and right. Each is unbranched until it reaches the soil and then it branches profusely. Anatomically the vascular cylinder of the aërial part arises from the vascular system of the stem at the junction of the stem-cords. The aërial portion, as has been already pointed out by several authors, is centroxylic (Pl. XX, Fig. 17), and remains so until the subterranean parts are reached when the root becomes normally monarch. *S. Kraussiana* has hitherto been regarded as the solitary exception in this respect. *S. Poulteri*, Veitch, and *S. delicatissima*, A. Br., however, show precisely the same centroxylic condition in the aërial roots, like *S. Kraussiana* becoming monarch in the subterranean portions.

Turning now to the species usually designated as tristelic, it may be said that they agree in almost all respects with the majority of the species already described in the monarch character of their root-cylinders.

The root of *S. canaliculata*, Bak., in its aërial part shows a slightly crescentic xylem and a protoxylem situated in the middle of the crescent. The mode of origin of the steles of the root is as follows:—From the upper and lower steles of the stem vascular strands are isolated (Pl. XXI, Fig. 24, 1), then one from the middle strand, and at the same time one for the ventral leaf (2); the middle stele then broadens and forks and a strand is given off the lower stele (3); the upper stele then bends down and unites with the upper branch of the fork of the middle stele, the lower branch uniting with the offset of the lower stele (4). The middle stele is now isolated and the fork portion is still united with the upper stele (5); the three steles of the lateral branch are thus distinct. The vertical strand divides into an upper part which goes to the upper root and a lower part which goes to the lower and functional root (6, 7). As in *S. helvetica*, the upper and middle steles of the stem, before giving off the strands to the vertical band which supplies the roots, become centroxylic on that side, again becoming perixylic when the root-strands are isolated.

In *S. Wallichii*, Spr., the roots are very short and not related in all cases to the branching of the stem, but generally arise from the under side of the rhizome just at the junction of the minor and major branches, but from the latter. The stele of the aërial root in section is similar to that of *S. atroviridis*, save that the protoxylem is almost isolated from the xylem. The endodermis is well defined, the pericycle is two or three layers thick, and there are abundant root-hairs right up to the margin of the root-cap.

In the general anatomy of the root similar features to those exhibited by *S. Wallichii* are shown by *S. chilensis*, Spr., *S. viridangula*, Spr., *S. Victoriae*, Moore, *S. inaequalifolia*, Spr., and *S. gracilis*, Moore. In *S. Willdenowii*, Bak., the root arises as in *S. Wallichii*. There is an abortive root on the upper side of the stem, which has a small prominence of vascular tissue arising from the strand of the functional root near its junction with the stele of the stem. The lateral branch is isolated farther back. The abortive root, as in *S. inaequalifolia*, is sometimes functional. The xylem of the root-stele is slightly crescentic, with the protoxylem almost isolated from the xylem but accompanied by some metaxylem. The subterranean part of the root is normally monarch with a sclerotic cortex and plentiful root-hairs. *S. laevigata*, Baker, var., *Lyallii*, Spr., which exhibits so many anomalies in its stem-structure, is normal in its root-structure. The roots arise singly at the bases of the erect shoots, and their vascular strands are inserted on the cylindrical stele of the rhizome.

In *S. Lobbii,* Moore, the only other species which I have examined in detail, the roots arise at the forkings of the stem, but not at all of them. The roots are developed at each fork, the ventral one becomes functional but the other develops into a leaf-bearing shoot. The functional root forks at a variable distance from the stem in a plane at right angles to the long axis of the stem, the next forking taking place at right angles to the previous one, and so on. The dorsal papilla develops in most cases into a leafy shoot from which at its base a functional root arises (Pl. XX, Fig. 11). A section taken between the origin of the root and the main axis shows a central cylinder with an extended protoxylem and a slight lacuna. Just before the origin of the root the protoxylem breaks up and is distributed round the metaxylem. Beyond the point of origin of the root the stele differentiates into the usual three steles of the ordinary branch. A transverse section of an old aërial root shows a well-marked epidermis, a slightly sclerotic external cortex, followed by a thick cortex of large elongated cells. The stele has an endodermis with radial cuticularization, a pericycle three or four cells deep, then one or two rows of sieve-tubes followed by three or four layers of phloem-parenchyma. The xylem forms a crescentic band of scalariform and sometimes reticulate fibres, the largest elements being on the convex side, viz. that towards the apex of the shoot from which the root arose. The phloem-parenchyma turns the horns of the crescent and is continuous with the parenchyma, which entirely lines the concave side and separates the proto- and metaxylem by three or four layers of cells. The protoxylem is thus aggregated in a strap-like mass in the hollow of the crescent. The sieve-tubes stop abruptly at the horns of the crescent, but the pericycle is continuous round the horns and outside the protoxylem. In sections of smaller roots taken close to the stem the endodermis is not so well marked, the pericycle is thinner and the sieve-tubes are more numerous. The xylem is horse-shoe shaped with a break at the convexity and with an isolated protoxylem. Previous to the forking of the root the protoxylem-band also divides, and the two protoxylems take up positions one-third and two-thirds of the way along the concave margin of the xylem. The isolation of the protoxylem in this species is a peculiar feature which I can find no parallel for amongst other members of the genus, although the condition is led up to by the semi-isolation of the protoxylems in such species as *S. Wallichii.*

GENERAL CONCLUSIONS.

1. The root of *Selaginella* is either subterranean only, or partly aërial and partly subterranean.

2. The view held by some authors that the aërial part of the root is of cauline value, and should be distinguished from the underground portion as a 'rhizophore,' is not supported by sufficient morphological, anatomical, or developmental evidence.

3. The root anatomically is monarch, both in its aërial and underground regions, with well-defined endodermis.

The branching of the root is dichotomous, and the first dichotomy is at right angles to the long axis of the stem.

4. In several species the vascular cord of the stem at the origin of the root is centroxylic.

5. A centroxylic condition of the aërial part of the root occurs in *S. Kraussiana*, *S. delicatissima*, and *S. Poulteri.*

6. At every forking of the root the protoxylems of the two branch roots face each other, having revolved through an angle of 90 degrees.

7. Certain exceptional positions of the protoxylems are also referred to.

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EXPLANATION OF FIGURES IN PLATES XX AND XXI.

Illustrating Professor Harvey-Gibson's paper on the Anatomy of the genus *Selaginella.*

PLATE XX.

Fig. 1. Origin of the vascular cords of the roots of *Selaginella atroviridis*, Spr. × 2. *a.* lateral branch ; *b.* dorsal abortive root ; *c.* main stem ; *d.* ventral root.

Fig. 2. Root-system of *S. atroviridis.* Nat. size.

Fig. 3. Transverse section of the root of *S. atroviridis* just previous to the third forking. × 350. Lettering as in Fig. 4.

Fig. 4. Transverse section of the aërial part of the root of *S. atroviridis.* × 350. *a.* endodermis ; *b.* pericycle ; *c.* sieve-tubes ; *d.* phloem-parenchyma ; *e.* metaxylem (see Fig. 3).

Fig. 5. Transverse section of the cortex of *S. involvens*, Spr. × 350. *a* endodermis ; *b.* cortex ; *c.* hypodermis ; *d.* piliferous layer.

Fig. 6. Transverse section of the root of *S. oregana*, Eat., showing piliferous layer and hypodermis, sclerotic outer and thin-walled inner cortical cells, endodermis and monarch vascular cylinder. × 350.

Fig. 7. Portion of the axis of *S. Galeottei*, Spr., showing the alternate origin of roots to right and left. Nat. size.

Fig. 8. Vascular cords of *S. Galeottei.* Nat. size. *a.* vascular cords of the lateral branch ; *b.* of the root ; *c.* of the main axis. The arrow points towards the apex of the stem.

Fig. 9. Root-system of *S. caulescens*, Spr. Nat. size.

Fig. 10. Successive positions taken by the protoxylems at the bifurcation of the root of *S. molliceps*, Spr. Diagr.

Fig. 11. Origin of the roots in *S. Lobbii*, Moore. Nat. size. *a.* adventitious shoot in the position of the dorsal root ; *b.* root arising from the adventitious shoot ; *d* and *c.* right and left branches of the shoot axis.

Fig. 12. Transverse section of the root of *S. Vogelii*, Spr. × 350.

Fig. 13. Root-system of *S. Vogelii.* Nat. size.

Fig. 14. Transverse section of the root of *S. grandis*, Moore, taken just before the forking. × 350.

Fig. 15. Origin of the normal root of *S. Lobbii.* Nat. size.

Fig. 16. Transverse section of the root (aërial) of *S. Lobbii* at the point of forking. The metaxylem has divided but not the protoxylem. × 350.

Fig. 17. Transverse section of the aërial part of the root of *S. Kraussiana*, A. Br. × 550. *a.* metaxylem ; *b.* phloem-parenchyma ; *c.* sieve-tubes ; *d.* pericycle ; *e.* endodermis ; *f.* protoxylem.

Fig. 18. Origin of the root in *S. Wallichii*, Spr., in transverse and longitudinal view. Diagr.

Fig. 19. Centroxylic condition of one of the marginal bundles of the stele of the shoot at the origin of a root of *S. helvetica.* × 350.

Fig. 20. Transverse section of one of the smaller roots of *S. Wildenowii*, Baker. × 550.

PLATE XXI.

Fig. 21. Root-system of *S. Lyallii*, Spr. Nat. size.

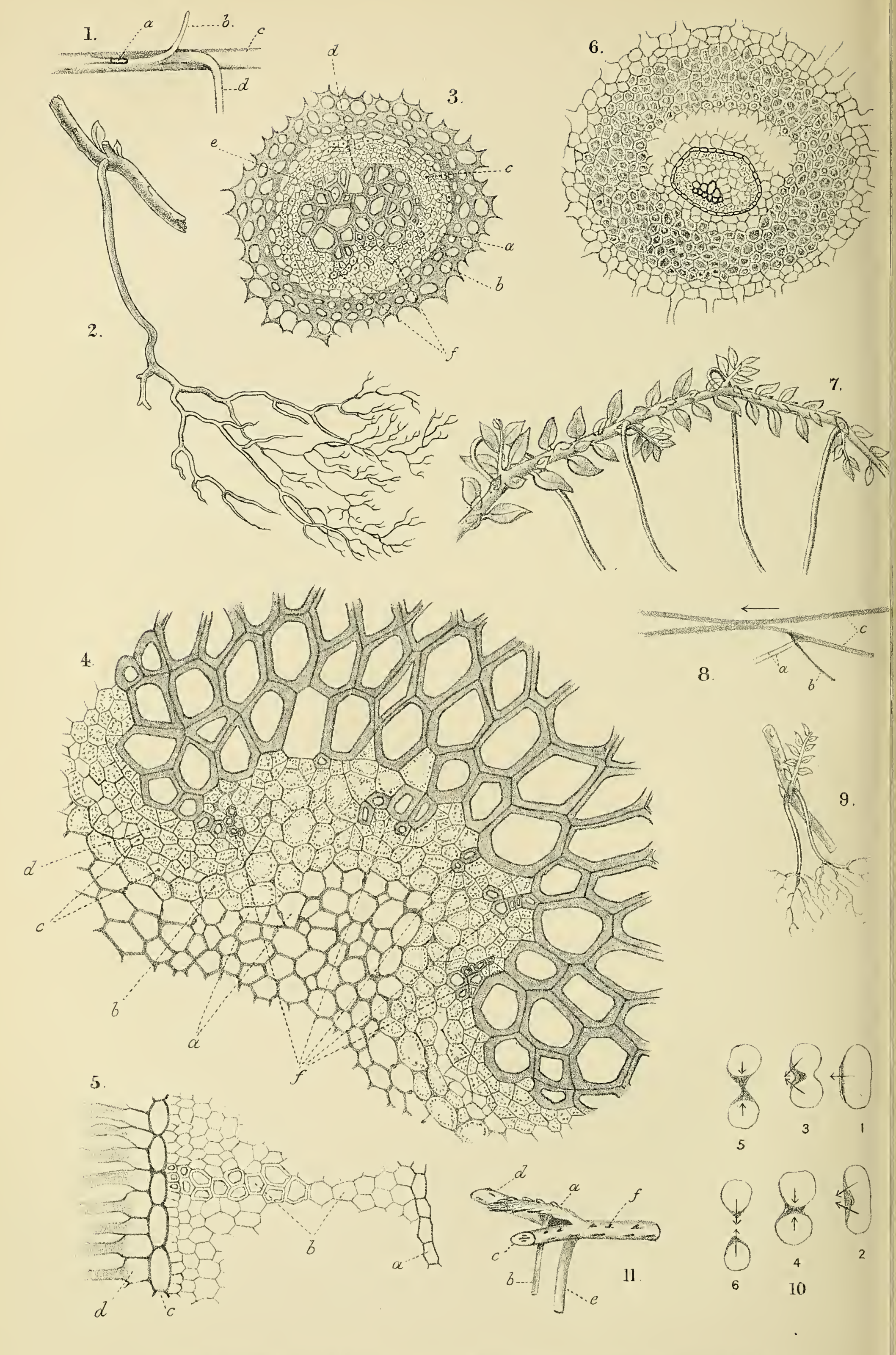
Fig. 22. Forking of the root-stele in *S. Lyallii*. × 350.

Fig. 23. Root-system of *S. Kraussiana*, A. Br. Nat. size.

Fig. 24. Successive sections showing the mode of origin of the steles of the lateral branch and root in *S. canaliculata*, Baker. Diagr.

Fig. 25. Transverse section of the root of *S. Willdenowii*, Baker, showing the almost isolated protoxylem. × 350.

Fig. 26. Successive sections of the stem of *S. Willdenowii*, Baker, showing the mode of origin of the vascular systems of the root and lateral branch. Diagr.



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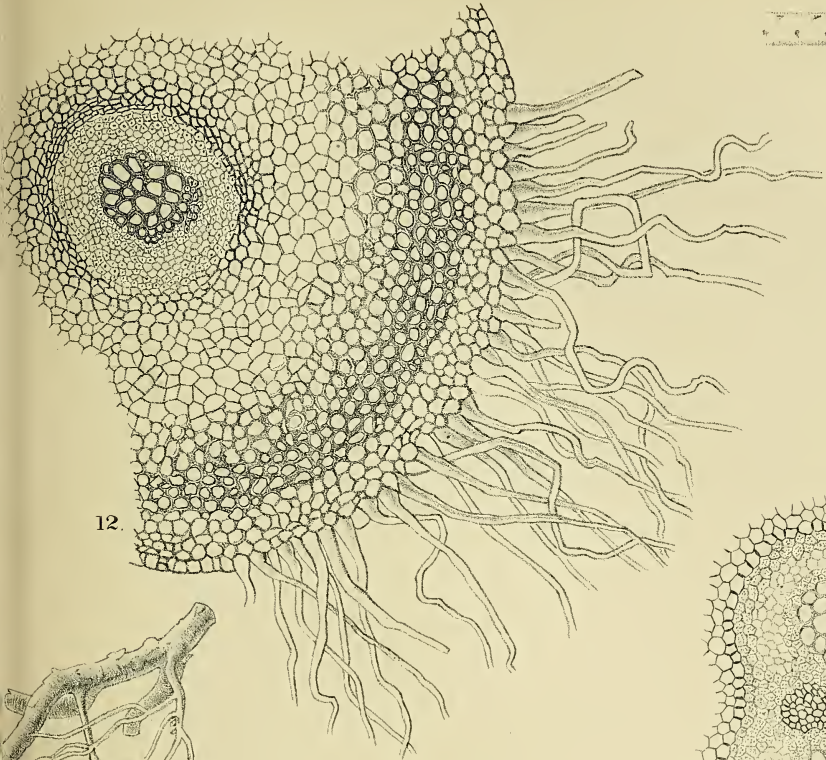

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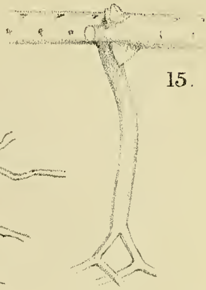

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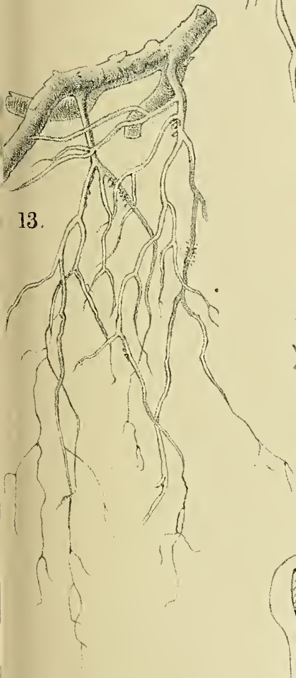

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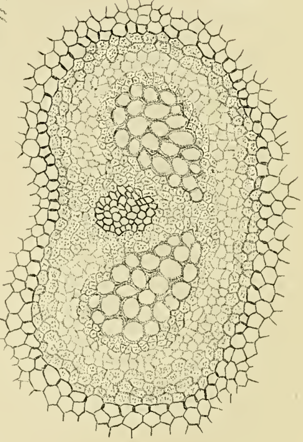

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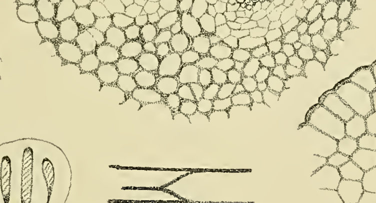

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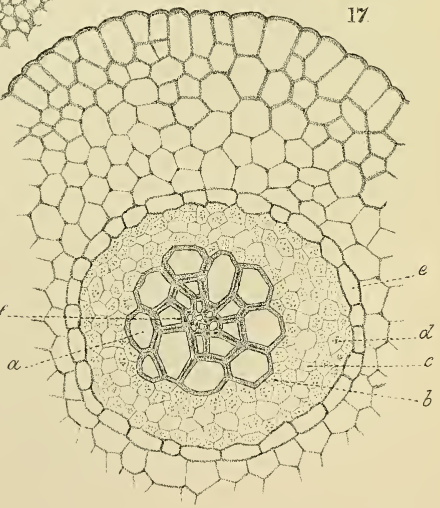

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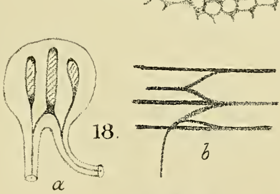

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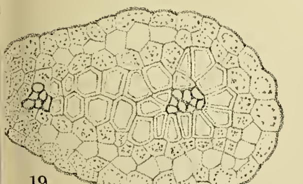

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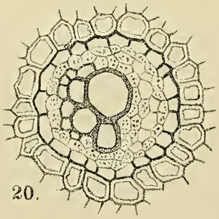

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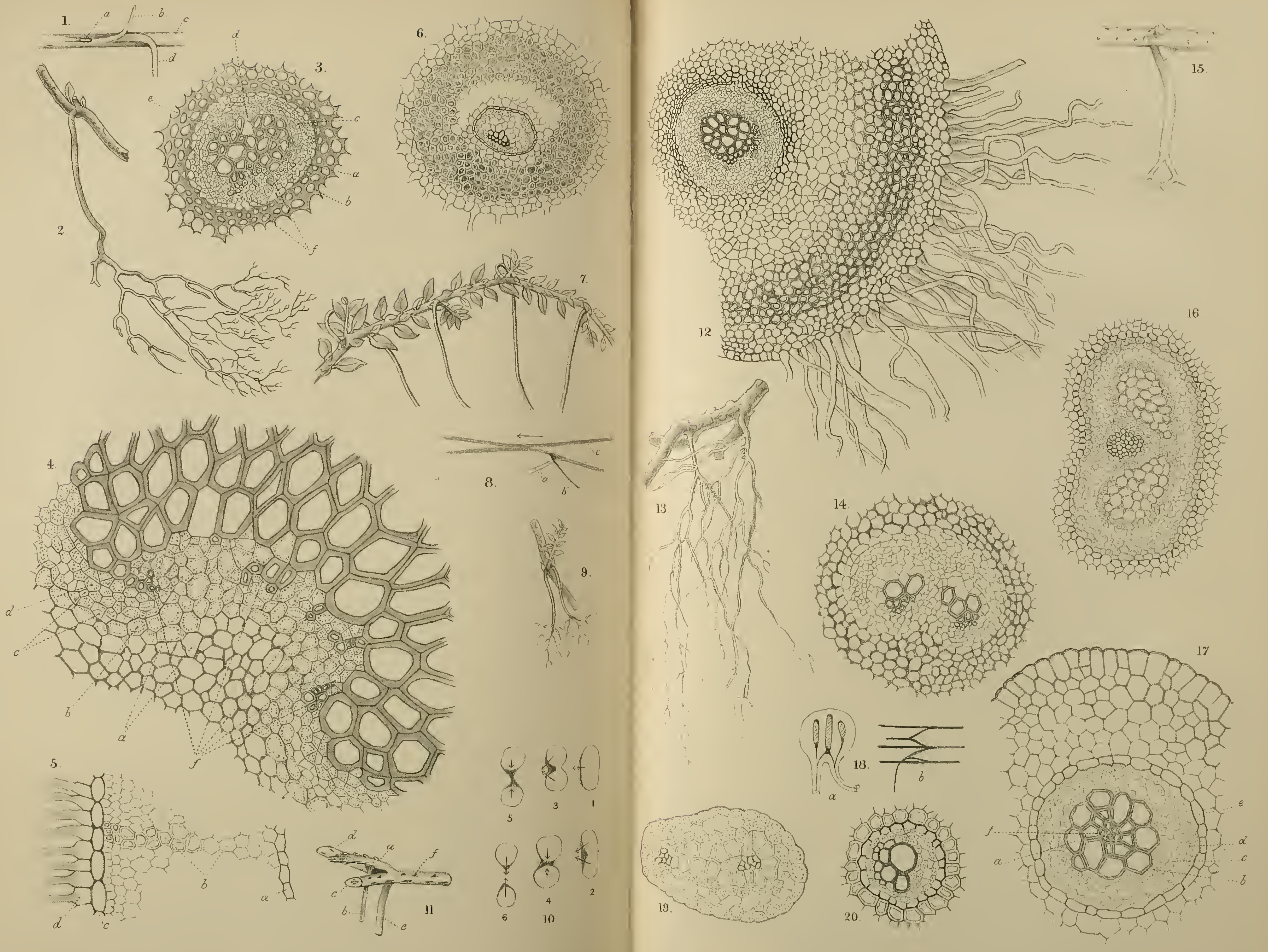

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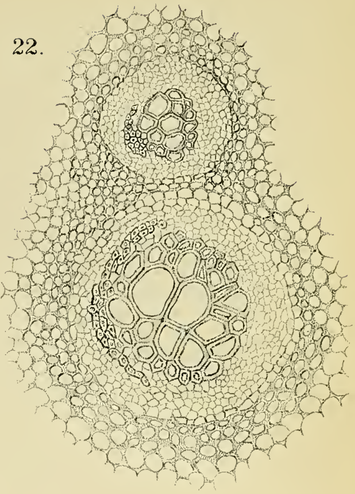

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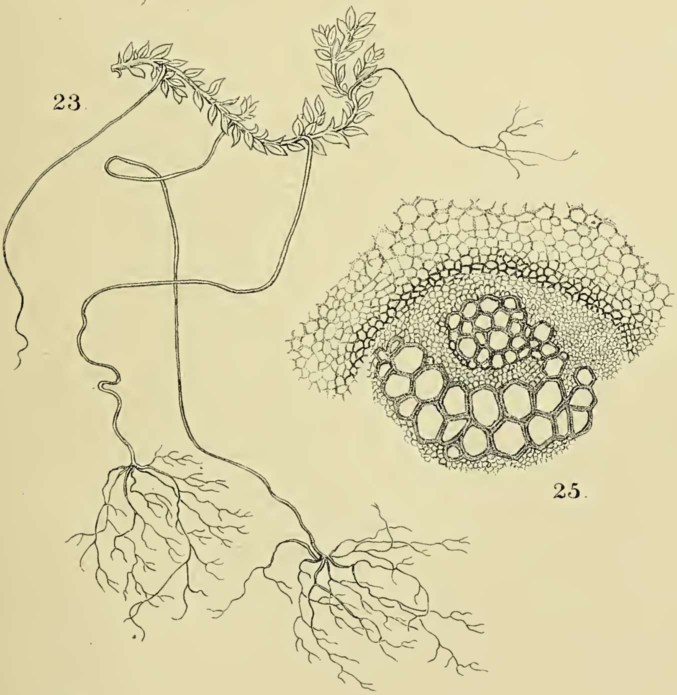

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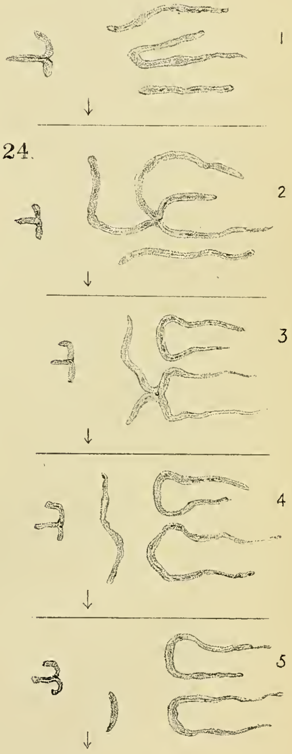

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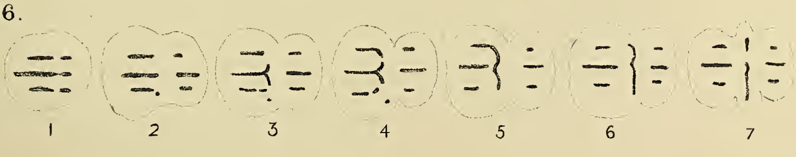

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HARVEY-GIBSON —— ANATOMY OF SELAGINELLA.

The Structure and Development of the young plants in Oedogonium[1].

BY

F. E. FRITSCH, B.Sc., Ph.D.

With three Figures in the Text.

ALTHOUGH the young plants of *Oedogonium* have not infrequently been figured[2] in various species, not many observations on their structure and mode of development have been published[3]. I propose therefore in the present paper to discuss the structure of the young plants in five species of *Oedogonium*[4], obtained from different parts of the Royal Botanic Gardens at Kew.

On the other hand, the formation of the zoospores in this genus has already formed the subject of much investigation. The curious details of their liberation were first clearly described by Braun ('49, pp. 150 and 173) and Pringsheim ('58, pp. 25–29). The observations of these two investigators were so reliable, that later botanists have been able to add little thereto, and chiefly occupied themselves with theories regarding the derivation of the thin membrane, which is formed round the emerging zoospore, and within which the latter remains for a short time, when fully liberated from the zoosporangium, until the dissolution of this membrane enables

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[1] From the Jodrell Laboratory, Royal Botanic Gardens, Kew.

[2] Cf. Kützing, '43, Tab. 10 and 12; Thuret, '50, Pl. XIX, Figs. 8 and 9; Wolle, '87, Pl. LXXIII, Figs. 24–30; Pl. LXXIV, Figs. 12 and 13; Pl. LXXXI, Figs. 4 and 5; Borge, '94, Figs. 66 and 67 (*Oed. diplandrum*, Jur.).

[3] See Pringsheim, '54, p. 70, foot-note; Poulsen, '79; Wille, '87; Fritsch, '02.

[4] Namely, *Oed. capillare*, Ktz., *cardiacum* (Hass.), Wittr., *stagnale*, Ktz., *calcareum*, Cleve, and in an undetermined species from the river Severn.

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the zoospore to commence moving actively. Under abnormal circumstances the phenomena connected with the liberation of the zoospore and its germination are somewhat modified, and I shall refer to some of these modifications below.

The zoospores were generally allowed to germinate in a slow but continuous stream of water on the stage of the microscope (Zimmermann, '92, p. 3). In a few cases a weak (2°/₀) solution of cane-sugar was employed.

1. THE STRUCTURE OF THE YOUNG PLANTS.

I will commence by describing the structure of the young plants in *Oed. capillare*[1], in which the end cell of the filaments bears a distinct pointed tip. The species was growing on a mass of *Nitella syncarpa* contained in a glass vessel in the Herbaceous Department. When I first observed it, numerous young plants of very variable size were attached to the sides of the vessel about the level of the water. Most of these were unicellular, but some consisted of two or even three cells (see Fritsch, 1902, Fig. 23, *f*) ; all were provided with a very prominent tip[2], which was hollow in its lower portion and solid towards the apex. Many of these young unicellular plants had again emptied their contents without undergoing division, the upper part of the cell-wall, together with the tip, being pushed on one side like a hinged lid[3]; in some cases this lid became quite disconnected. Sometimes, however, no lid was formed (owing probably to abnormal external conditions), and the contents of the cell then became rounded off and surrounded themselves with a new membrane, being unable to escape as a zoospore (Fig. 25, *a*) ; under these circumstances a considerable decrease in bulk usually took place, the contents only occupying a small portion of the cell. It is of interest that I once or twice found that these contents had passed over the motile stage and had germinated directly

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[1] The germination of the zoospores in this species formed the subject of a note in the last Number (cf. Fritsch, '02).

[2] Not infrequently this tip is dilated into a slight knob towards its apex.

[3] Cf. Fritsch, '02, p. 414 and Fig. 23 *e*.

within the mother-cell (Fig. 27, *c*). A branched, root-like organ had been formed at the one end, but the reverse end did not bear a tip as in the normal condition. It is worthy of note that the polarity of the inner individual is just diametrically opposed to that of the mother-cell (cf. Poulsen, '79, p. 2). Usually, however, if unable to escape, the contents of these young plants die off.

The cells of the young plant have the chlorophyll arranged in longitudinal bands in the manner characteristic of the adult cells of *Oedogonium*. Several large pyrenoids (*p* in Fig. 26, *a* and *b*) are present in each cell, being closely surrounded by numerous starch-grains. The nucleus—a large rounded body, about twice the size of a pyrenoid, and generally parietal in position—often shows up well without staining (cf. Fritsch, 1902, Fig. 23, *f*), especially in plants which have been kept indoors for a few days. With Chlor-zinc-iodide the walls of the cells and the tip, which in the fully developed young plant appears quite solid, stain blue; the same colour is taken on by the basal disc. In all the species of *Oedogonium* examined, I found the cellular structure of the young plants to conform to the above description, except that in some of the smaller species (e.g. *Oed. calcareum*) the cells have only one pyrenoid apiece. The arrangement of the chlorophyll also varies slightly—apparently only irregularly though, and according to external conditions.

The young plants in *Oed. capillare* were found to possess two chief types of root-ends: the first strongly branched and expanded chiefly transversely to the long axis, the second slightly or not at all branched, and greatly elongated in a longitudinal direction. The first type—the attaching-disc (Fig. 25, *n*)[1]—was mostly to be found in the young plants, which were attached to a firm substratum (such as the sides of the vessel); the second type, on the contrary, occurred invariably in the young plants floating on the surface of the water or in such as were not attached to any definite object (Figs. 25, *a* and 26, *a*). It is a fact that Wille ('87, p. 456)

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[1] Cf. also Fritsch, '02, Fig. 23*f*.

has already noticed that only those plants which have a firm substratum, and therefore a branched basal disc, continue to grow and divide; whereas those of the second type almost invariably form zoospores before undergoing even a single division. Wille (p. 456) pointed out that this is doubtless of

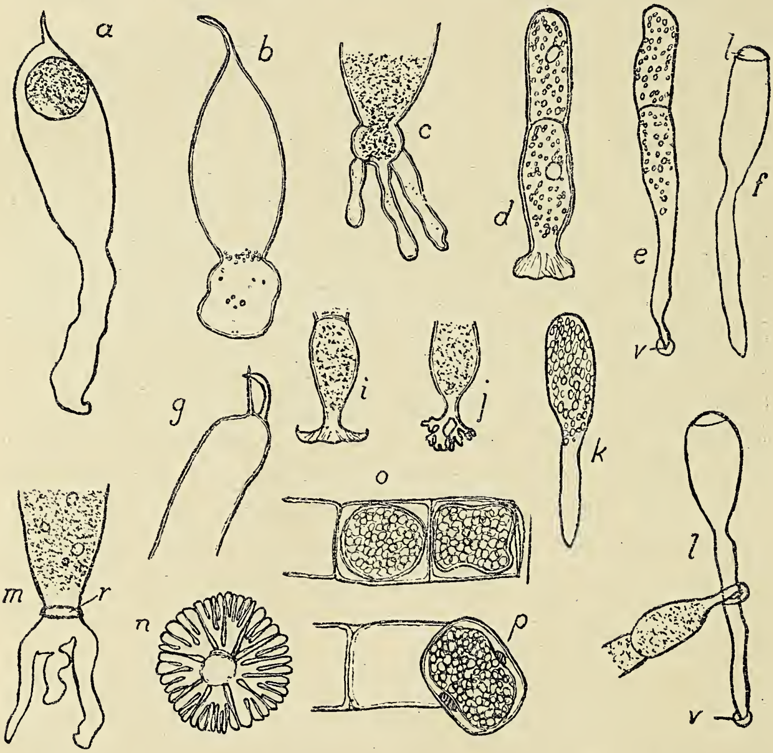

FIG. 25. *a*, *b*, *c*, *g*, and *n*, *Oedogonium capillare*, Kütz. *a*. Young floating plant with rhizoid; the contents have rounded themselves off. *b*. Young unicellular plant with a sack-shaped root-end. *c*. The sack-shaped root-end has grown out to form three long rhizoids. *g*. Apex of young plant, showing two tips. *n*. Attaching-disc seen from below. *d*, *e*, *f*, *i*, *j*, *k* and *l*, *Oedogonium spec.* from River Severn. *d*. Two-celled plant with basal disc. *e*. Two-celled plant with normal type of root-end; *v* = mass for attaching plant to substratum. *f*. Empty unicellular plant with lid, which has returned to the position it had before liberation of the contents of the cell. *i*. Basal disc with upturned ends. *j*. Branched root-end. *k*. Unicellular plant with rhizoid; not yet fully-developed. *l*. Young plant, whose rhizoid has firmly curled itself round another empty individual; *v* = same as above. *m*. *Oedogonium cardiacum*, Wittr., usual type of root-end in floating plants; *r* = ring of brown matter. *o*, *p*, *Oedogonium Vaucherii*, Braun. *o*. Abnormal zoospore formation. *p*. Liberation of abnormal zoospores. (×415.)

great value for the maintenance of the species, since only individuals which are able to attain a definite footing are capable of further development. However, this is not invariably the case, for sometimes I met with short floating filaments of from 5–10 cells, which had only a long rhizoid-like process basally (see Fig. 26, *a*, in which the lower part of a 6-celled individual is figured), and later on I even found filaments of considerable length with such a basal termination. In *Oed. stagnale* and *calcareum* this difference between the root-ends of floating and attached individuals is also observed. At the end of the long root-processes (rhizoids) I frequently found a small, round, hyaline mass, which, according to Wille ('87, p. 458) and Pringsheim ('58, p. 55), consists of a substance for attaching the plant to the substratum (*v* in Fig. 25, *e* and *l*).

In an as yet undetermined species of *Oedogonium*[1] I found the formation of a long rhizoid basally to be the rule, even in the plants attached to a firm base (see Fig. 25, *e*, *f*, and *l*). An attaching-disc, found so frequently in *Oed. capillare*, was comparatively rare here (Fig. 25, *d* and *i*). These young plants also behaved differently to those of the last-named species in that many, although attached, had emptied their contents as zoospores (Fig. 25, *f* and *l*); the larger number, however, had already formed 2–3 celled individuals (Fig. 25, *e*). The young plants of this and the other species examined do not possess the tip which is so characteristic for those of *Oed. capillare*[2], their apex being perfectly smooth and rounded.

The lid in the species from the river Severn and in *Oed. stagnale* is not always so readily discerned as in *Oed. capillare*. The emerging zoospore seems[3] to have pushed it on one side, whilst it still remained attached to the adjacent part of the

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[1] Growing in a glass-vessel in the Herbaceous Department, which contained a water-moss from the river Severn.

[2] Tips occur at the apex of the filaments in a number of species of *Oedogonium* (cf. Figs. in Wolle, '87, cited in foot-note 2 on p. 467); other species (*concatenatum*, var. *setigerum*, *Huntii*, *ciliatum*) have the apex of the filaments thinning down into a hair (cf. also Chodat, '02, p. 48).

[3] I did not observe the emission of the zoospores in this species.

wall at one point, as in the last-named species. But after the complete emergence of the zoospore it evidently sprang back into its original position (Fig. 25, *f* and *l*), and it requires careful observation of the empty mother-cell to make out the line along which the wall gave way for the emission of the contents. In other cases, however, the lid, just as in *Oed. capillare*, was cast off as a whole.

I found considerable variation in the form of the root-ends in *Oed. capillare.* The normal type of attaching-disc (Haftscheibe) is figured in Fig. 25, *n*; it is no easy matter to reproduce its delicate divisions in a drawing. A sack-shaped basal end (as in Fig. 25, *b*) was not at all rarely observed; it was found in individuals lying freely in the water (cf. next paragraph) and under rather abnormal conditions, large numbers of bacteria having formed in the cultures. Not infrequently I found this sack-shaped root-end growing out into three or more rhizoids (Fig. 25, *c*), which, as it were, were searching for a substratum. Probably this is always the result of further development of the type of base shown in Fig. 25, *b*, unless the cell dies off soon (as in the case figured) or empties its contents as a zoospore.

Such a sack-shaped basal termination, which not infrequently is almost spherical, occurs as a rule and under normal conditions in *Oed. cardiacum*[1] (Fig. 26, *c*). This species forms an attaching-disc very like that of *Oed. capillare* (cf. Fig. 27, *a*), provided the zoospore attains a definite substratum before coming to rest. Otherwise the sack-shaped root-end is formed, never an elongated rhizoid as in the species discussed above. These basal portions are generally only slightly dilated, and in nearly every case grow out into a number of rhizoids, which can extend for a considerable distance and are not rarely successful in reaching a definite footing (Figs. 25, *m* and 27, *h*); in such plants with well-developed rhizoids, the original almost-spherical shape of the basal end is often hard to recognize[2].

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[1] Growing on leaves of *Vallisneria spiralis* in the chief tank of the water-lily house.

[2] In a few cases a transverse wall was observed cutting off this basal part as a special root-cell from the part above.

There is only a slight constriction at the point at which the colourless root-end goes over into the chlorophyll-containing part of the plant ; at this point, coinciding almost with the former position of the cilia, I very frequently saw a ring of brown matter extending right round the cell (*r* in Fig. 25, *m*).

I found considerable numbers of young plants of *Oed. cardiacum* with this type of base floating on the surface of the water, and most of them exhibited a striking peculiarity. I found that each of these was in intimate connexion with an air-bubble of variable size. The connexion was not alone a mere cohesion, but a closer examination showed that the otherwise spherical air-bubble was drawn out to a distinct point of attachment, coinciding usually with the ring of brown matter, mentioned above (cf. Fig. 27, *h* ; *a* is the bubble). It would thus appear as though there were some connexion between the presence of the air-bubble and this brown matter, for the two nearly always occurred side by side. The curious shape of the bubble suggests its having been formed on the plant itself, which was by this agency enabled to float to the surface of the water[1]. All my attempts to elucidate this point have as yet proved unsuccessful, as the bubbles break up soon after the plant is removed from its floating position. The substance forming the brown ring is undoubtedly ferric oxide or some ferric salt. The same is very commonly found forming a coating on the basal disc of this and other species of *Oedogonium*. It is often present in considerable quantity at places where young plants of this genus are attached to other filamentous Algae. If treated with a solution of potassium ferrocyanide, to which a trace of hydrochloric acid has been added, this brown substance is dissolved, and in its place a precipitate of Prussian blue is formed (cf. Zimmermann, '92, p. 66).

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[1] Cf. also Chodat, '02, p. 92 : 'C'est ainsi qu'on rencontre très communément les Ulothriciacées, les Palmellacées, les Confervacées, les Oedogoniées et les Conjugées constituant des écheveaux denses de filaments suspendus . . . par les bulles d'oxygène qu'ils exhalent au soleil. . . .'

In the other species examined the above-described feature was not observed, although the floating individuals are frequently found aggregated in large numbers (being then often almost radially arranged) round a single large air-bubble, which, however, exhibits a perfectly circular outline. The floating plants form a bacteria-like scum on the surface of the water, and large numbers may be obtained by dipping the tip of the finger into the water and conveying a drop on to a slide.

It is unnecessary to mention all the variations in the types of basal-end observed in *Oed. capillare*; this species seemed the most variable of all in this respect. The simple rhizoid not infrequently divides irregularly after some time, thus giving rise to a structure like that figured by Poulsen ('79, Tab. 1, Figs. 2, 3, 4, and 6); also Cohn ('54, Tab. 20). I occasionally saw the rhizoid of a young plant, which had attached itself to another (empty) one, divide up into a number of small processes, each of which twined itself round the substratum; somewhat similar cases were also found in the species from the river Severn (Fig. 25, *l*). Apically the filaments of *Oed. capillare* sometimes terminated in a swollen cell (Fig. 26, *b*), the cell below then bearing a large number of caps, thus indicating that the terminal cell had not divided since its first formation. In a few cases two tips were present (Fig. 25, *g*).

The undetermined species from the river Severn also showed a certain amount of variation in the structure of its root-end. The attaching-disc, when found here, is frequently slightly turned upwards round the edge (Fig. 25, *i*). Delicately branched roots are not uncommon (Fig. 25, *j*), and form an intermediate step between the basal-disc and the unbranched rhizoid.

In order to complete my description of the root-ends of *Oedogonium* I must make mention of the hemispherical basal cells, whose curious mode of development has been recently worked out by Lemmermann ('98, p. 504) and Schefferle (1901). Hirn (1900, p. 15) has shown that they occur in a large number of species of *Oedogonium*[1]. Hence it is surprising that I have not come across this type in the course of my investigations; possibly, however, it only develops under certain external conditions.

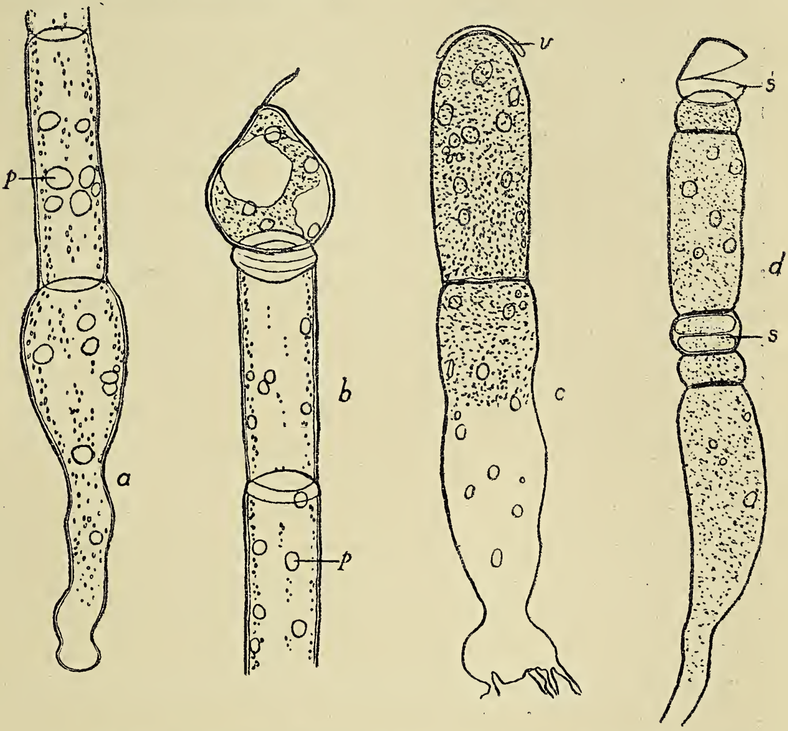

FIG. 26. *a, b, Oedogonium capillare*, Kütz. *a*. Base of a six-celled filament, showing rhizoid; the green matter extends down a considerable distance into it. *b*. Filament of young plant with swollen apical cell, active cap-formation going on in the cell below. *c. Oedogonium cardiacum*, Wittr., two-celled plant; the first cap has been thrown off and lies loosely at the apex. *d. Oedogonium stagnale*, Kütz, young two-celled plant, which is already forming spermatozoids. (× 375.)

Lemmermann ('98, p. 502) mentions the occurrence of chlorophyll in the hemispherical basal cells of *Oed. africanum*, Lagerh., and *spirogranulatum*, Schmidle. I have not infrequently observed small amounts of chlorophyll in the

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[1] Such young plants differ from all I have described above in that the attaching portion consists of an entire cell and not of only the lowermost modified portion of a cell.

root-ends of the species investigated, and the protoplasm extends down into them, often even into their finest branches. Sir W. Thiselton-Dyer was kind enough to let me inspect some drawings he had made about thirty years back of young plants of an *Oedogonium*, collected in Ireland ; they exhibited attaching-discs and more or less elongated and slightly branched rhizoids, and the protoplasm extended in a radiating manner into all the branches of the former.

I append a brief discussion of the literature and figures published on the structure of the young plants in *Oedogonium* : Léon de Clerc ('17, p. 462) speaks of a collar (' collet ') at the point of constriction (Fig. 2′, *e*) without saying exactly what it consists of. He figures young plants with rhizoids very like those of *Oed. cardiacum*, and possibly his ' collet ' is the brown ring. He further figures 1–3 celled plants, which are attached to a filament and show but little indication of a basal disc (Figs. 2 and 2′). Figs. 5′ and 5″ show developing plants of *Oed. Boscii*, including apparently some abnormal forms (cf. below).

Kützing ('43, Tab. 10[1], Figs. 4–10) figures young plants of *Oed. vesicatum* attached to a water-plant. These merely terminate in a point of attachment, but it seems probable to me that there was a small basal disc present, which was overlooked.

Thuret ('50, pp. 226 and 227, Pl. 19, Figs. 8 and 9) briefly mentions the germination of the zoospores and figures a number of young plants, all of which have divided root-ends (crampons radiciformes) ; Fig. 9 shows two empty unicellular plants with lids.

Cohn ('54, Tab. 20) figures the liberation and the development of the zoospores in *Oed. capillare* (Fig. 16). All the young plants have more or less branched rhizoids ; no attaching-disc is shown.

Pringsheim ('54, p. 70, foot-note) describes the development of the root in a young plant in the following words : ' Die Zoosporen der Oedogonien sind nicht nur nicht nackt, sondern

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[1] Cf. my Fig. 25 *m* and 27 *h*.

besitzen wie alle Zoosporen sogar zwei Membranen. . . . Die innere Haut der Zoospore hat wachsend die äussere Haut der Zoospore schon vor ihrem Austritt aus der Vegetationszelle so durchbrochen, wie die Tochterzelle die Mutterzelle bei der Theilung durchbricht, dadurch entsteht die Öffnung der äusseren Haut; dieses Verhältniss ist an der keimenden Spore nachweisbar, wo jedesmal die Öffnung der äusseren Sporenhaut sichtbar wird, und zugleich auch die an ihr befestigten Cilien noch später wenigstens in Rudimenten gefunden werden können.' On Pl. IV, Figs. 26–31, he figures the development of the young plant, exhibiting this collar round the upper part of the root-end (cf. also Hartig, '55, p. 415). I have observed nothing of this nature in my cultures.

Wolle ('87) figures on Plate LXXIV, Figs. 12 and 13, one and eight-celled plants of *Oed. crispum*, var. *rostellatum*, both with an attaching-disc and a distinct tip. On Plate LXXXI, Figs. 4 and 5, a unicellular plant of *Oed. autumnale* with a long rhizoid and another with an attaching-disc is shown.

This is not intended to be by any means a comprehensive discussion of the literature involved. I have merely mentioned those observations which seemed to me of interest in connexion with the species discussed above.

2. THE FIRST CELL-DIVISION IN THE YOUNG PLANT.

I have already discussed (cf. Fritsch, 1902) the first cell-division in connexion with Poulsen's[1] observation that the first cap of the young plant is cast off. At the time I had not yet observed this phenomenon, although I had carefully investigated this point in three species[2]. Since then I have seen the casting-off of the first cap in a number of species, and have found that, although fairly constant for some, in others the cap is just as often retained. Thus in *Oed. cardiacum* the casting-off of the first cap is the rule (*v* in fig. 26, *c* and 27, *a*), nearly all the two-celled plants showing the cap still in

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[1] Poulsen, '79, p. 1, &c.; cf. also Hartig, '55, p. 417; Tab. IV, Figs. 12, 13 and 14.

[2] Namely, *Oed. capillare*, the species from the river Severn, and another undetermined species.

position, though evidently no longer in organic contact with the rest of the cell-wall. It is frequently so closely applied to the top cell, however, that it could be easily overlooked. In other cases it is cast right off and is found lying loose in the water. I observed the structure of the first ring in this species; it agreed with the description given by Poulsen (loc. cit.), going over into the inner layer of the wall above with a gradual curve. I also followed its division into two layers and the casting-off of the outer one as a cap. In *Oed. stagnale* as a rule no cap is cast off, as is sometimes also the case in the first-discussed species. In *Oed. calcareum* I was not successful in finding a cap at the apex of the two-celled plants, although one is frequently found covering the top cell of four or five-celled individuals. It would seem as though this casting-off of the first cap depended to some extent on the shape of the apical cell; when this is acutely rounded the cap is often cast off (cf. however Poulsen, '79, p. 5).

3. ABNORMAL DEVELOPMENT OF THE YOUNG PLANT.

In the course of my investigations on the young plants of *Oedogonium* I came across a number of interesting abnormalities, which I will now briefly discuss. Fig. 26, *d* shows a young plant of *Oed. stagnale*, which, although consisting of only two vegetative cells, has already commenced to form spermatozoids (*s*). I found this individual amongst other normal ones of the same species, scattered in between the adult filaments, from which the zoospores for their formation had been derived. These adult filaments were engaged in very active spermatozoid formation, there being five or six antheridia between almost each of the vegetative cells. In this point the young plant differed from the adult, for there were only two antheridia present in each group. The conditions were evidently very suitable for spermatozoid-formation, and hence probably the precocity of the individual figured. The lower group of antheridia are still developing, in the upper group one has already liberated its contents. Such an abnormality may show how the dwarf-males originated, for the smaller androspores on germinating would naturally have a still more reduced vegetative portion. In fact, if we suppose the individual shown in Fig. 26 *d* to have been situated on an

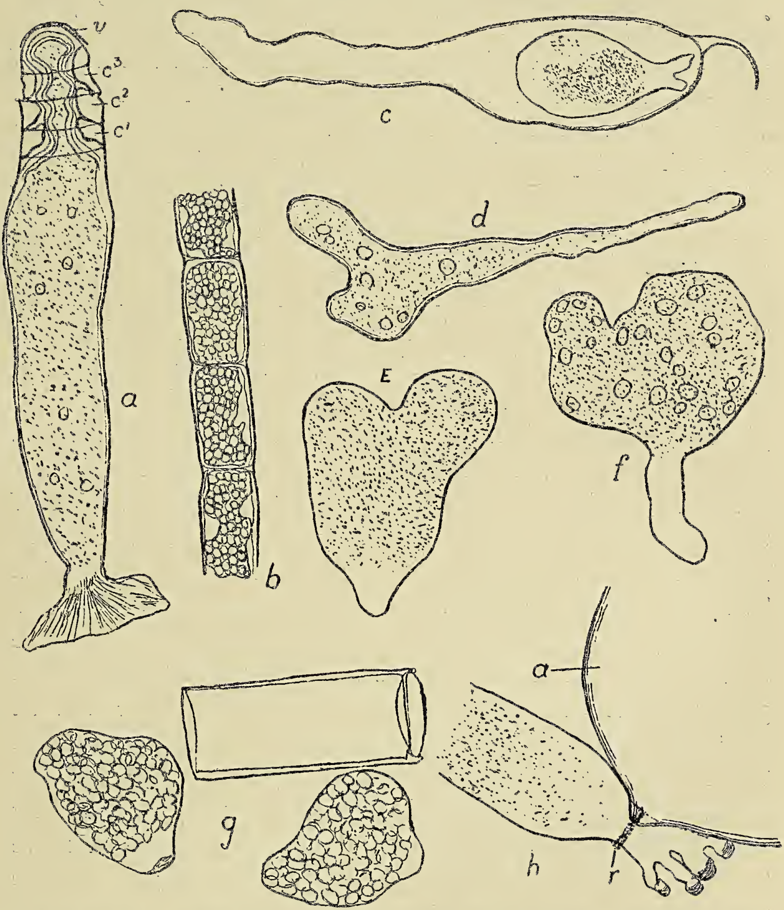

FIG. 27. *a*, *e*, *f*, and *h*, *Oedogonium cardiacum*, Wittr. *a*. Young plant with basal disc, which has formed successive rings, c_1, c_2, and c_3 without corresponding formation of transverse walls; v = first cap, which has been cast off. *e*, *f*. Abnormal germination of zoospores. *h*. Floating plant, in intimate connexion with an air-bubble *a*, which is joined to the plant at the point where a ring of brown matter, *r*, surrounds the cell. *b*. *Oedogonium Vaucherii*, Braun, irregular thickenings in cells of filaments, cultivated in a 2% solution of cane-sugar. *c*, *g*, *Oedogonium capillare*, Kütz. *c*. Germination of a zoospore within a young unicellular plant. *g*. Abnormal germination of zoospores. *d*. *Oedogonium stagnale*, Kütz, abnormal germination under almost normal conditions. (× 420.)

oogonium, it would differ from a dwarf-male only in size and development of the vegetative structure, due to its origin from a normal, chlorophyll-bearing zoospore.

Another interesting abnormality is shown in Fig. 27, *a*. This young plant was derived from a zoospore of *Oed. cardiacum*, which was being grown in a 2 per cent. solution of cane-sugar, in order to further the formation of oogonia[1]. Although the conditions were unfavourable to the formation of much protoplasm and consequently to the growth and division of the plant, it was able to form large amounts of cellulose, which resulted in the formation of successive rings (c^1, c^2, c^3). The first ring had been of the kind mentioned above and after its formation the plant must have stretched itself, for there is the usual cap (*v*) loosely covering the apex of the cell. The following rings (c^3, c^2, c^1) were then successively formed without any further stretching of the cell taking place. Several such cases were observed in the sugar solution, the upper part of the cell presenting a truly elegant design.

Finally, I wish to make mention of a curious condition of the young plants, observed chiefly in *Oed. calcareum* and *capillare*, but also to a less extent in one or two other species. The former species had been kept in a glass vessel in the laboratory a month or so, and numerous zoospores had come to rest and germinated on the sides of the vessel. In the young plants thus formed only the basal cells contained chlorophyll, those higher up being filled with starch grains. The cells of these plants were considerably elongated, narrowing down more and more the further they were situated away from the base, the cells at the apex being often not more than a quarter of the diameter of the basal cell ; so that the plants looked as though they narrowed down into a hair apically, especially as the uppermost cells had generally almost lost their contents. Such a condition of *Oedogonium* has been recently described in America (Keller, 1901), and interpreted as a kind of resting-stage. I do not think this very probable, and rather look upon it as a gradual dying-off of

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[1] Cf. Klebs, '96, pp. 279, 280.

the plant. *Oedogonium* is one of the hardiest genera of freshwater Algae, and it is likely that unsuitable conditions would take a long time to put an end to its vital activity, unless they were extremely fatal in their action. As a matter of fact, if cultivated in very strong solutions of cane-sugar the above-described appearance can be called forth in a few days, and, although then returned to fresh water, not a single filament becomes green and active again.

A glass vessel in the Herbaceous Department contains a mass of *Oed. capillare*, which has been in this condition for some months, and I do not think is likely to recover. I first noticed a change in the filaments in March of this year. I then found that the (still green) contents of the cells were aggregated chiefly about the transverse walls, and sometimes so closely that these could only be recognized on a close perusal. The side-walls also were lined by a thin layer, but the whole interior of the cells was either quite empty or only contained a few strands of protoplasm. At the time of writing all the cells are absolutely colourless and many are crowded with starch-grains ; the arrangement of the protoplasm, however, indicates that most are still living. As to the external conditions, which cause this change, I can say nothing ; *Nitella syncarpa* growing in the same water is perfectly healthy, but some *Closteria* present are in a similar state of degeneration.

4. Abnormal Formation of Zoospores and their Development.

The adult filaments of *Oedogonium* almost invariably form zoospores after being kept in a slow stream of water (Zimmermann, '92, p. 3) for some time[1]. The emission of the zoospores takes place very abundantly for some days, but then as bacteria gradually collect in the cultures and the filaments of the *Oedogonium* itself become exhausted, the process slackens down again[2]. Under these final (abnormal) conditions the zoospores formed often present curious characters (Fig. 27, *e, f, g*).

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[1] These experiments were carried on during the months January to June, 1902.

[2] Fritsch, '02, p. 415.

They assume a very irregular shape on coming to rest and only move a very little distance away from the mother-cell, and some are apparently even whilst still moving surrounded by a definite membrane. As far as I could make out, germination of these abnormal zoospores does not usually take place[1].

Somewhat similar phenomena were seen in a species of *Oedogonium*[2] (*Oed. Vaucherii*, Braun), which was cultivated in a 2 per cent. solution of cane-sugar, placed in direct sunlight as much as possible. The contents of the cells had rounded themselves off more or less after some days (Fig. 25, *o*), frequently taking on exactly the shape of a zoöspore in course of development (see Fig. 25, *o* ; the cell on the right). However, the conditions in the sugar solution must be unfavourable to the liberation of zoospores, for in most cases the contents remained within the mother-cell, surrounding themselves with a thick membrane (of two or three layers). Only in one or two cases was the liberation of the zoospore observed (Fig. 25, *p*), which then took place quite abnormally. It was already at that time surrounded by a thick membrane and came to rest immediately outside the sporangium. The latter dehisced in the ordinary manner, but the zoospore showed no vibrating cilia, nor was naturally the formation of the thin membrane, usually connected with the liberation of zoospores in *Oedogonium*, observed. If the cells are treated with a watery solution of Iodine when in this condition, neither the external wall of the cell nor the thick membrane of the zoospore is perceptibly coloured ; whereas in the cavity of the cell between these there lies a substance, which is stained a deep violet and which is undoubtedly a kind of mucilage[3]. This pheno-

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[1] Fig. 27 *d* shows a zoospore of *Oed. stagnale*, which germinated under relatively normal conditions, and which has formed a well-developed rhizoid. The irregularity at the apex amounts almost to branching.

[2] From the pools in the Temperate House. The same species later on produced oogonia and antheridia in the sugar solution (cf. Klebs, '96, pp. 279, 280).

[3] Klebs (loc. cit., p. 264) took the appearance of this mucilage as indicating the commencement of zoospore formation. He says: 'Die Hülle hat die Eigenschaft sich mit wässeriger Iodlösung violett zu färben, . . . infolgedessen erkennt man die Bildung der Zoospore auch dann, wenn diese nicht austritt . . . Gewöhnlich verfuhr ich dabei in der Weise, dass ich die Fäden kurz in konzentrierte Salpeterlösung

menon has been observed and described by Hirn (1900, p. 14), although he experimented with a 12 per cent. solution of cane-sugar in order to plasmolyse cells suddenly, in which zoospore formation was already going on. He considers this mucilage to be homologous with the membrane, which normally surrounds the zoospore during its liberation, but it seems to me probable that this membrane is entirely suppressed here, and that mucilage is always (even normally) present between the zoospore and the wall of the mother-cell, though probably not in such quantities as in this case. Sporangia of *Oed. capillare* with the zoospores half out were stained with Chlor-zinc-iodide, and it was found that the empty half of the cell became stained with a deep violet colour (much darker than that due to the cellulose-walls), which is undoubtedly caused by an aggregation of mucilage behind the zoospore. The latter was surrounded by the typical thin membrane. Most probably this mucilage is of use in effecting the liberation of the zoospores; at all events I do not think that it has anything to do with the membrane of the emerging zoospores.

Not all the cells of *Oed. Vaucherii* formed abnormal zoospores in this manner when cultivated in a 2 per cent. solution of cane-sugar; in some filaments the cell-contents merely contracted irregularly, whilst the walls presented curious and irregular thickenings (Fig. 27, *b*). With Iodine or Chlor-zinc-iodide these thickenings stain a deep reddish-brown, whereby they are clearly differentiated from the original cell-wall. I also observed such thickenings in *Oed. capillare*, where, however, they took on no colour with the above-mentioned reagents. These masses seem to consist of different kinds of mucilage, which is formed under abnormal conditions[1] and differs from the mucilage above described as existing between the mother-cell and the zoospore. In *Oed. Vaucherii* the

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legte und dann mit Iod tötete. Dann traten an den plasmolysierten Zellen, soweit sie in Zoosporen umgewandelt waren, die violetten Hüllen deütlich hervor.' The 'violette Hülle' is in my opinion not the same as the 'Hüllblase' of the zoospore.

[1] These thickenings also appeared in old cultures of *Oed. capillare*, in which, however, common tap-water had been employed.

membrane of the zoospore itself sometimes presented such thickenings (Fig. 25, *p*), and the difference in colour between the two kinds of mucilage on the addition of Iodine is then readily perceived.

5. SUMMARY.

The more important results obtained in the present paper may be briefly summarized as follows:—

1. Certain types of root-ends are characteristic for certain species of *Oedogonium*; thus the attaching-disc and rhizoid for *Oed. calcareum*, *capillare*, and *stagnale*, the rhizoid alone for the species from the river Severn, and the attaching-disc and sack-shaped basal end for *Oed. cardiacum*.

2. The brown substance, which is so frequently found in connexion with the young plants of *Oedogonium*, consists of ferric oxide or of some salt thereof.

3. The casting-off of the first cap is by no means the rule in this genus, although occurring fairly constantly in some species (e.g. *Oed. cardiacum*).

4. The colourless state, into which the filaments of this Alga sometimes pass over, is probably a gradual dying-off of the plant.

It remains for me to express my sincere thanks to my friend, Mr. L. A. Boodle, F.L.S., for several valuable suggestions made in the course of this work.

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Experiments on the Brown Rust of Bromes (Puccinia dispersa).

BY

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THE experiments from which the following results have been obtained were carried on in the botanical laboratory of Cambridge University, and I take pleasure in the acknowledgement of my indebtedness to Professor Marshall Ward for his many valuable suggestions and helpful direction, as well as for the excellent laboratory facilities afforded me. The experiments were undertaken for the purpose of obtaining, if possible, evidence on the brown rust of Bromes correlative to the recent work of Professor Ward[1], viz. to test the infection capabilities of numerous species, among which were several whose systematic position in the genus has been somewhat doubtful, with spores from *Bromus sterilis* and *B. mollis*, using the reaction of plant and Fungus as an indication of the systematic affinities. The work was begun March 19 and closed June 18. The method of procedure was in general that used by Marshall Ward. Upon the first foliage leaf of seedlings of Brome plants, usually less than two inches high, were rubbed spores of the Uredo of *B. sterilis* and *B. mollis* respectively, a short distance from the apex of the leaf, or the spores were placed in the water-drop exuding from the water-stomata at the tip. The plants were then placed under moist bell-jars or beakers and kept in the laboratory for about twenty-four hours; they were then placed out

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[1] Proc. Camb. Phil. Soc., vol. xi, pt. v; Proc. Roy. Soc.; Annals of Botany, xv, No. lix, 1901.

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of doors, where the bell-jars were removed gradually to harden the plants to change of conditions. The spores used for infection were obtained from plants (both wild and cultivated) of *B. sterilis* and *B. mollis* from the University Botanical Gardens at Cambridge. Care was taken to prevent the admixture of leaves of other species. The cut-off leaves were placed in closed glass chambers for twelve to thirty-six hours before the spores were used. The determining condition of germination of the spores in distilled water are still enigmatical and have evidently narrow limits. Spores from the material used for each separate infection were tested in distilled water twenty-four to forty-eight hours. In most cases germination is abundant. Occasionally, however, apparently excellent spores may, under seemingly favourable conditions, almost utterly fail to germinate in distilled water, while spores from the same or neighbouring sori of the same leaf may successfully infect a Brome plant. Experiment 77 q''' is a very good example in point[1], where no spores germinated in distilled water, while the infection of *B. mollis* with the same material was in each case (i. e. four out of four) successful. For this reason the negative results in the distilled water tests are not always an indication that the spores were incapable of germination. Dry spores were used in most cases, and in rubbing them on to the leaves of the host there arises the danger of dropping or shooting spores on to other parts of the plant or upon the control plants. Such may explain the infections of control plants in Experiments 94–96, in which cases an abundance of spores was used. Such infection may also be caused by the rubbing together of two leaves upon one of which spores have been placed (Marshall Ward, l. c.). The plants after infection were examined at intervals of several days from about the eighth to twelfth day onward.

The weather throughout almost all of these experiments was colder than normal, and the long incubation period of most infections as compared with those noted by Marshall

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[1] These numbers refer to the tables of details of the experiments not published here in full.

Ward is undoubtedly due to this cause. The rainfall though not excessive was evenly distributed, and sunshine less than normal throughout. The drying up of the infected leaves, though, in all probability, usually accelerated by the action of the Fungus, was in many cases due largely to severe weather conditions.

The results confirm in general those obtained by Marshall Ward, but under different seasonal conditions. The success of the infections under the unfavourable conditions encountered adds interest to the result, since it accentuates the possibility of natural field infections throughout the winter season. The following is merely an account of the experiments; the bearing of the results will, it is hoped, be more fully discussed in a future paper by Professor Marshall Ward.

The following tables sum up the results obtained during the progress of the experiments. The column 'host' includes the species upon which infections were made; then follow the species from which the brown rust spores were taken, viz. *B. mollis* and *B. sterilis.* About one half of the plants in each pot were infected and their position marked, so that the control and host plants could later be distinguished. This is of some importance, as in Experiment 94 *q*[1], although five of ten plants were infected and five plants subsequently bore pustules, two of the pustules were on control plants and not due to the artificial infection unless accidental as indicated above. The germination of the spores in distilled water after twenty-four to forty-eight hours was classified as 'very poor' when only a few tubes can be found in the watch-glass; as 'excellent' when there are only a few spores which do not germinate. The intermediate conditions are self-explanatory. Records were kept of experiments in which all of the spore material was taken from the same leaf; and the numbers in the columns under the various dates indicate the number of plants whose infected leaves produced one or more pustules of brown rust.

The formation of yellow flecks in the leaves, which often

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[1] See footnote, p. 488.

precede the sorus formation, is not always noted ; they may in some cases be due to other causes than the infecting Fungus. It happens very frequently that the tip of an infected leaf dries up. When this extends to or past the point of infection it is noted as 'tip-dried.' It is not a matter possible of exact determination how far the success of the infection is impaired in such cases. In many, pustules arise in the dried portions and in others below the point of infection. Those cases only are noted where it seems possible that the drying may have interfered with the growth of the Fungus. 'Leaf dried' denotes that the whole leaf has dried up. The unusually large number of dried leaves in Experiment 84 and 85 was due to very low temperature and a too sudden exposure of the plants to external conditions after infection.

When more than one leaf on a single plant shows pustules, it is in almost every case, without a doubt, due to a falling of spores from the infected leaf on to the leaf below; such are not included in the totals. Occasionally, pustules are reported and subsequently lost; this may be due to one of two reasons. First, the infection material may, when in bulk, simulate a sorus, even under a lens, and the error may not be detected until a later examination ; and second, the leaf may become dried, and if the pustule is small the latter may disappear.

Leaves 'missing' have been cut off by slugs or accidentally torn off in handling.

Each experiment was continued about three weeks; the incubation period of about twelve days prevents a second infection from the earliest pustules.

The following tables summarize the results. They include those plants with 'dried tips,' &c., which were possibly incapable of forming pustules so that general averages only must be reckoned.

Series A gives twenty-two species. In 11, 12, and 19, and also in 15 and 16, the number of plants worked with is too small for generalization. The same applies to several species included in the following series. In *B. pitensis* and *B. unioloides* large yellowish flecks were very easily produced but

SERIES A. Unsuccessful with spores from both *B. sterilis* and *B. mollis.*

Host.	*Spores from B. sterilis.*			*Spores from B. mollis.*		
	Total No. of Plants.	*No. infected.*	*No. successfully infected.*	*Total No. of plants.*	*No. infected.*	*No. successfully infected.*
1. *angustifolius*	6	5	0	5	4	0
2. *arvensis*	29	15	0	29	15	0
3. *asper*	65	33	0	69	35	0
4. *Biebersteinii*	20	11	0	23	12	0
5. *breviaristatus*	28	14	0	40	20	0
6. *carinatus*	54	27	0	58	29	0
7. *ciliatus*	16	9	0	12	8	0
8. *condensatus*	14	8	0	8	4	0
9. *erectus*	56	30	0	71	37	0
10. *Hookerianus*	10	5	0	15	8	0
11. *inermis*	3	3	0	2	2	0
12. *Kalmii*	1	1	0	7	4	0
13. *laxus*	29	17	0	35	18	0
14. *parviflorus*	10	5	0	20	10	0
15. *fibrosus*	8	4	0	6	4	0
16. *pitensis*	9	6	0	14	8	0
17. *pungens*	23	13	0	29	16	0
18. *pumpellianus*	51	26	0	59	30	0
19. *segetum*	2	1	0	6	3	0
20. *unioloides*	26	14	0	35	19	0
21. *valdivianus*	29	17	0	24	13	0
22. *virens*	70	35	0	70	35	0

SERIES B. Successfully infected with spores from *B. mollis*, but not with *B. sterilis* spores.

23. *adoensis*	24	14	0	17	10	9
24. *arduennensis*	6	4	0	10	6	6
25. *commutatus*	24	13	0	28	14	3
26. *grossus*	58	30	0	60	30	15
[1] 27. *inermis* (*arvensis*)	36	19	0	36	19	3
28. *macrostachys*	14	7	0	14	7	1
29. *mollis*	106	53	1 ?	127	62	53
30. *multiflorus*	5	3	0	11	6	3
31. *patulus*	27	14	0	16	8	4
32. *squarrosus*	19	11	0	25	13	11
33. *squarrosus*, var. *villosus*	25	14	0	23	12	9
34. *arvensis* (*inermis*)	33	17	0	20	10	1

SERIES C. Successfully infected with spores from *B. sterilis*, unsuccessfully with *B. mollis* spores.

35. *sterilis*	94	48	44	115	58	0

SERIES D. Successfully infected with spores from both *B. sterilis* and *B. mollis.*

36. *Gussoni*	118	60	37	102	53	6
37. *Krausei*	51	29	14	53	27	27
38. *molliformis*	48	25	1	50	26	2
39. *pendulinus*	101	53	12	98	50	30
40. *vestitus*	7	4	1	6	4	3

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[1] Is probably same as 34 and both are probably incorrectly named (see next page).

it is very doubtful if these were due to the infecting Fungus; no pustules were produced. The results with *B. arvensis* are at variance with those of Marshall Ward, who has found a successful infection of about 37 per cent. It is possible that at least some of the negative results of series A are due to weather conditions.

Series B contains about eleven species. In *B. adoensis*, *B. arduennensis*, *B. mollis*, *B. squarrosus*, and *B. squarrosus* var. *villosus*, the percentage of successful infections is notably high. *B. arduennensis*, although the number of plants used is small, seems to be decisive in its results. *B. grossus*, *B. multiflorus* and *B. patulus* are also decisive but show more resistance to *B. mollis* spores, about 50 per cent. being successful. *B. commutatus* and '*B. inermis* (*arvensis*),' which latter is probably identical with No. 34, shows still less liability to infection. *B. macrostachys* requires more study, the single successful infection being insufficient for generalization.

Number 27 (and 34?) are Canadian forms and are probably *B. arvensis*, which, although my experiments give negative results, are according to those of Marshall Ward occasionally infected with *B. mollis* spores. In series D, *B. Krausei*, *B. pendulinus* and possibly *B. vestitus*, are more susceptible to *mollis* infection than to *sterilis*.

Series C contains only *B. sterilis*. In the following series *B. Gussoni* has a much higher percentage of *sterilis* infections than of *mollis*.

Series D contains five species. *B. Gussoni* infects very readily (over 50 per cent.) with *sterilis* spores and over 10 per cent. with *mollis*. On the other hand, *B. vestitus* and *B. pendulinus* show greater susceptibility to *mollis* spore infection than to *sterilis*, but good percentages with both. In *B. molliformis* the percentages are too low and the differences insufficient for generalization, while *B. Krausei* infects with both species with remarkable ease. In the latter case infection with *mollis* spores is effected as easily if not more so than upon *mollis* itself, and the pustules are remarkable for size and vigour. With *sterilis* spores almost 50 per cent. were successfully infected.

It has been previously pointed out by Marshall Ward that the infection capacities of the brown rust spores are profoundly affected by conditions of formation and also by the host upon which they fall, and furthermore, that the optimum condition arises from infecting a species with spores formed on that species, which infection is least likely to succeed with spores of a species on those farthest removed in systematic position.

The results of series A are negative and valuable only in connexion with further work on these species. In series B one would expect to find species with at least not very remote relationships with *B. mollis*.

Such species as *B. commutatus*, *B. inermis* (*arvensis*?), and *macrostachys* may have closer affinities with one of the other groups of Brome species than with the *mollis* group, but no close affinities with the *B. sterilis*. It will be seen by an examination of the members of the series that the expectations as to systematic position are in general realized. That intermediate forms between *B. mollis* and *B. sterilis* exist is an inference which may perhaps be drawn from series D; i.e. at least *B. Gussoni*, *B. Krausei* and *B. pendulinus* are quite susceptible to infection with spores from both species. *B. Gussoni* leans notably toward the *sterilis* side, while *B. pendulinus* and perhaps *B. Krausei* and *B. vestitus* would seem to be nearer to *B. mollis*. *B. Krausei* is remarkable in the case of infection from both species, and there is probably some other factor to be considered besides the morphological and biological factors involved in the systematic position, because if *B. Krausei* is an intermediate form, one would not find such extraordinary susceptibility to either species as is actually shown to exist toward *mollis* spores. If this additional factor is not all-important, and there is no reason to believe such to be the case, one would seek in the *mollis* group for the closer affinities of *B. Krausei*.

The above results are all those of averages and there are several possible sources of error which must be borne in mind. The chief of these is to be found in the possibility of the admixture of stray spores from other species of *Bromus* than that experimented with; there is also the danger from foreign spores after the Brome seedlings expose their leaves to the air. Care in selection of spore material should reduce the former to a very small error. There is no control of the second condition, except in the selection of a place free from Bromes, if the plants are to be kept as nearly normal as possible, and this is essential. Since the pustules on an infected leaf in a great majority of cases arises in the immediate vicinity of the infection spot, there may be at least an indication when foreign contamination has taken place. Confusion is also possible with the uredos of other species of *Puccinia* growing on Bromes. Errors resulting in negative results, e. g. poor spore material or the presence of conditions which are unfavourable for germination and of which the limits and exact nature are as yet unknown, are less easy to detect, so that chief reliance is perhaps to be placed upon the positive results.

The 'Sadd' of the Upper Nile: its Botany compared with that of similar Obstructions in Bengal and American waters.

BY

C. W. HOPE.

INTRODUCTORY.

THE Cataracts on the Nile are well-known obstacles to navigation between its mouth and the Soudan, but they are beginning to yield to the attacks of modern engineers, who are throwing dams across the river, and providing side channels through which navigation will be carried on by means of locks. These cataracts are caused by barriers of granite rock which cross the bed of the river. But it is not so well known that an almost more serious obstruction to navigation is caused by the accumulation of a few species of plants floating in the Bahr-al-Jebel, or Mountain Nile, beginning about 435 miles south of Khartum, and extending thence southwards for about 250 miles; and that this accumulation also seriously reduces the flow of water northwards to the Lower Soudan and Egypt. The great Equatorial Lakes store the rainfall of vast catchment basins, and so regulate its off-flow northwards by means of the Mountain Nile; but this function is greatly neutralized by the vegetable accumulation which begins 715 miles northward, in a comparatively flat country, and which reduces the velocity of the current, and also causes the water of the river to spill right and left over the country and go to waste in shallow lakes and lagoons, where it is subject to evaporation to a serious extent.

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Previous to 1863 both the Bahr-al-Jebel, or Kir, and its eastern branch, the Bahr-al-Zaráf, had been navigable, but in March of that year the Nile, below their junction with the waters coming in from the west and northward—thence northwards called the White Nile, or Bahr-al-Abiad—was found to be blocked by 'an accumulation of vegetable flotsam, and it cost the crew of the Tinné Expedition two days' hard labour to take their vessel through a channel which had been partially cleared by their predecessors. The obstruction rapidly increased, and thirty vessels had to be employed for five weeks to open a permanent passage. Matters went from bad to worse, till, in 1874, Ismael Ayub Pasha cleared the main route by the White Nile and the Kir. But in 1878 the White Nile rose to an unusual height, and enormous quantities of vegetable debris were carried off by the current. A formation of bars (blocks) on an unprecedented scale was the result, and communication between the Upper and Lower Nile was not restored until 1880.' If the Kir and the White Nile, with their comparatively strong current, were thus obstructed, it was natural that the more sluggish Bahr-al-Ghazál should contain more extensive though less compact accumulations. 'In 1881 Gessi Pasha spent three and a half months on a part of the voyage westward usually performed in five hours, and lost half of his men by starvation. Between the mouths of the Kir and the Bahr-al-'Arab there were twenty distinct dams.'

The above information has been found in the 'Encyclopædia Britannica'; but—fully to realize what the Nile 'Sadd' is—it is necessary to read the Report by Sir William Garstin, K.C.M.G., as to Irrigation projects on the Upper Nile, &c., accompanying a despatch by Lord Cromer, His Majesty's Agent and Consul General at Cairo, which was published as a Blue Book in July, 1901. In Part II of his Report, 'Points for future Study,' we find a section 'The Sudd.' (The spelling of this word is various in these papers, and the pronunciation consequently uncertain; but it seems probable that 'Sudd' is a transliteration into English, and that the word ought to be pronounced like the first syllable of 'sudden,' and therefore, to all but Britons, 'Sadd' would be the better guide.) Sir William Garstin says that his Report is the result of his observations made during three consecutive years. In 1900 he had 'the advantage of studying the actual process of its formation on the spot,' as he was imprisoned for three days in the Gebel River, owing to the 'Sudd having burst in' (from the side lakes and lagoons) 'and blocked the channel downstream of the steamer.'

In 1890–91 a reconnaissance survey of the Bahr-al-Gebel (or Jebel) from Lake No southwards to Gondokoro was finished ; and a map to the scale of 1 inch to 10 kilometres is given with Sir William Garstin's report : it shows very clearly the features of the river's course ; the lakes and lagoons met with ; the positions of the 'Sadd' blocks then found, and the nature of the swamps, whether papyrus or grass. The last block met with, the nineteenth, was just above the 400 kilometres point from Lake No, near Ghaba Shambé, one of the Nile Posts of the Bahr-al-Ghazál Province. Papyrus swamps ceased at about 460 kilometres, and the plant does not seem to have been found south of about 520 kilometres.

'In the Bahr-al-Jebel,' says Sir William Garstin, 'the main factors of the "Sadd" are—the papyrus, and the "um-soof" (or omm-soof) reeds. These two, with the earth adhering to their roots, form the real obstacle. Many of the smaller swimming plants, such as the *Azolla*, the *Utricularia*, and *Ottelia*, are mingled with the others ; but they certainly do not play any important part in the formation of the obstacle. The ambatch, too, has been unjustly accused of assisting in forming the barrier. This is not the case. This plant does not grow in any great quantity in the vicinity of the Bahr-al-Gebel, and its stem is so light and brittle that it would break when subjected to great pressure.

'On the Bahr-al-Ghazal, on the contrary, the sudd is chiefly composed of the swimming plants above mentioned. Their breeding places are Lake Ambadi and the other lakes to the south. The Ghazal sudd is much lighter in texture than that of the Gebel, and is consequently much easier to remove. At the same time, even in the former river the sudd is at times dangerous, especially if it forms down-stream of a vessel, and if the latter has to work upon it from its up-stream end. The accident to Gessi Pasha's expedition in 1881 proves that even the Bahr-al-Ghazal sudd can be an impassable obstacle under such circumstances.'

How these various plants come to be so massed, in the respective rivers, as to form the barrier called 'Sadd,' or 'Sudd,' is very graphically explained by Sir William Garstin; but the account will not bear abridgement, and it must be read in the Report itself.

THE BOTANY OF THE 'SADD.'

The mention, in Sir William Garstin's Report, of certain plants, as inhabitants of the swamps and lagoons of the Upper Nile and its branch the Giraffe Nile, and its tributary the Gazelle Nile, and as constitutional parts of the 'Sadd,' has led to an investigation of these plants from a botanical point of view, and the following are the identifications which have been made, and notes as to their characteristics.

The Papyrus Plant.

The Papyrus plant—*Cyperus Papyrus*, Linn.—was, in ancient times, widely cultivated in the Egyptian Delta, where it was used for various purposes, but especially in making a writing material; but it is now extinct in Lower Egypt, and it is believed that it was not indigenous there, but probably had been introduced from Nubia. A clump of it grows in the tank-house in the Royal Botanic Gardens, Kew, with many stems, some of which are 9–10 feet in height above the water, while others, also in flower, are only about 6 feet high. A very characteristic picture of a large clump, backed by a tall grass or reed, is to be found in the Gardeners' Chronicle for 1870, p. 314, which was taken from a photograph of the plant as it grew on the Anapo River in Sicily. The plant has been recently and authoritatively dealt with by Mr. C. B. Clarke, F.R.S., in the 'Flora of Tropical Africa,' Part II, vol. viii. Mr. Clarke gives *Cyperus Papyrus*, described by Linnaeus in his 'Species Plantarum,' as the typical species, and names *Cyperus syriacus* of Parlatore (which grows on the Jordan) and *Papyrus sicula*, Parl., and *P. antiquorum*, Link, as synonyms; and he separates, but only as a variety, *P. antiquorum*, C. B. Clarke. He gives the habitats of the typical plant as Africa: Upper Guinea, Lower Guinea, South Central Africa, and the Mozambique District; and the habitats of his variety as, in Asia—Palestine; and in Africa—Nile Land, the White and Gazelle Niles, Mozambique, and Zanzibar. Mr. Clarke refers to an article by Mr. Thiselton-Dyer, in the Gardeners' Chronicle of January 16, 1875, p. 78. In that article Mr. (now Sir William) Thiselton-Dyer says: 'Probably few persons in this country are prepared to regard the *Papyrus* as a European plant, yet it has long been known to occur in many parts of Sicily, and it is more than likely that it is from this source rather than from the East that the specimens in various botanic gardens have been ultimately derived.' Mr. Thiselton-Dyer quoted a description given in a previous number of the Gardeners' Chronicle (1870, p. 314) by E. O. Fenzi, of the *Papyrus* in the Anapo River, where it grows to the height of from 12 to 15 feet. Macgregor, in the Illustrated London News, April 24, 1869, describing the *Papyrus* on the waters of Merom, Syria, said:—'On this (morass) is a vast floating forest of *Papyrus* and cane, perfectly dark inside. I could never penetrate more than 3 feet. Many of the stalks of the *Papyrus* are as thick as my arm. The water percolates below and through the spongy mass, and there loses at least half its volume by absorption and evaporation. This impassable barrier is about a mile wide.'

In the transactions of the Edinburgh Botanical Society, vol. x, 1868–69, will be found a very interesting and instructive paper of notes on the Botany and Agriculture of Malta and Sicily, by Dr. Hugh Cleghorn, late Conservator of Forests, Madras, who spent three months of the winter of 1867 and

1868 in those islands. In February 1868 he visited Syracuse, but had not time to visit 'the renowned station of *Papyrus antiquorum*, the celebrated fountain of Arethusa,' on an island close to the harbour. Dr. Cleghorn said: 'The *Papyrus* grows luxuriantly on the banks of the Cyane (see illustration in "Le Tour du Monde," 1866), amongst flags, reeds, and water plants. . . . There appears to be no other spot in Europe where this interesting plant flourishes in a natural state. The clumps are very thick, attaining a height of 15 to 18 feet. It is supposed to have been sent from Egypt by Ptolemy Philadelphus to Hieronymus II, 250 B.C. . . . Paper is now prepared as a curiosity by Signor Politi in the same way' (as described by Pliny, Book xxi, Sect. 12).

Afterwards, Dr. Cleghorn visited Palermo, and saw the locality where it is said the *Papyrus* formerly grew, now called the *Papireto*. 'The *Papyrus* of Sicily,' he said, 'is not mentioned by Theophrastus, Dioscorides, Pliny, nor Ovid, nor even by Diodorus Siculus and Theocritus, who were Sicilians. The first notice of it is contained in a translation by Professor Amari, quoted by Professor Parlatore, from the Arabic of Ibn Hankal, a learned Arab, who visited Palermo in the tenth century. The following is an extract: "Among these marshes (on the streams about Palermo) there is a bottom covered all with *Papyrus*, from which writing-paper is made. I had not believed that it grew anywhere on the earth except in Egypt, but here I have found it in Sicily. The greater part is twisted into ship cables, and the remainder serves to make paper for the Sultan, who, however, hardly gets as much as he requires. The place, now dry, and partially filled up, retains the name of *Papireto*." Till 1591 it was a vast swamp, full of *Papyrus*.'

Mr. Thiselton-Dyer, in the paper quoted above, said that Bruce found the *Papyrus* at Lake Zana (Tsana) in Abyssinia, in 12° N. Lat. Lake Tsana, as we learn from Sir William Garstin's Report, lies at an altitude of 1,775 metres above sea-level, over 5,800 feet.

'Um-soof.'

The other main factor in the composition of 'Sadd' is, according to Sir William Garstin, the 'um-soof' reed. That is the Arab name of the plant: the botanical name is, according to Dr. Georg Schweinfurth (the author of 'Beitrag zur Flora Aethiopiens,' Berlin 1867, and other works on the botany of the Nile Region), *Vossia procera*, a grass belonging to the tribe *Rottboellieae*. But, says Sir William Garstin, 'the sample of this grass sent to the British Museum was identified as *Phragmitis communis*.' The specimens of *Vossia procera* in the Kew Herbarium show a thick stem, with long and broad sheaths from the nodes which at first envelop the stem and make it appear thicker than it really is. It throws out roots from each node (or joint), which draw nourishment from the water in which it grows, and also from the mud should the stems lie prostrate, as probably they at first do. Schweinfurth, in the book presently to be quoted from as to 'Ambatch,' mentions *Vossia procera* as one of the plants which have a share in the formation of the floating 'Sadd' islands. This must be a comparatively new identification, for in the 'Treasury of Botany,' 1870, it is stated that *Vossia cuspidata*, a native of the West Indies, is the only species of the genus.

'Ambatch.'

This plant, *Herminiera elaphroxilon*, Adanson, the only species of the genus, belongs to the order Leguminosae, and has 'thorny branches, abruptly pinnate leaves, and large orange-coloured flowers, succeeded by linear oblong compressed legumes, which become at length spirally twisted.' Sir William Garstin, as has already been mentioned, says that this plant has been unjustly accused of assisting to form the 'Sadd' in the Bahr-al-Jebel; that it does not grow in any great quantity near that river; and that its stem is so light and brittle that it would break when subjected to pressure. But this is not the view Dr. Schweinfurth takes of it. In his very interesting book of travel, 'The Heart of Africa,' a translation of which into English was published in 1873, we find full information about 'Ambatch,' which will now be quoted or abridged :—

'What, however, most interested me was the unlimited variety in the kinds of water plants which abounded in the floods, the sport of the winds and waves. Among them the *Herminiera*, known under the native name ambatch, has already been the subject of general remark ; it plays so prominent a part in the waters of the Upper Nile that it might fairly be designated the most remarkable of the aquatic plants.

'My predecessor, Kotschy, who did not know that it had already been observed by Adanson in Senegambia, named it *Aedemone mirabilis*, which was corrupted into the still more wonderful name of *Anemone mirabilis*, and so appeared in many books which treated of Africa. The ambatch is distinguished by the almost unexampled lightness of its wood, if the fungus-like substance of the stem deserves such a name at all. It shoots up to fifteen or twenty feet in height, and at its base generally attains a thickness of about six inches. The weight of this fungus-wood is so insignificant that it really suggests comparison to a feather. Only by taking it into his hands could any one believe that it were possible for one man to lift on his shoulders a raft made large enough to carry eight people on the water. The plant shoots up with great rapidity by the quiet places of the shore, and since it roots merely in the water whole bushes are easily broken off by the force of the wind or stream, and settle themselves in other places. . . . This is the true origin of the grass-barriers so frequently mentioned as blocking up the waters of the Upper Nile, and in many places making navigation utterly impracticable. Other plants have a share in the formation of these floating islands which daily emerge like the Delos of tradition ; among them in particular the Vossia grass, and the famous papyrus of antiquity, which is at present nowhere to be found either in Nubia or in Egypt.'

'As we progressed farther the river islands became more and more narrowed by the surrounding masses of impenetrable grass. The ambatch is here almost excluded by the Vossia grass, but only to appear at the mouth of the waters. . . . Here we came across numbers of Shillooks fishing in their light canoes of ambatch, darting through the water almost as quickly as the fish themselves. . . . So light are these canoes that one man can carry three of them on his shoulders, although each canoe is capable of holding three men. From a dozen shoots of ambatch of about three years' growth a canoe of this kind can easily be produced; at about six feet high the stem goes off rapidly to a point, so that a bundle of them needs only to be tied together at the extremities, and there is at once obtained a curve that would grace a gondola.'

Here then is a direct conflict of testimony. On the one hand Dr. Schweinfurth, a great traveller and explorer as well as an eminent botanist, states from personal observation that the 'Ambatch,' *Herminiera elaphroxylon*, is the true origin of the 'grass-barrier' which blocks up the Upper Nile; and, on the other hand, we have Sir William Garstin, an eminent engineer, holding a high post under the Egyptian Government, who spent months on the Upper Nile, and watched the operations carried on for the removal of the 'grass-barriers' (the 'Sadd'), stating that the main constituents of the 'Sadd' are the Papyrus and the 'um-soof' (*Vossia procera*) reeds, and that the 'Ambatch' has been unjustly accused of assisting in forming the barrier. Possibly Dr. Schweinfurth's observations were not made just where Sir William Garstin investigated the composition of the barrier. And Dr. Schweinfurth says that in places the 'Ambatch' was almost excluded by the 'um-soof.' Also it is quite conceivable that in some places as good a block may be made by *Papyrus* and *Vossia* alone as by all three plants combined in other places. And the objection that the stem of the 'Ambatch' is too light and brittle to withstand great pressure does not seem to have been verified by experiment and may not be fatal. The lightness and brittleness are admitted; but would it be possible for a plant to have a stem generally six inches thick at the base, and to shoot up to fifteen or sixteen feet in height, unless the stem had a certain degree of strength? And doubtless the 'Ambatch' attains its height above the water by the support which the *Papyrus* and *Vossia* afford it. It must therefore be flexible enough not to mind pressure.

But Dr. Schweinfurth is not the only observer and botanical authority who may be quoted against Sir William Garstin on the side of the 'Ambatch.' In 'Plantae Tinneanae,' by Theodori Kotschy and Joannis Peyritsch, 'Ambatch' is not botanically figured, that having been done before by Heuglin; but a lithographed frontispiece shows a landscape with 'Ambatch' and papyrus and other plants growing together in the foreground. The 'Ambatch' is growing much higher than the papyrus, and the stems are bent down or broken off at various heights. The stems are therefore brittle; but one can easily imagine that they form a substantial woof in the entanglement of which the papyrus and 'um-soof' form the warp. And the branches and twigs of the plants, being thickly set with stout prickles like those of a rose plant, would add to the trouble.

In the 'Proemium' M. Kotschy tells us that, according to Lejean, 'les deux rives sont couvertes de Papyrus, mais surtout de l'arbre aquatique appelé Ambadj, qui, pendant l'époque de la fleuraison, c'est-à-dire en février et mars, relève encore la beauté de son feuillage vert et étoilé par des fleurs d'un jaune brillant.'

The Tinné botanists say that it is in the neighbourhood of Mt. Dinka (Njemati) one first sees thickets (or bushes) of Ambadj (*Herminiera elaphroxylon*) which become more and more frequent as one travels towards the south, and are associated with *Pistia stratiotes*, and Nymphea round about them; and, near Hille-Kaka, a fern equally floating, *Ceratopteris thalictroides*, comes in their company. At the mouth of the River Sobat much of the surface of the water is covered by reeds, and there, round the reeds and other plants above mentioned, one meets with *Azolla nilotica* growing very large, which is figured on Plate 27 of the work. Further on the botanists say:—

'L'Herminiera, qui porte le nom d'Ambadj, pousse pendant 5 ans de ses grosses racines principales, qui sont horizontales, placées constamment sous la surface de l'eau, et garnies de radicelles capillaires très-nombreuses, ses troncs coniques qui atteignent souvent une hauteur de 20 à 25 pieds: pendant les cinq années suivantes, ces troncs dépérissent, et une nouvelle période de végétation commence à se produire.'

In the dry season, fires in the neighbouring jungle frequently reach the 'Ambatch,' and thus seriously endanger the boats of the inhabitants.

Herminiera elaphroxylon was first described by Guillemin, Perrotet, and Richard, in their Flora of Senegambia, and was therein figured: and it again appeared in Speke's book, 'The Source of the Nile,' in the botanical Appendix by Thomson. In Kotschy and Peyritch's book the authors remark as follows:—

'In stagnantibus aquis ad ripas Nili et Bahr-Ghasal planta haec mirabilis radicibus intertextis cum quibusdam aliis plantis insulas format, quae ventis huc atque illuc agitantur.

'Crescit in fossis Nili albi inter Schilluk insulas necnon in Bahr-Ghasal copiaque navigantibus impedimento est. Arabice Ambadj dicitur.'

Of *Pistia stratiotes* MM. Kotschy and Peyritch say that it is very abundant in the Bahr-Ghazál, 'où il constitue des îles flottantes, en société des *Cyperus colymbates*, des *Herminiera elaphroxylon*, des *Nymphaea*, et divers autres plantes.' Besides *Cyperus colymbates* of Kotschy and Peyritch, Mr. Clarke shows another floating *Cyperus* of the Nile, namely, *C. nudicaulis* of Poiret, collected on the White and Gazelle Niles by Schweinfurth. These are small plants, with long, pendent roots; but in quantity they must play a considerable part in the formation of 'Sadd.'

On referring to the Botanical Appendix to Speke's work, 'The Source of the Nile,' we find in its place in the order Leguminosae, *Herminiera elaphroxylon*, Guill. and Per., the 'ambash' or pith tree of the Nile from 3° to 8° N. lat. There can therefore be no doubt as to the identity of ambatch, or ambadj, or ambash, with *Herminiera elaphroxylon.* And, when we find Schweinfurth's account of the habits and propensities of 'Ambatch' thus corroborated by the evidence of Kotschy and Peyritch, we cannot but find it guilty of being a chief constituent of 'Sadd.'

Smaller Plants of the 'Sadd.'

Those mentioned in Sir William Garstin's report are—*Pistia stratiotes*, *Utricularia*, *Azolla*, and *Ottellia.* These are said to grow mingled with the larger plants we have discussed, but not to play an important part in forming the blocks in the Bahr-al-Jebel; while, on the contrary, on the Bahr-al-Ghazál the 'Sadd' is composed chiefly of them. They are, there, bred in Lake Ambadi and other shallow lakes adjoining the river into which they are swept by floods.

Pistia stratiotes has already been mentioned as floating down the Nile far above the 'Sadd' region, from the Victoria Nyanza (Lake), probably, and again as being a plant of the 'Sadd' region of the Mountain Nile: it was absent in 1900, but in 1901, when the river was open, there was a continuous stream of it floating down. 'It is a very common tropical water-weed, out of which many species and even separate genera have been made. It is referred to the same order as duckweed . . . but is very different in appearance, and very much larger. . . . Like duckweed, it propagates itself with great rapidity, and frequently completely covers tropical ponds and water-tanks with a coating of verdure, keeping the water underneath fresh and cool. It floats on the water and sends down a quantity of long feathery roots, which very rarely reach the bottom. The plant consists of a rose-shaped tuft of wedge-shaped leaves, two to five inches long. . . . Each plant sends out several runners, and upon the ends of these other similar plants are formed, which again send out runners, until in a short time the surface of the water is covered.' It was figured in the Botanical Magazine, No. 4564.

Utricularia is a genus, containing several floating species, the roots, stems, and leaves of which are furnished with numerous membranaceous vesicles or small bladders, which during the early stage of the plant are filled with water, but when the flowers are ready to expand become filled with air. The British species, at least—called Bladderwort—are thus floated upwards, but only sufficiently to let the flowers rise above water, the rest of the plant remaining submerged. 'After the season of blossoming the vesicles become again filled with water, and the plant descends to ripen its seed at the bottom,' where, on the Nile, it probably fraternizes with the roots and stems of the other 'Sadd' plants. Another group of *Utricularia* consists of species which grow at higher altitudes, and have quite a different habit from that just described.

Azolla is a very curious genus, belonging to the fern allies. The species found in the Upper Nile is *A. nilotica.* The few species all float upon water, forming green or reddish patches, frequently several yards across, and they have creeping rhizomes which throw down roots towards the bottom of the pool or stream. 'The species occur from Australia and New Zealand as far as New York. One has been found in Western Africa by Vogel.' *A. filiculoides*, found in California, often grows in densely crowded masses, the plants being usually much larger than those of the Eastern species. *A. nilotica* was got on the Shiré River, in East Central Africa, by Dr. (now Sir John) Kirk, who noted it as 'small, creeping' (on the surface of the water), 'and sending down roots all along,' and also by him on the Luabo River, 'floating, with *Pistia* and *Trapa*.'

Ottellia, another genus of 'Sadd' plants named by Sir William Garstin, consists of 'perennial herbs inhabiting the mouths of the Nile, Ganges, and Australian rivers, and eaten as potherbs in India. They are quite stemless.' The size as well as the shape of the leaves varies much. The Indian plant is *O. alismoides*, Persoon.

One other minor 'Sadd' plant is mentioned by Sir William Garstin, namely *Aldrovanda.* This is a genus of Droseraceae

(Sundews) containing, says Lindley, only a single species, *A. vesiculosa*, found in Southern Europe, and growing in still waters. The leaves are pellucid, and are widened at the extremity into two lobes which in Europe are generally found closed. In 1873 Stein discovered that the bilobed leaves open under a sufficiently high temperature, and when touched suddenly close and thus entrap aquatic animals. The leaves sometimes contain bubbles of air, and were formerly supposed to be bladders: hence the specific name of *vesiculosa*. *Aldrovanda* is destitute of roots and floats freely in the water. ('Insectivorous Plants,' Darwin, 1871, p. 321.) The leaf-stalk is flat, not inflated. Mr. Clarke says the plant is only rarely met with in the 'Sundribans' of Bengal, but he cites it as an instance of a genus occurring on both the Nile and Ganges.

Ceratopteris thalictroides, Brongn., mentioned by Kotschy and Peyritch as being one of the floating components of the 'Sadd' in the Gazelle Nile, is a fern, but very anomalous in its structure, placed by Hooker and Baker in the tribe, or family, *Pterideae*, but considered by other botanists as so paradoxical that it ought to be placed in a tribe, or even a sub-order, by itself. It is the only species of its genus, but it was originally named by Linnaeus *Acrostichum thalictroides*. It has since been characterized by later authors under no less than nine different genera, and a dozen specific names. The fern grows in separate plants. The stipes or stalks of the fronds are thick, inflated, filled with large air-cells. The fronds are of two sorts, one barren and floating, the other longer, erect and fertile, and succulent in texture. The plant is found widely spread in the tropics of both hemispheres, growing, said Mr. John Smith, in wet places or even in shallow water, the sterile fronds viviparous; and the ready germination of the spores, and rapid growth of the fronds, make it abundant in its habitats. Mr. Smith says this is one of the few ferns that are annual. Colonel Beddome, the authority on Indian ferns, says it grows throughout India, Ceylon, and the Malayan Peninsula up to 3,000 feet elevation, and is common in tanks (ponds), ditches, and swampy places, or even on dry ground in the rains. And he does not think it is an annual, at least in cultivation, if kept very moist or in water, as he kept the same plant growing for some years at Ootacamund in the Nilgiri Mountains, 7,000 feet or so above the sea. Mr. C. B. Clarke, who, in the Transactions of the Linnaean Society published a 'Review of the Ferns of Northern India,' notes regarding this fern :—'In rice-swamps, floating ; but much more commonly erect, tufted, in ditches, or even in dry spots during the rains. The floating and erect forms both produce their barren and floating fronds. In ditches the rhizome is somewhat creeping and stout.' T. Moore wrote :—'Either floating or attached to the soil in shallow, still, or slightly moving waters.' The plants in the Bahr-al-Ghazál must be quite off the ground. The present writer found the plant growing gregariously in the Dehra Dún, North-Western India, in briskly running shallow water, and there it was well-rooted in the ground, and liable to be submerged with the rise of the water. In Florida, U. S. A., it is recorded as floating. The late Rev. C. S. Parish found *C. thalictroides* growing in his garden in Maulmain, Burma, on gravel walks during the rainy season ; and the late Mr. H. C. Levinge, a very distinguished amateur collector of Indian ferns, gathered it 'on an old wall at Siliguri in the Darjiling Terai.'

VEGETATION IN THE SWAMPS OF LOWER BENGAL.

When consulted as to the plants which form the Nile 'Sadd,' Mr. Clarke was led to think back to his life long ago, in Lower Bengal and Assam, when in the course of duty he had to travel about in a boat through the great swamp which extends over the *zillas* (counties) of Sylhet, Comilla, and Maimensingh. These water plants of many sorts unite to form not only barriers in streams, but, during the annual floods of the Ganges, Brahmaputra, and Surma Rivers, a dense mass of floating vegetation, extending perhaps 100 miles from east to west, and as much from north to south ; and Mr. Clarke very kindly furnished some notes in which he contrasted the conditions prevailing in Bengal with those on the Nile, and showed how similar the vegetation is in the two localities. During the floods, Mr. Clarke says, the only means of communication is by water; and away from the main streams the inhabitants can get about nowhere except from point to point where the villages are built on isolated, artificially-raised, mounds, or on river banks. This they do along straight lanes through the floating vegetation, which are kept open by the boat traffic.

Mr. Clarke points out that the main difference between the Bengal floating vegetation and the Nile 'Sadd' is that the first-named grows in water which is practically at rest (it really moves in mass, though extremely slowly, from north-west to south-east), but the floating vegetation if forced into the main rivers is lost owing to their vast width; whereas the 'Sadd' plants of the Nile, though reared in the still waters of the lakes and lagoons, are broken off into clumps and carried into the river by the strong winds which accompany the annual rise of the river, and there become potent for mischief. The interesting point to Mr. Clarke is the remarkable way in which some of the African 'Sadd' plants are represented in Bengal by closely allied 'representative' species. The two 'Sadd' floating species of Cyperus (*C. colymbates*, Kotsc. and Peyr., and *C. nudicaulis*, Poir.), have in Bengal two representatives, *C. cephalotes*, Vahl., and *C. platystylis*, R.Br., the seeds of which float and germinate in the water. The seeds of *C. papyrus*, and some other species which at all events begin their life rooted in the ground, are heavy and sink to the bottom, there to germinate in the mud.

The representative of 'Ambatch' (*Herminiera elaphroxylon*, Guill. and Perrot) in Bengal Mr. Clarke finds in *Aeschynomene aspera*, Linn., also a leguminous plant, of a genus which stands next to *Herminiera* in Bentham and Hooker's 'Genera Plantarum.' *Herminiera* is, he says, only *Aeschynomene* writ large. The wood, or 'pith,' of this shrub is the well-known 'Sola' of Bengal, which is used for making sun-hats, swimming-jackets, and covers under which to keep iced drinks cool, and for many other purposes where elasticity and lightness are required, such as for floats for fishing nets. To construct some of these articles the soft corky stem is cut into thin slices and pasted together. It is sold in the bazars of Calcutta, being brought from the neighbouring marshy places, where it grows to a great size.

Aeschynomene aspera ('Sola') itself seems to be a Nile plant, for in the Botanical Appendix to Speke's book is an entry—*Aeschynomene indica*, L., 'Solah' of India, in marshes generally 5° S. to 2° N. lat. But this range is all south of the 'Sadd' region. In September, it is said (the height of the dry season), at 3° S. lat., this plant lies dead on the dry mud; it grows erect 7 feet high, and is used for floats for nets. *Ae. Schimperi*, Hochst., is another equatorial African plant, and is said to be a species of Indian Solah (pith), a bushy tree, growing 20 feet high.

Azolla nilotica is represented in Bengal by *A. pinnata,* R. Br., and the Nile *Ottellia* by *O. alismoides,* Pers.—if indeed the plants are specifically different.

Plants which are identical on the Nile and in the Bengal swamps are *Vossia procera*, *Trapa natans*, Linn., *Pistia stratiotes*, L., *Aldrovanda vesicularis* (very rare, though perhaps plentiful in places), *Nymphaea Lotus* and *N. stellaris*, and *Ceratopteris thalictroides.* Mr. Clarke is inclined to consider *Pistia stratiotes* as the chief constituent of the rotting vegetation in the Bengal swamps and *jheels*, which in the middle of the rains forms a floating mass from 6 to 24 inches thick, on which birds run and which will often carry a man. And he says that most of the plants which float, or grow on floating masses of *Pistia*, other weeds and earth mixed, can also grow on mud; while the whole of the rice-field weeds *may* grow on such floating masses. Even seedlings of trees, as of *Bombax* and *Erythrina*, sometimes appear plentifully on the floating mass.

It is by notes such as these which Schweinfurth, Kotschy and Peyritch, Mr. Clarke, and other botanists who have been great travellers, give us of the habits and habitats of plants, that the dry bones of systematic botany are made to live and be interesting to the general reader.

'SADD' IN AMERICA.

In conclusion, a comparison may be added with the American 'Sadds,' which have an entirely different composition. Mr. T. A. Sprague, of the Herbarium in the Royal Gardens, Kew, who has travelled across South America by way of the Amazon Valley, says that neither on the Amazon nor on the Orinoco do masses of floating plants occur in sufficient bulk to hinder navigation. This was not to be expected in such wide and deep rivers. But Mr. Sprague pointed out that something of the sort occurs in Guiana, and referred the writer to the very interesting book, 'In the Guiana Forest,' by Mr. James Rodway, F.L.S. (T. Fisher Unwin, London, 1895), from which it appears that serious, though temporary, obstructions to the flow of the great rivers in that region (the Essequibo, &c.) are caused chiefly by two plants, *Montrichardia arborescens* and *Panicum elephantipes*. At p. 107 of his book Mr. Rodway says: 'The tall trees cannot hold their own in the mud; therefore they give place to a different type which has little or no trunk, and sits down as it were to anchor itself by means of special contrivances. Several species of Leguminosae, including *Drepanocarpus lunatus*, *Muellera moniliformis*, and *Hecastophyllum Brownii*, form dense thickets and extend as far from the bank as they dare. In front of these is an advance guard of mocca-mocca (*Montrichardia arborescens*), which is as it were drawn up in rank to keep back the flood. Growing in the water, this monster arum develops great club-like stems, which come up as close to each other as they can pack, and rise like rows of palisades to the height of twelve feet or more above the surface. As if this were not a sufficient encroachment on the open space, the floating island grass (*Panicum elephantipes*) anchors itself to the mocca-mocca or bushes, and extends just as far across as the rapid current will allow. In dry weather, when the water is low and the stream has little power, the extensions from either side meet in the centre, and close the passage-way for a time—only, however, to be torn away in great masses as the floods come. At such times great patches, fifty feet or more in diameter, are seen floating down stream, sometimes carrying with them monster camoudies (*Boa murina*) or other snakes.' Mr. Clarke caps this by telling how a rhinoceros was carried down a Bengal river to near Chittagong, and there caught and sent to the London Zoological Gardens, where it was described as a new species by Mr. Sclater (*R. lasiotis*). 'As these masses are caught by the sea-waves they are thrown back upon the beach, where they lie in great heaps until, dying, they go to help make up that extension of the coast-line which is continually driving back the waves to a greater distance. Sometimes a great tree, whose timber is light enough to float, gets entangled in the grass and becomes the nucleus of an immense raft, which is continually increasing in size as it gathers up everything that comes floating down the river. The grass extends over the whole mass and mats it together until a formidable obstacle is produced ; but, notwithstanding all its efforts, the dam is imperfect. When eight or ten inches of rain fall in a day, and the river rises sixteen to twenty feet, the barrier must go. However (much) it may be attached to the bottom by a thousand anchors, it has to give way when the rise takes place, and here the hollow stems help in its destruction. By their great numbers they act as buoys, drag the great tangle of trees and bushes to the surface, unloose their own anchorage, until the mass sails away, ever on and on, to be broken in pieces and dashed on the shore, or perhaps carried far out to sea.'

It sometimes happens that a very obstinate obstruction succeeds in withstanding the flood, which by and by comes and deposits fresh masses of similar material on the fast-forming bank until it becomes an impenetrable barricade, narrowing the channel to a considerable extent. 'The waters become higher, and the current swifter. Something has to go, but it is not this late erection. The opposite bank is undermined, one bush after another goes down with the flood, trees fall over and are also carried away, and a few months later the great river has a new bend.' And sometimes such an obstruction is formed in the middle of the stream, in a shallow place.

Then a little island is gradually formed, and mocca-mocca roots get stranded and begin to grow, and in a year or two a dense living palisade of *Montrichardia* protects the small island from being washed away. 'The little island lengthens down stream to a considerable distance. The semicircle of gigantic arums is sufficiently elastic to bend before the weight of water; the plants may be torn off by the roots, but never broken off.'

'The great rivers of Guiana all contain islands of different sizes, some as many as ten miles long, and it may be confidently stated that nearly all have been built up in this way, by means of the mocca-mocca, with the assistance of the host of thorny Papilionaceae.'

From Mr. Rodway's description it appears that the obstructions caused on the Guiana rivers are caused or intensified by the mocca-mocca being stranded in the water, or growing up in it from roots which have sunk to the bottom, and by the interlacing of floating grass with its thickly planted stems, and the 'host of thorny Papilionaceae.' On the other hand, the 'Sadd' of the Upper Nile consists mainly of plants which grow in the lateral lakes and lagoons, or on the banks of the main channel, and are forced in masses into the river by floods and winds and swept down by the current until they unite and find a point on the bank or in a narrow part of the channel which brings them to a stand, when they form a floating block under which further supplies of material coming from up-stream are sucked in and go to increase the vertical thickness of the mass both above and below water. The consequence of a block of 'Sadd' on the Nile is increased flooding of the land on either side of the river, and disastrous loss of water in the lakes and lagoons, and by evaporation, for it does not appear that there is any such solid ground, within reach of the current, into which the river can eat and form a new channel, as there is in the case of the Guiana rivers; and the floating power of the hollow-stemmed and buoyant mocca-mocca prevents the blocks formed by it and the floating grass from being anything like so permanent as those on the Nile.

Another case of obstruction by aquatic vegetation in America is found in Florida, U. S., North America, where—originally introduced from tropical South America for its beauty as a flowering plant—the so-called Water Hyacinth has become naturalized, and has increased to such an enormous extent in the St. John's River as to cause serious apprehension that navigation may be altogether closed. A Report to the U. S. Department of Agriculture, Division of Botany, by Mr. H. J. Webber, published as Bulletin No. 18 of the Department (Washington, 1897), gives full information concerning the vegetation which causes the obstruction, and the nature of the damage, of various sorts, caused by it. The Water Hyacinth, *Eichhornia speciosa*, Kunth (syn. *E. crassipes* (Mart.), Solms=*Piaropus crassipes* (Mart.), Britton), is the main factor in the block. It belongs to the Pontaderiacea Order. The leaves form a rosette one to two feet high, which remains above water as the plant floats; the basal portions of the leaf-stalks of young plants are strongly swollen, but as the plant becomes older the swellings gradually disappear, and the petiole lengthens. The swellings on the petioles of the young leaves act as air-reservoirs, and thus ensure the stability of the young in water. Old plants become thoroughly entangled, and are in no danger of being overturned. The long petioles are full of air. The roots form a dense, bushy mass, reaching in many cases a length of over two feet. The plant bears spikes of light-blue or violet flowers, and blooms freely, and this has led to its being widely cultivated in America and Europe. Plants, now coming into flower (July 1902), may be seen in the tank in the *Victoria Regia* house in the Royal Gardens, Kew.

The water hyacinth is mostly limited in its growth to sluggish fresh-water streams, bayous, lakes, ponds, &c. In Florida the plants are generally found lining the shores of lakes and rivers in immense numbers. In certain lakes the entire shores are lined with a solid mass for fifty to several hundred feet wide, and small tributary creeks of the St. John's River are entirely covered. The main channel of the river remains clear unless masses of the plants become so packed together as to produce a block. In most places the hyacinth grows to some extent on the muddy shores of the rivers and lakes, and the stolons become so entangled that the plants whose roots penetrate the soil serve to moor large floating masses to the shore. Masses get loose and are blown by the wind, even 25 miles, up stream, and there form solid masses. Other large masses are carried by the current down to the sea. Mr. Clarke says that the American *Eichhornia* is represented in the Bengal swamps by the allied genus *Monochoria*, which has the same habit and mode of growth.

Mr. Webber describes the method of self-propagation of the plant, and notices its introduction into Florida and its present distribution in the State. He gives a graphic account of the damage caused by obstruction to the rafts in which timber is brought down the river, and to fishing with nets, and an illustration in his Report, from a photograph, shows at once the great width of the St. John and the extent to which it is in places covered by *Eichhornia*, with large river steamers imbedded in it. Masses of the plant floating down stream get banked up against the long low bridge which carries a railway across the river, or estuary, and act as a dam to the water. Another illustration shows how the weed, floating down stream, is diverted by booms into docks similarly constructed, whence it is taken on shore and used as manure. Observations are recorded as to the effect on health of so much vegetation collected together in the water, and along the river banks; but it may be doubted whether the weed does any harm while floating and growing. In its manner of growing and spreading over the surface of sluggish water in a continuous sheet the *Eichhornia* strikingly resembles *Pistia stratiotes*, which plays no mean part in the 'Sadd' of the Upper Nile, and is so striking a feature in the great swamps of Bengal; but there does not seem to be any tall-growing plant in Florida at all corresponding to the Papyrus, Um-soof, and Ambatch of the Nile, or to the mocca-mocca of the Essequibo.

On the Anatomy of Danaea and other Marattiaceae.

BY

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With Plates XXII and XXIII, and Text-Figures 28 and 29.

INTRODUCTION.

THIS investigation was begun in the Jodrell Laboratory, Royal Botanic Gardens, Kew, in 1893, at the suggestion of the Honorary Keeper, Dr. D. H. Scott. In connexion with it two papers were published, one on the development of the mucilage-canals of the Marattiaceae[1], and another on the prothallus and embryology of *Danaea simplicifolia*, Rudge[2]. It was originally proposed to make the general anatomical part a comparative study of the then known genera of the Marattiaceae. Its completion, however, was unavoidably delayed, and now it is found desirable to limit its scope somewhat on account of some recent detailed work on the Anatomy of *Angiopteris evecta*[3].

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[1] Journ. Linn. Soc., xxx.

[2] Annals of Botany, x, 1896.

[3] R. F. Shove, On the structure of the stem of *Angiopteris evecta*, Annals of Botany, xiv, 1900. J. Bretland Farmer and T. G. Hill, On the Arrangement and Structure of the Vascular Strands in *Angiopteris evecta* and some other Marattiaceae, Annals of Botany, xvi, 1902.

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For the purposes of this investigation, material, more or less complete, was available of species of *Danaea*, *Angiopteris*, *Marattia* and *Kaulfussia*, for which the writer is greatly indebted to Sir William Thiselton-Dyer, Director of the Royal Botanic Gardens, Kew, Professor F. O. Bower, Glasgow University, Professor F. W. Oliver, University College, London, and the late Mr. George S. Jenman, British Guiana. The writer likewise had the privilege of cutting a section of the petiole of a herbarium specimen of the new genus *Archangiopteris*, discovered by Henry in 1899[1].

The subject will be dealt with in the following order:—

(1) Development of the vascular system of *Danaea simplicifolia*, Rudge.

(2) Comparative anatomy of the frond, stem and root of the Marattiaceae.

The importance of the Marattiaceae as a group and the desirability of studying it both from the developmental, anatomical and palaeontological aspects has been so well set forth in the important recent contributions just referred to, that further dwelling on this point is unnecessary. It is hoped that the present paper will help to fill up another gap or two in our knowledge of this interesting section of the Pteridophyta, although from the nature of all such investigations there can be no finality.

It will be well, however, before beginning the descriptive part of this paper, to say a few words about the stelar terminology to be used. The exceedingly valuable advance made by Van Tieghem in emphasizing the importance of the vascular conducting cylinder as a whole by his stelar terminology has been recognized by the general adoption of his terms. Also, owing to the influence of the fresh position thus assumed, a great step forward has been taken in the study and comprehension of the vascular system of plants. This study, in its turn, has led to the recognition of the fact, that a certain number of the terms did not fit the resulting new views. Further, fresh terms have been devised to express

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[1] Christ u. Giesenhagen, Flora, 1899.

the new theoretical interpretations. Strasburger's term *phloeoterma* and Jeffrey's *siphonostele* may be cited as examples of these. The original, as well as the later terms, have in some respects the unfortunate character that they are not merely descriptive, and therefore cannot be used in many cases where they would be very useful if they did not commit the user to expressing homologies which he did not wish to imply. It seems desirable therefore, in this connexion, that certain names should be found, which denote definite structures without necessarily involving any idea of homology. The advantages of some such way out of the difficulty seem to counterbalance the disadvantages of a further multiplication of terms.

In the terminology to be used in the present paper the word 'stele' and several of its compounds will be employed in their original sense, in most cases, but several others have been devised to fill certain apparent gaps.

The Dicotyledons are looked upon as the highest expression of plant life, and it therefore seems appropriate to apply the term *eustele* to their well-known type of vascular cylinder, i.e. a ring of collateral vascular bundles surrounding a pith and limited on the outside by the pericycle. *Eustele* is therefore equivalent to Van Tieghem's 'monostele' in one of its applications. This definition is adopted so that E. C. Jeffrey's term of *siphonostele* may not be interfered with, because from his point of view the pith is extrastelar. In most roots the arrangement of the xylem and phloem is 'radial,' hence the term *actinostele* seems appropriate. Its application, however, would not be confined to roots (cf. stem of *Lycopodium*). Certain supposed primitive steles have been called *protosteles*, but at least two distinct kinds are included under this name, viz. what is here called an actinostele and also another simpler type in which a ring of phloem surrounds a mass of central tracheids (e.g. most Hymenophyllaceae). On account of its structural simplicity *haplostele* will be used for the latter type, and, if a central mass of parenchyma is present, the structure can be spoken of as a *medullated haplostele* (e.g. most Lepidodendreae). The adoption of this word leaves *protostele* and *protostelic* to be used as previously. When distinctly present, and developed from the procambium-strand along with the other elements, the 'pericycle' would be included in this or any other type of stele[1]. It is difficult to find a suitable word to express the idea of scattered vascular strands as typically found in Monocotyledons. As indicating irregular arrangement, *atactostele* may serve for this type, whether the individual bundles lack or possess a cambium. An *atactostele* therefore consists of a number of more or less irregularly arranged vascular bundles together with the ground tissue in which they are imbedded. It is now known that a large number of Dicotyledonous plants have scattered vascular bundles, and, as already indicated, they would be said to be *atactostelic*. In certain of them the vascular bundles are all of one type, and the stele in that case would be said to be *homodesmic*. In other cases, however, there are 'medullary' strands which consist of phloem only (e.g. in Gentianaceae and Melastomaceae), and then the steles might be called *heterodesmic*. *Cucurbita* may be taken as an example of *atactostely* among the Dicotyledons and *Habenaria bifida* of *eustely* among Monocotyledons. The term *solenostele* as defined by Gwynne-Vaughan[2] will be retained for the continuous amphiphloic tube with widely separated leaf-gaps[3]. Another and closely allied type of 'siphonostele[4],' in which a tubular network of vascular tissue results from the overlapping of the leaf-gaps, seems well described by the term *dictyostele*. This is a common condition found in Ferns, and well illustrated by the vascular system of *Aspidium*, with

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[1] It would perhaps be better to fix the phloem as the outermost limit of the stele on account of the want of constancy in origin of the 'pericycle,' but in the meantime, at any rate, the other definition is adopted.

[2] Gwynne-Vaughan, Observations on the Anatomy of Solenostelic Ferns, Annals of Botany, xv, p. 73, 1901.

[3] Neglecting the internal endodermis as a morphological criterion, it might be well to include it and the rest of the central parenchyma in the definition of the *solenostele*, but at present Van Tieghem's term, as revived and defined by Gwynne-Vaughan, will be retained.

[4] Jeffrey applies this term to the *eustele* of Dicotyledons and the *solenostele* of certain Vascular Cryptogams and also to the network-like stele of others.

which all are familiar. The word would apply whether the dictyostele were tubular as a whole (*Bündel-Rohr* of De Bary), as in *Aspidium*, or consisted of an irregular compound network of anastomozing strands as in *Pteris aquilina* and *Angiopteris evecta.* Jeffrey[1] has proposed the term *adelosiphonic* to describe the 'siphonostelic central cylinder' when it 'ceases to be obviously tubular.' Adopting his terms, the clearly tubular *dictyostele* would then be described as *siphonic* and the more irregularly constructed form as *adelosiphonic.*

In certain cases the central cylinder seems to be clearly reduced, or modified, as a result of habitat, e. g. in *Hottonia*, aquatic stem, and in *Potamogetons*, &c. The term *hysterostele* would distinguish these forms satisfactorily. Having thus named and described the chief types of stele, the question remains to be considered how to speak of the individual strands of any of those steles. The term *meristele* would seem to answer, but modified from its original meaning as used by Van Tieghem and Strasburger. A sense in which it has been used and in which it is proposed to be used here is due to Jeffrey, who applies the word to the individual strands of any vascular system. The application of the term will not be confined to the vascular strands of the stele only, but will be extended to those of the outgoing leaf-traces and their continuation into the leaves. This is done purely as a matter of convenience, on account of the apparent identity in structure, in most cases, of those strands, not on account of any theoretical considerations as to how the leaf bundles become continuous with those of the stem or vice versa. The terms collateral, bicollateral and concentric, can be just as well applied to the same types as under the old vascular bundle terminology, with this gain that haplosteles and actinosteles are not included. The 'steles,' or now meristeles, of some of the 'polystelic' *Primulas* and *Gunneras* are reduced eusteles in structure, and if desired could be simply described as *eumeristelic*, and those of the simple fern-

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[1] E. C. Jeffrey, The Structure and Development of the Stem in the Pteridophyta and Gymnosperms, Phil. Trans. Royal Society, vol. cxcv, 1902, p. 144.

type as *haplomeristelic*. In speaking of outgoing leaf-traces the prefixes *mono*, *di*, *tri*, &c. could be used, to simplify description. The use of meristele in the ways suggested is illustrated by a description of the behaviour of the outgoing leaf-traces in *Danaea simplicifolia*: e.g. in the very young seedlings the outgoing leaf-trace-meristeles are collateral, but the later-formed ones are concentric, just like the dictyomeristeles. The leaf-traces themselves are at first monomeristelic throughout their course, then dimeristelic through dichotomy, subsequently they are dimeristelic from the first, then they are trimeristelic, and finally in the most advanced seedlings examined they were found to be tetrameristelic.

The aim in suggesting, and adopting, the above modifications in and additions to the stelar terminology was to get words which had as little as possible of theoretical connotation, and were at the same time fairly descriptive and clearly defined. Complete avoidance of theoretical connotation is of course impossible, nor is it always desirable. Time, which tests all things, will show if this attempt to simplify stelar terminology by increasing the number of terms was a wise one.

SYNOPSIS OF TERMS.

Eustele. The 'monostele' of a typical Dicotyledonous plant. It consists of a ring of collateral or bicollateral meristeles, and includes the pericyclic and medullary ground tissue.

Actinostele. The 'monostele' of most roots and the similarly constructed stele of certain stems. It consists of alternating, or 'radially' arranged groups of xylem and phloem, surrounded by a pericycle. Pith may or may not be present.

Atactostele. The monostele of typical Monocotyledons. It consists of a number of scattered vascular bundles imbedded in conjunctive ground-tissue. Also applied to the stele of Dicotyledons with meristeles not arranged in a single ring. In the latter, if the meristeles are all of one kind, described further as *homodesmic*, if of different kinds, as *heterodesmic*.

Haplostele. A simple type of stele, frequently found in seedling Pteridophyta, rhizome of Hymenophyllaceae, &c. It consists of an axial rod of tracheae surrounded by a ring of phloem. The 'pericycle' is included if differentiated from the procambium-strand. If central parenchyma is present, then to be described as a medullated haplostele.

'Solenostele.' A continuous amphiphloic tube of vascular tissue with widely separated leaf-gaps. Pericycle present and the tube delimited by an external and internal endodermis.

Dictyostele. A vascular tube with large 'overlapping' leaf-gaps, so that the whole structure becomes a network of vascular strands or meristeles. The meristeles are concentric. This is closely allied to the preceding, the difference being due to the approximation and overlapping of the leaf-gaps. The dictyostele is further defined as *siphonic* when the network is simple and tubular, *adelosiphonic* when complex, i. e. ceasing to be obviously tubular.

'Protostele.' A stele which is supposed to be primitive in structure. Has been applied to both haplo- and actinostelic types.

Hysterostele. A stele which is supposed to be reduced in structure, e. g. in *Hippuris*, *Potamogeton* and *Hottonia* (aquatic stem).

Meristele. The vascular bundle in the old sense, except that it does not include actino- and haplosteles as formerly. It therefore applies to the vascular bundles of the stem of Dicotyledons and Monocotyledons, the 'concentric vascular bundles' of Pteridophyta, and vascular bundles of outgoing leaf-traces and leaves.

DEVELOPMENT OF THE VASCULAR SYSTEM OF DANAEA SIMPLICIFOLIA.

A number of seedling plants of various ages were available, and these were examined chiefly by means of microtome serial sections. The sections were usually doubly stained with haematoxylin and safranine and mounted in Canada balsam. The advantage of this method of staining, when successfully carried out, is that the endodermis shows up well, being distinctly stained red, thus contrasting with the dark purplish-blue of the cellulose-walls of the ground-tissue and phloem. In cases where sieve-tubes were required to be distinguished, dilute glycerine (50–70 per cent. glyc.) and safranine, or glycerine jelly and safranine were used.

Beginning at the base of a very young seedling, or older one if the base is not decayed, the vascular axis of the stem is found to consist of a *haplostele*[1]. The mode of transition from the diarch actinostele of the root to the haplostele of the stem was described in a paper on the prothallus and embryo of *Danaea simplicifolia*, Rudge[2], and agrees in every essential respect with the state of matters found by Farmer and Hill in *Angiopteris*. With regard to the first and earlier roots of *Danaea*, the protoxylem not infrequently abuts directly on the endodermis, or is separated from it by one pericyclic cell either at one or both ends of the diarch xylem-plate, but in this it does not show any essential difference from many other roots. The following quotation from Farmer and Hill's paper[3] might have been written for *Danaea simplicifolia*:—'The diarch xylem-plate of the root loses its definite outline owing to a considerable increase in the number of its tracheids that appear at the sides of the plate, which causes the wood to be roughly circular in transverse section ; at the same time the protoxylem loses its individuality and the diarch character becomes entirely lost. The phloem also extends over the periphery of the wood.' In *Danaea*, as in all the Marattiaceae, the sieve-tubes are distinguished by their relatively thick and glistening walls, and by the proteid-granules applied to their pitted areas. The sieve-tubes, however, often do not show up well in Canada balsam preparations, although the phloem as a whole is nearly always readily distinguishable. In seedlings they are very small, compared to the size they attain in the older plants, but are of the usual Marattiaceous type. In *Danaea* seedlings, unlike *Angiopteris*, the pericycle[4]

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[1] See definition in Introduction.

[2] Loc. cit.

[3] Loc. cit., p. 384.

[4] Cf. Farmer and Hill, loc. cit., p. 385.

is frequently not a well-marked tissue (cf. Fig. 9, Pl. XXII). It may even be represented by an isolated cell or two[1], the endodermis abutting directly on the phloem. If, as seems to be the case, the so-called pericycle consists of sister-cells of the endodermis, then it is not a pericycle by the definition that makes that layer the outermost one of the stele. Not infrequently the inner of the two sister-cells has cuticularized radial walls as well as the outer. In one or two cases undoubted phloem-parenchyma cells likewise had cuticularized cell-walls. On that account it would seem that there is very little constancy in the position of the histologically differentiated endodermal cells. In the seedlings of *Danaea simplicifolia*, however, the endodermis is on the whole a well-marked layer, and, as a matter of convenience, it will be treated as the boundary-layer between the stele or meristeles and the rest of the extrastelar tissue. At the next stage to the constitution of the haplostele there seems to be a distinct difference between *Danaea simplicifolia* and *Angiopteris*. The observations of Leclerc du Sablon are confirmed by Farmer and Hill with regard to the appearance of parenchyma in the centre of the xylem of the haplostele, which increases in amount till what they call a pith is present. In *Danaea* there is no such distinct pith differentiated, and the very small amount of parenchyma which does appear is clearly to separate the xylem of the outgoing leaf-trace from that of the haplostele (Plate XXII, Figs. 1–3). The earlier leaf-traces are usually separated off before the first lateral root joins the stele, tracing from below upwards[2], consequently

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[1] Cf. Fig. 20, prothallus of *Danaea*, &c., loc. cit.

[2] In all cases the development is described from below upwards, and hence the roots will be spoken of as coming in to the stele, but at the same time it has to be clearly borne in mind that the roots arise from the endodermis (this has not yet been definitely proved) and pass outwards and downwards. It is also important to remember that there is a large area of junction between the stele of the root and that of the stem, and that the root-junction very considerably affects the structure of the xylem not only in the immediate neighbourhood of the anastomosis, but for a considerable distance upwards and downwards. The texture of the xylem is much looser on account of the presence of a considerably greater amount of parenchyma.

matters are not complicated so early by the influence of the root as is the case in *Angiopteris*, which gives off a root nearly opposite the first leaf-trace[1]. The parenchyma marked *p.* in Fig. 13, Pl. XVI (Farmer and Hill, loc. cit.), and called pith, is probably simply due to the root-junction and preparation for the departure of the leaf-trace. In *Danaea simplicifolia*, then, the xylem of the first leaf, or cotyledon-trace, is marked off from that of the haplostele by a layer of parenchyma, and this increases in amount till the leaf-trace becomes free. The leaf-trace is collateral, and phloem appears on the side of the haplostele facing the departing trace-meristele, and thus becomes repaired or restored. This repairing phloem, at higher levels, sometimes makes its appearance in the intrastelar parenchyma before the leaf-trace becomes free, and might be interpreted as phloem appearing in pith. This process of giving off a leaf-trace with restoration of the haplostele is repeated several times, varying in number with the seedling and more or less affected by the junction of roots with the haplostele[2]. This is, therefore, nothing more nor less than the usual mode of departure of a leaf-trace from a simple rod-like stele, i. e. haplostele. Although, in the early stages of development of the vascular system, the successive departure of leaf-traces with resumption of the haplostelic condition seems to be the rule, one seedling showed a striking variation. It had in all six leaf-traces fully differentiated. Instead, however, of the usual mode of behaviour, the xylem soon showed parenchyma among the tracheids, which was at first irregularly distributed, but later occupied a central position (cf. Fig. 6). The appearance at this stage somewhat resembles the state of matters figured by Leclerc du Sablon for *Angiopteris*[3], and the central parenchyma might be called a pith. The unusual condition was due to abortion of the cotyledon-trace, and preparation

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[1] Farmer and Hill, loc. cit., p. 376.

[2] In this there seems to be no essential difference from what happens in *Angiopteris* (Farmer and Hill, loc. cit., p. 385) except for the presence of a pith in the latter.

[3] Loc. cit.

for the almost simultaneous departure of the next three leaf-traces. At a higher level the whole thing has resolved itself into a state of matters such as shown in Fig. 5, with the difference that there are three outgoing leaf-traces instead of two. The remaining leaf-traces were given off in the usual way, and there was only one cauline root. This seedling is mentioned on account of its apparent pith, but it is so abnormal that much importance cannot be attached to it. It is interesting to note that sieve-tubes, &c. appear in the central parenchyma. As already mentioned, the earlier leaf-trace meristeles are collateral, but those developed later are concentric, hence according to Van Tieghem's terminology, the former would not be 'steles' and the latter would. With regard to the leaf-traces themselves, the earlier ones are monomeristelic[1] and collateral; later they become concentric. The next step is that the xylem becomes separated into two masses as the leaf-trace passes out, but without actual dichotomy. Later, i. e. at a higher level, the originally single meristeles dichotomize, and finally they are given off separately *ab initio.* To take a concrete example:—One of the seedlings microtomed had thirteen leaves and therefore leaf-traces. The first six outgoing leaf-traces were monomeristelic and monoxylic, the seventh was at first monoxylic and became dixylic. The eighth was monomeristelic and then became dimeristelic through dichotomy. The ninth behaved much as the eighth, the tenth was dimeristelic from the start. The meristeles of the tenth leaf-trace, when they reached the leaf-base, each gave off a strand to the stipules, which were now distinctly developed. The eleventh, twelfth and thirteenth leaf-traces behaved as the tenth.

The following is a short account of the general sequence of events in the formation of the dictyostele from the haplostele. First of all, there is the haplostele with a solid core of tracheids, this becomes somewhat oval in outline, a layer of parenchyma divides the xylem into two more or less equal halves; this parenchyma increases in amount till it

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[1] See Introduction, p. 522.

extends right across the stele and the cotyledon-trace is cut off. The phloem reappears on the side of the haplostele facing the leaf-trace, and the endodermis is differentiated in the ground-tissue between the two [1]. This process is repeated a variable number of times, the haplostele showing a fluctuating tendency to become crescentic, especially about the place of junction of a root. When the stele does become definitely crescentic, it is not due to the departure of a 'sector' from a medullated haplostele, but because it is laid down in that shape by the differentiating meristem, hence there is no leaf-gap, in the ordinary sense, at first. After this crescentic stage has been reached, the next leaf-trace may go off from the convex side of the crescent (Fig. 28, diagram I), leaving two meristeles behind with a portion of extrastelar ground-tissue between them. The space [2] facing the previous leaf-trace is closed (diagram II) at the time a root comes in, and another leaf-trace is soon given off (diagram III). Thus the beginnings of the dictyostele are laid down, and it practically amounts to the branching of the haplostele through the formation of leaf-gaps. Up to this stage the leaf-trace is monomeristelic, only becoming dimeristelic through late dichotomy, but succeeding traces soon become dimeristelic from the first. Diagrams V, VI, VII, show how this takes place. After the crescent has been restored by the closing of the leaf-gap, the root R, coming in as usual, a portion is again separated off (m', diagram V), and rejoins the opposite horn of the horseshoe at a higher level (m', diagram VIII). From each of the tips of the crescent or horseshoe a leaf-trace meristele is now separated off, and the leaf-trace is dimeristelic from the beginning (diagram VIII, *l.t.*). Once this stage has been reached, or earlier in some cases, the central

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[1] In the Figs. 1, 2, 3, Pl. XXII, the endodermis is not represented round the leaf-trace meristele, because the preparation did not show it, either through defective staining or because the seedling was too young. It was quite clearly seen in other cases, however, e. g. Fig. 7.

[2] This space, i. e. on the right of the diagram, is not a leaf-gap, but due to the change from a haplostele to a crescentic one, subsequently to the departure of the leaf-trace.

strand (Centralstrang[1], commissural strand[2]) makes its appearance as a branch from the inner face of the more or less crescentic meristele, diagram IX, *c.s.* (cf. E. C. Jeffrey, Phil. Trans. B. Vol. cxcv, Pl. I, phots. 4 and 5). It traverses the ground-tissue, passing obliquely upwards (diagram X), joins the stelar-tissue of the opposite side usually at the same time as an incoming root (diagram XI). The leaf-gap is now closed, and there is what might be called a transitory solenostelic condition[3]. In *Danaea* this amphiphloic ring, with external and internal endodermis, has been found in all the seedlings which were old enough to have it, but it does not seem to occur at the corresponding level in each, nor is it so clearly developed in all. In most cases, moreover, there is a suggestion of an abortive attempt at its formation at a lower level. The central strand also may make an abortive attempt at formation, as in one seedling it was found to consist of phloem only. Farmer and Hill[4] found exactly parallel conditions in *Angiopteris*. From the point of view of development it is important to note that the central parenchyma, with or without a mucilage-canal, is extrastelar in origin, and not continuous with any parenchyma formed within the haplostele as a pith. In this, *Danaea simplicifolia* differs both from *Angiopteris* and *Aneimia phyllitidis*[5]. A study of the microtome-series shows the mode of development clearly. As has

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[1] R. Kühn, Untersuchungen über die Anatomie der Marattiaceen und anderer Gefässkryptogamen, Flora, 1889, p. 463.

[2] Farmer and Hill, loc. cit., p. 376, par. 3.

[3] Fig. 3, Farmer and Hill, loc. cit., illustrates a distinct solenostelic stage in *Angiopteris*, for the leaf-gaps do not over-lap. It is impossible to decide from the text whether the tube is amphiphloic or not. In the latter case it would be what these writers call pseudosolenostelic.

[4] Loc. cit., p. 387, par. 1.

[5] L. A. Boodle, Annals of Botany, xiv, p. 389. After all, it may be only a difference in degree, through the reduction or loss of the central parenchyma in the case of *Danaea simplicifolia*, which is a very small plant compared to *Angiopteris*, in its seedling as well as in its adult condition. It might also be that it is *Danaea*, which is the more primitive, and that the parenchyma, which in the first instance appeared simply to cut off the leaf-trace, grew to be a 'pith' for conducting and storing purposes as plants advanced in complexity and size. The writer does not feel competent to express any opinion as to which of these two views is the more rational.

FIG. 28.

FIG. 28. The diagrams illustrate horizontal sections of a hand-cut series of a seedling stem of *Danaea simplicifolia* at successively higher levels.

Diagrams I to VIII are in fairly close sequence, but not consecutive.

Diagrams IX to XI are in sequence after a considerable gap between VIII and IX.

FIG. 29. Sections from the same series as Fig. 28. Diagrams XII and XIII are near each other; XIV is isolated; XV–XIX are in sequence, but not consecutive.

Smooth contours mark outer limit of phloem. Shaded parts indicate xylem. Dotted contours indicate mucilage canals.

Abbreviations in Figs. 28 and 29: *c.s.* central strand or commissure or a branch from it; *c'.s'.*, branch of central strand; *K.σ.* original commissure after giving off

FIG. 29.

branch ; *σ*. meristele which is upward continuation of *K.σ.* ; *l.t.* and *l.t.'* leaf-trace meristeles ; *m.'* meristele of stem ; *R*. root ; *a. b. c. d. e. f.* meristeles which sooner or later pass out as leaf-traces.

been already stated, no 'pith' appears in the centre of the haplostele, but the ground-tissue is embraced by the conversion of the rod-like haplostele into a crescentic one. Then by the formation of leaf-gaps and their subsequent closure the 'extrastelar' ground-tissue comes to lie in the centre of a more or less complete ring of meristeles, as seen in transverse section[1].

In the series of sections from which Figs. 28 and 29 were drawn, the very transitory solenostelic condition did not appear till after the leaf-trace had become dimeristelic, but in two other cases (one of which is illustrated by Fig. 19, Pl. XXIII) it took place while the leaf-trace was still monomeristelic. A little above the level at which diagram XI was drawn, the solenostelic ring opens out at the side opposite to the anastomosis of the central strand, and then from the tip of each horn of the crescent a leaf-trace meristele is cut off, one apparently much ahead of the other[2]. While these changes have been going on, the central strand again frees itself. Its nature is well expressed by Farmer and Hill's term 'commissural column.' At the most peripheral part of its course it comes to occupy the centre of a leaf-gap, and it, with the other meristeles, forms a sort of ring, Fig. 29, diagram XV. It seems that this is the nearest approach to internodal structure attained, and, from the time it first appears, it repeats itself at intervals with but slight modifications. Shortly after the stage just described has been reached, certain of the meristeles pass off as leaf-traces and others anastomose and form a long slightly curved meristele (gamomeristele), as seen in transverse section. This is usually more or less directly associated with the incoming of a root. The central strand fuses with, or be-

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[1] This central, so-called extrastelar, parenchyma is developed from the central parenchyma of the differentiating meristem, so that it might not be so far-fetched to call it a pith in the ordinary sense. Whatever was its phylogeny, the pith of the normal Dicotyledon is also formed from the central part of the apical meristem. It is difficult to understand, except on account of the fetish endodermis, why the one should be called intrastelar and the other extrastelar.

[2] The meristeles of a leaf-trace do not always depart simultaneously from the dictyostele; but a little obliquity in the plane of section, which is often unavoidable, considerably emphasizes the discrepancy.

comes merged in, this curved plate of tissue (for such it is in reality), only to be again given off higher up. The next commissural branch may, however, be given off before the previous one is merged in the curved plate, Fig. 29, diagram XII, K.σ., central strand, *c.s.*, new commissural branch. In the next diagram σ. is the upward continuation of K.σ., and at a slightly higher level it will anastomose with the meristeles on each side of it and the incoming root, R. In these two diagrams the small meristele, *l.t.*, is one of a leaf-trace pair, the other will be given off from the long meristele opposite at the end marked *l.t.* The next diagram, XIV, shows the formation of a trimeristelic leaf-trace referred to above. The small strand, *l.t.*, became free at a considerably lower level, and the two remaining strands of the trace will be given off from the large meristeles marked *l.t.* at their outer ends. This trimeristelic leaf-trace was formed twice, before the tetrameristelic condition was attained in this seedling. Diagrams XV–XIX show a further modification in the behaviour of the central strand, and the formation of a tetrameristelic leaf-trace. In this case the central strand, after it reaches its peripheral position in the centre of the leaf-gap, gives rise to two branches, *c.s.* and *c.′s.′* These branches unite at a higher level, and the central strand is restored (diagrams XVIII, XIX). This state of matters was found in two different seedlings. Diagrams XV to XIX are not consecutive sections, but are in sequence, and show a typical and frequently recurring state of matters. Diagram XV illustrates the nearest approach to internodal structure met with, and already referred to. Diagram XVI shows the maximum number of meristeles present at this phase, *a–f*. The strands *a*, *b*, *c*, *d*, will become leaf-trace meristeles. They, however, do not leave the dictyostele without first anastomozing and again separating before passing outwards as the leaf-trace meristeles, as seen in the succeeding diagrams. In Diagram XIX the four leaf-trace meristeles have now definitely left the dictyostele, and the two branches of the central strand have completed their fusion. The meristeles, *e.* and *f.*, together with branches from σ will give rise to the next leaf-trace, which also consists of four meristeles. The meristeles, *e. f.*, in their turn, behave as *a. b.* did at the lower level. After this stage is reached there is little further complexity attained as far as the oldest seedlings available showed. Judging from the adult rhizome of *D. alata*, such changes as do occur are due to an increase in the number of the leaf-trace meristeles and the tendency of the meristeles generally to branch and anastomose, as is so strikingly illustrated in the case of *Angiopteris*.

In this way, then, the somewhat irregular or adelosiphonic dictyostele of *Danaea* is established, viz. by a process which is, to all intents and purposes, a branching of a haplostele, due to the departure of the leaf-traces of closely set, spirally arranged leaves. The complications which arise are due to a tendency of the meristeles themselves to branch, to the formation of a central commissural column, and to the presence of an abundance of cauline roots.

It will be appropriate to note here a few remaining points of interest in the anatomy of these seedlings. It was mentioned that the central strand sometimes begins as a phloem-commissure only. It is therefore not surprising to find meristeles losing their xylem and continuing their course as phloem-strands, till they rejoin the system at a higher level. Farmer and Hill found that the central commissures sometimes ended blindly in their upward course. That was not observed in *Danaea*, but the time and manner of its branching varies a good deal. For instance in the seedling from which Figs. 28 and 29 were drawn, at a stage subsequent to that of the double branch shown in Diagrams XV–XVII, first one branch was given off, and then another followed, the latter anastomozing with the former on the way upwards and across. In the oldest seedling cut, not more than two commissural branches were given off at any level, and the later ones only differ from those figured in their greater size and importance.

The root (R. in Figs. 28 and 29) behaves in a fairly constant manner. When the leaf-trace is paired, it generally, though not always, comes in medianly, and there is frequently one root for each leaf. Its fusion[1] with the dictyostele is usually associated with the closing of a leaf-gap, and synchronizes with the junction of the central commissure with the dictyostele[2]. The meristeles, whether of the dictyostele, the outgoing leaf-traces, or the fronds, are all built very much upon the same plan, viz. the usual Marattiaceous type. The phloem of the seedlings is so narrow in the radial direction, that it is practically impossible to distinguish proto- from a later formed phloem, as can be done in the case of older and adult plants. The protoxylem in the leaf and leaf-trace meristeles is endarch, as usual for the family, and more or less clearly mesarch in the dictyomeristeles. There is very little sign of what Farmer and Hill call *secondary thickening*, or of secondary merismatic division of the ground-parenchyma, except as a result of injury or undue pressure. The Marattiaceae generally have a great tendency to form what seems to be wound-periderm, but more will be said of this when dealing with the comparative anatomy. A small peculiarity that might be noticed *en passant* is the occurrence of an isolated tracheid in the ground-tissue in a leaf-base. It is of no great importance except in helping to show that the line to be drawn between stelar and extrastelar tissue is not a hard and fast one. This question will be dealt with under the heading 'Review of Terminology in Relation to Morphology.'

The study of the transverse sections of the seedlings of *Danaea simplicifolia* inevitably leads to a belief in the importance of the central strand or 'sympodial commissural column.' It is undoubtedly the one part of the dictyostele which is purely cauline. If the parts of it, where it is continuous with the other meristeles, be included, it may be said to follow a somewhat zigzag spiral course, because its points of junction move through the same angle which is described

[1] It has constantly to be borne in mind that this is only a descriptive *façon de parler*.

[2] If one were to imagine a transverse section across Fig. 4 (Farmer and Hill, loc. cit.) at the level of the lettering *rt.* 3, one would have a very good idea of the state of matters in *D. simplicifolia* as described, but generally the root is more median, and opposite the commissure.

by the leaf-spiral, roughly 144°. As the roots in nearly all cases join the dictyostele at or near the most peripheral position of the central strand, they are pretty obviously attached to the stem meristeles, as distinguished from the outgoing leaf-trace meristeles. This brings *Danaea* into line with the observations of Lachmann[1] on the behaviour of the roots of Ferns generally. As the result of a very careful and extensive piece of work, he came to the conclusion that the roots of Ferns were developed from the stem (stele ?) not the leaves (outgoing leaf-trace meristeles ?). The only case in which he found a direct connexion of the root with petiolar meristeles was that of *Ceratopteris thalictroides*[2].

The physiological meaning of the central strand is pretty obvious. As has been seen, it directly connects the root-bearing gamomeristeles at one level with the corresponding part at the next higher level, and so on. As the leaf-traces are given off from these curved plate-like masses, it is obvious that a considerable portion of the water absorbed can do what corresponds to 'short circuiting' in electrical terminology. But that is probably not all, for the roots, which are thus developed in close relation to the leaf-traces, probably do not reach the soil till some time after the related leaf has unfolded, hence the special advantage of such a central strand or commissural column is obvious. Finally the central strand also behaves as a reparatory strand ('Ersatzstrang') helping to close the leaf-gap.

COMPARATIVE ANATOMY OF THE MARATTIACEAE.

The Frond.

The anatomy of the frond of the following species of Marattiaceae was examined and compared:—

Angiopteris evecta, Hoffm.	*M. alata*, Smith.
Marattia fraxinea, Smith.	*Danaea simplicifolia*, Rudge.

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[1] J. Paul Lachmann, Contribution à l'histoire naturelle de la Racine des Fougères. 8°, 199 pp., 5 pl., Lyon, 1889.

[2] Cf. text, fig. 1. S. O. Ford, The Anatomy of *Ceratopteris thalictroides*, Ann. of Bot., xvi, 1902.

M. cicutaefolia, Kaulf.
M. Kaulfussii, J. Sm.
M. laxa, Kze.
Danaea alata, Smith.
Danaea elliptica, Smith.
Kaulfussia aesculifolia, Blume.

Sections were made from them at all the important levels, as far as the material permitted. As is well known, the fronds of the Marattiaceae have a broad leaf-base with large stipules. From the top of the leaf-base springs the pulvinus, which then tapers into the rest of the petiole [1].

Secondary and tertiary pulvini are found at the bases of the secondary and tertiary axes. In some cases the leaflets of the pinnules are practically sessile, but even then the base of the midrib is swollen. A pulvinoid swelling is sometimes present above the insertion of the lateral axes. This is of some slight importance, because occasionally in *Angiopteris* and *Marattia*, and frequently in *Danaea*, there are pulvinoid swellings or 'nodes' on the petiole. In the last-named genus there are often quite a number of these nodes normally present in some of the species. These swellings have been interpreted, apparently with good reason, as representing the position of lost pinnae. The internal structure of these 'nodes' is practically identical with that of a basal pulvinus.

Miss Shove (loc. cit.) has illustrated the structure and arrangement of the meristeles of the leaf-base and stipules of *Angiopteris*. There is no important difference in *Marattia*, or in the new genus *Archangiopteris*, so far as observed. Most of the fronds had been cut just below the pulvinus, so that the leaf-base was wanting, but the whole of a fair-sized plant of *M. alata* (reared from a stipule) was available. In this species there is a very distinct and considerable narrowing of the leaf-base at its insertion, and there is no reason to suppose that this feature is exceptional. Careful examination of the leaf-base showed no sign of a stipular commissure, which is, however, stated to be present by Kühn. His

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[1] The fronds of the Marattiaceae are too well known to require general description here, so only those parts will be specially mentioned which are concerned with anatomical features to be described. For the diagnoses of the various species the reader is referred to the 'Synopsis Filicum,' Hooker and Baker.

description leaves some doubt about the matter, and it is possible that the absence of a stipular commissure may be a generic difference. *Archangiopteris*, *Angiopteris* and *Danaea* have distinct, not to say well-marked, commissures. *Kaulfussia* was not examined for this feature. In *Marattia alata* only a very few, three or four, meristeles pass into the leaf-base from the stem, but they then branch very freely, so that they become very numerous. They are not very definitely arranged in the leaf-base, but, by the time they have reached the pulvinus, they have taken up a definite and characteristic position. In the case of a frond of *Marattia alata*, about three and a half feet long, three or four meristeles passed into the leaf-base; there they branched freely, giving rise to 33–34 meristeles, as seen in transverse section of its middle region. In the middle region of the pulvinus there were likewise 34 meristeles. Their arrangement in the pulvinus and petiole is illustrated by Figs. 11 and 12 (Pl. XXII) from *M. fraxinea*, which is a much smaller plant than *M. alata*, and therefore there are correspondingly fewer meristeles. The arrangement is essentially the same in all the species of *Marattia* examined. In this genus, as also in *Angiopteris* and *Danaea*, the meristeles (*ms.* in the figures) form a ring, somewhat flattened towards the upper surface, and besides there is a sort of indentation formed by a single, or a few, meristeles (*ms.*′). In all these vascular strands the protoxylem is directed towards the centre. Then further there is a small number of meristeles (*ms.*″) nearer the middle of the pulvinus, or petiole, in which the protoxylem faces upwards, or outwards towards the ring. As already said, there is the same general arrangement in all the Marattiaceae, but in *Angiopteris* there are several almost concentric sets of meristeles. In a petiole of *Angiopteris*, $\frac{5}{8}$ in. thick, there were three such sets. The possession of more than one set of concentrically arranged meristeles in the petiole seems to be generically distinctive of *Angiopteris*. It may be that, in the full-sized fronds of the larger species of *Marattia*, the same thing may be found, but in the absence of the necessary material it could not be decided. There is nothing peculiar about the meristeles themselves in this region. They are comparatively small and anastomose at not very frequent intervals. Figs. 11 and 12, Pl. XXII, are from the primary axis; Fig. 13 is just below the first pair of pinnae; Figs. 15–17 represent the pulvinus and rachis of one of these pinnae, and Fig. 14 the pulvinus of the other. In the last named there is a gamomeristelic ring, which in its structure recalls the solenostelic stage of the *Danaea*-seedling, or the solenostele of *Marsilia*. In the leaf, however, there is no external nor internal endodermis. The absence of mucilage canals in Figs. 14 and 15 shows that these structures are not continuous from the primary to the secondary and succeeding axes.

As is well known, the collenchyma of the pulvinus passes into the pale yellowish (sometimes even faintly brownish) sclerenchyma of the rest of the petiole and the rachis [1].

In the leaf the mucilage-canals do not seem to have any very definite arrangement. They generally pursue a fairly continuous longitudinal course, sometimes branching and forming an occasional horizontal anastomosis. They sometimes also end blindly. Tannin-sacs are abundant and are usually arranged round the meristeles. The black dots in Figs. 12, 13, 15, 16, 17 represent the tannin-sacs.

One of the chief objects of the investigation was to ascertain if there were any anatomical features which by their form, position, variation in presence or absence, afforded means of generic or specific distinction. It has already been pointed out that the arrangement of the petiolar meristeles of the older fronds of *Angiopteris* distinguishes it from the other genera. In addition it was found that to a certain extent (1) the sclerenchyma, (2) the mucilage-canals, and, in a less degree, (3) the tannin sacs yielded means of anatomical, specific or generic distinction.

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[1] It may be as well here to again emphasize the fact that the sclerenchyma in *Danaea* is of the usual Marattiaceous type, and not brown like that of the leptosporangiate Ferns. This was verified in the fronds of three different species, and the rhizome and roots of *Danaea alata*. Cf. Kühn, Ueber den anatomischen Bau von *Danaea*, Flora, 1890.

(1) *The sclerenchyma.* The petiolar sclerenchyma in most of the Marattiaceae is a simple continuous band of thick-walled elements a little below the epidermis, Fig. 13, *scl.*, but in *Angiopteris* its inner margin is sculptured owing to circular groups of the sclerenchyma projecting inwards. There is no such sculpturing in any of the five species of *Marattia* studied, so that as far as they are concerned the genus is distinguished from *Angiopteris* by this histological feature. In *Danaea elliptica*, however, an almost identical state of matters is met with in the fertile, but not the barren fronds. This is very curious and difficult to explain. It is evident therefore that the arrangement of the elements of the sclerenchyma may have some diagnostic value. This difference in the sclerenchyma of the fertile and barren fronds of *Danaea elliptica* is one example of the many pitfalls and snares which beset the path of the palaeophytologist.

(2) *Mucilage-canals.* Although in general there is no specially characteristic arrangement of the mucilage-canals, all the same, one species of *Marattia* showed a distinctive peculiarity in this respect, viz. *M. cicutaefolia.* In this species only was found in the pulvinus a ring of mucilage-canals lying between the collenchyma and the epidermis.

(3) *Tannin-sacs.* The number and arrangement of these structures vary a good deal in the different species, and it was at first thought they would be useful as systematic guides, but revision of the matter showed that there is not sufficient constancy and definiteness in arrangement to be of real value. However, careful plotting of their position and comparison of the arrangement in the different species might occasionally aid specific discrimination. Tannin-sacs, for instance, are abundantly present round the meristeles in the pulvinus of *M. cicutaefolia* and *M. attenuata*, and they are practically absent in the pulvinus of *M. fraxinea.* The section from which Fig. 11 was drawn had only two quite indefinitely placed tannin-sacs.

No attempt was made to test the distribution of crystals from this point of view, although in the hands of Radlkofer they have been shown to be of real use in aiding specific distinction in certain cases. The crystals and mineral deposits of the Marattiaceae have been studied by several observers, e.g. in more recent times Montverde, Kühn, and Radlkofer.

The structure of the meristeles, although distinctive of the group, does not afford means of generic or specific distinction. Taking the Marattiaceae collectively it may be said that they do not possess many diagnostically valuable histological characters.

The petiole and rachis are generally somewhat flattened on the upper surface. In the rachides, especially of the second and third order, there are projections from the angles, and there is a median ridge which becomes more prominent towards the apices. In some species the lateral ridges become wing-like, hence the specific term *alata.* These are specially mentioned because they are the only parts of the axes which have numerous rodlets projecting into the intercellular spaces from the walls of the cells. The rodlets however occur abundantly in the mesophyll of the lamina. It looks just as if there had been a viscid mass between the cell-walls, so that when the intercellular spaces were formed, it was drawn out into stringy masses, the threads of which parted in the middle as the walls receded from each other. According to Mangin[1] these rodlets consist of pectates, chiefly calcium pectate. Whereas these rodlets are very well marked in *Angiopteris*, *Marattia*, and *Kaulfussia*, they are almost, if not quite, absent in *Danaea simplicifolia* and *elliptica*, although present in other species.

In none of the genera do the meristeles of the leaf differ essentially from those of the stem. The chief difference is in the position of the protoxylem, which is normally endarch in the frond, endarch and mesarch in the dictyomeristeles[2]. In a few cases two or three xylem-elements (Pl. XXIII, Fig. 22, *mx.'*) were found to the inside of the protoxylem,

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[1] Mangin, Étude historique et critique sur la présence des composés pectiques dans les tissus des végétaux, Journ. de Bot., v. 1891, vi. 1892.

[2] Shove, loc. cit., p. 513.

so that the protoxylem becomes mesarch. Figs. 20, 21 and 22 show the structure of the leaf-meristeles in *Marattia attenuata*, *Kaulfussia aesculifolia* and *Danaea alata* respectively. These figures show that the structure of the meristeles is practically identical in the different genera. The difference in shape is not distinctive, because in any one species all these forms may be found, not to mention others. Fig. 20 was drawn from a secondary rachis of *M. attenuata* near its base, Fig. 21 from a leaflet-midrib of *Kaulfussia*, and Fig. 22 from the petiole of *Danaea alata*. The most interesting point in connexion with them is the extension of Miss Shove's interesting discovery of the endarch position of the protophloem in the meristeles of the stem of *Angiopteris* to the leaf-meristeles of the Marattiaceae generally. If the leaf-meristeles (in transverse section) of an adult frond be examined, there is very little evidence of the protophloem, but in stained preparations an irregular line of darker walls, especially thick at the angles where certain cells appear to meet, are noticeable near the outer border of the xylem. This layer was early observed but its cause was left for future investigation. In the meantime Miss Shove published her discovery in the stem of *Angiopteris*, and it at once became clear that this line (*pph.* in Figs. 20, 21, 22) was due to the obliterated protophloem. That this was really the case was subsequently proved in *Marattia alata, pph.* Fig. 18. Sections of young fronds of *Angiopteris evecta* and *Marattia cicutaefolia*, made in connexion with the mucilage-canal investigation, show this endarch position of the protophloem very clearly, but it was overlooked at the time.

The structure of the sieve-tubes themselves has been so exhaustively dealt with by Poirault[1], that it is superfluous to do more than quote his results. He found that there are two types of sieve-tubes, the *Cucurbita*-type, with a single plate on the transverse wall, and the vine-type with very

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[1] Georges Poirault, Recherches sur les cryptogames vasculaires, Ann. Sci. Nat., 2e sér., Bot., xvii–xviii, 1893, p. 138 et seq., and p. 192.

oblique end-walls, the number of plates varying with the obliquity of the wall. Besides these plates, isolated pits (*ponctuations*), or small groups of them, occur on the longitudinal walls. The contents of these sieve-tubes is a highly refringent liquid containing a number of refringent sphaerules in suspension, which are specially aggregated in the region of the pits. The wall consists of cellulose. The sieve-plates and pitted areas are actually perforated. No callus occurs.

The exceptional position of the protophloem in this group of Ferns is very remarkable, and it is matter for wonder and speculation why the Marattiaceae alone, so far as is known, possess it. A reason for its position can readily enough be found, viz. the more ready conduction of nitrogenous food-material to the developing xylem on the one hand, and the later formed phloem on the other. Once the advantage of such an arrangement is realized, the puzzle is not why should the Marattiaceae show this peculiarity, but why do not many other Pteridophyta and Spermophyta show it likewise? The internal phloem is developed a good deal later, and it has no protophloem, the protophloem only occurring on the outer face of the xylem and occasionally only just turning the corner at the ends of the xylem-plate[1].

In the Marattiaceae, as in other cases among Ferns, the concentric type of meristele which is characteristic of the frond generally, becomes collateral in the finer veins. In this there is a return to the condition found in the seedling, in which, at any rate in *Danaea simplicifolia*, the first veins have no phloem on the inner or upper side. Fig. 23 illustrates one of the lateral veins of a fair-sized frond of *Danaea simplicifolia*, near its base. The meaning of the xylem being broken up into three parts could not be ascertained. It was thought that it might be associated with the dichotomy of the veins, but the same arrangement occurs above as well as below the fork. Fig. 24 shows still further reduction of the phloem, and at the same time another case of endarch protoxylem. The section was made from a fine vein of *Marattia cicutaefolia*.

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[1] Cf. Shove, loc. cit., p. 513, par. 3.

Fig. 25 illustrates a similar vein in longitudinal section, and proves that the protoxylem is really endarch.

Finally, the occurrence of 'cavity parenchyma' in the leaf may be mentioned. A not particularly good example is shown at *cp.*, Fig. 22. The cavity due to the breaking down of the protoxylem is filled with parenchyma, owing to the increase in size, accompanied by a greater or less amount of division, of the adjacent living cells. It is practically a case of thylosis, only that the process is not accompanied by so much cell-division, and it is not the protoplasts but the cells as a whole that grow into the space. In this instance the internal xylem has been separated from the protoxylem in the process. It is probably not of any physiological importance, being simply a case of non-pathological hernia, so to speak.

The Stem.

In view of the recent work on the stem of *Angiopteris* and *Marattia* there is very little more to be said about its histology. The meristeles, as has already been pointed out by Kühn and others, whether of the dictyostele or the outgoing leaf-traces, are practically identical in structure in all the genera. Although not easily expressed in words, these meristeles have a sufficiently characteristic appearance to enable them to be distinguished from those of most other Pteridophyta. This is partly due to the absence of the endodermis round the outgoing leaf-trace meristeles of the stem, and its apparent[1] absence round the dictyomeristeles themselves. Besides finding it round the meristeles of the seedling, Farmer and Hill were able to demonstrate its presence in the older stem in *Angiopteris*, *Marattia* and *Kaulfussia*[2]. The fact that it is absent round the outgoing leaf-traces, after they have become quite free from the dictyostele, may account for the older observers having overlooked it, because they probably did not distinguish

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[1] The endodermis, even where most marked, as in the seedling-stem, cannot be detected without staining or other micro-chemical means.

[2] Loc. cit., p. 386.

between the outgoing leaf-trace meristeles and those of the dictyostele. Miss Shove, however, was not able to demonstrate the endodermis in relation to the 'stem steles' (dictyomeristeles) of the well-grown plant which she examined.

The arrangement of the strands in the stem, except in the case of *Danaea simplicifolia* seedlings, was not gone into. From the earlier, and especially more recent, work in this line it is now possible to form a good idea of the general arrangement of the vascular system of these plants. Farmer and Hill's models of the arrangements in *Angiopteris* and *Marattia* seedlings[1] mark an epoch in this study and are exceedingly helpful. To sum up then, these plants have a more or less complex adelosiphonic dictyostele, which is developed from a haplostele by the formation of leaf-gaps and a considerable tendency of the meristeles to branch and anastomose.

No further information was gleaned with regard to the apical cell by the work done on *Danaea simplicifolia* seedlings. Farmer and Hill (loc. cit., Pl. XVI, Figs. 14 and 15) seem to have got satisfactory evidence that in the seedlings of *Angiopteris* there is a single apical cell, and the writer came to the same conclusion with regard to the embryo of *Danaea simplicifolia*. But there is still room for further work in this direction. Farmer himself[2] and Bower[3] have both supported the oligocellular view. This is one of those questions to which it is very difficult to get a *definite* answer, perhaps because there is none, on account of the structures being still in a state of flux, so to speak.

The Root.

There is little variation in the root-structure throughout the group. Miss Shove, in her recent paper, has figured the

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[1] Loc. cit., Plates XVI and XVII.

[2] J. B. Farmer, On the Embryogeny of *Angiopteris evecta*, Ann. of Bot., vi, p. 267.

[3] Bower, Comparative examination of the meristems of Ferns, Ann. Bot. iii, pp. 324, 325.

polyarch actinostele of the aerial roots of *Angiopteris.* The subterranean roots only differ in the smaller number of the alternating groups of xylem and phloem, and slightly in texture of the cortex. The structure of the oligarch central cylinder of *Angiopteris* is practically identical with that of the fossil genus *Psaronius*, which is considered to have Marattiacean affinities[1]. It is unnecessary here to go into the structure of the actinostele of these plants since it has been so recently illustrated and described, nor is it desirable to give details of the varying number of the alternating protoxylem and phloem groups in the different genera. There remains, therefore, only to be mentioned one or two slight anatomical differences, which are of more or less diagnostic value. As noted by Harting, in the celebrated de Vriese and Harting monograph, there are very thick-walled sclerotic cells sparingly distributed in the cortex of the subterranean roots, and this seems to be generically characteristic. In *Danaea* Kühn found a sclerenchymatous pith[2] in the various species examined by him, but curiously enough a few specimens of *Danaea alata*, Sm., did not have it. The thick-walled fibres constituting this pith are differentiated early (cf. Fig. 26, Pl. XXIII). *Danaea* also has a continuous ring of sclerenchyma fibres two or three cells thick lying a few cell-layers below the epidermis. The protoxylem may abut directly on the endodermis in the older as well as in the primary and earlier cauline roots. In the figure this is seen to be the case with the protoxylem adjacent to the endodermal cell marked *en*.

In the article *Marattiaceae* of Engler and Prantl's Natürlichen Pflanzenfamilien, the development of the tracheae of the roots is said to be centrifugal[3]. After this was noticed there was no time to go into the matter practically, but the order of lignification of the tracheids is undoubtedly from without

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[1] Cf. D. H. Scott, Studies in Fossil Botany, p. 268 et seq., and Farmer and Hill, loc. cit., p. 268 et seq.

[2] R. Kühn, Ueber den anatomischen Bau von *Danaea*, Flora, 1890.

[3] Loc. cit., p. 430.

inwards, or centripetal (cf. Fig. 26). Moreover, it is difficult to understand what is meant by the statement that the tracheae are simultaneously developed in a quadri-radiate manner in the centre, and that subsequently smaller thick-walled tracheae are added partly in secondary rays[1]. There can be no question of a constantly quadri-radiate central differentiation, because all types of root from the diarch to the polyarch are formed in the course of the development of the seedling to the full-grown plant. The writer observed nothing in the many roots examined, both young and old, which suggested anything different from the normal development of a root central-cylinder, or actinostele.

Mucilage Canals.

The lysigenous view of the development of these structures has again found strong support, for Farmer and Hill[2] throw in the weight of their opinion in its favour.

The writer advocated the schizogenous view as a result of his examination of the development of those structures in the root and frond of species of *Marattia* and root of *Danaea simplicifolia*. A careful re-examination of the preparations originally made seems to the writer to still justify his belief in the schizogenous *origin* of these structures, but the sections were hand-cut, and there is always the risk that something may have dropped out. On the other hand, microtome-series made from material imbedded in paraffin and cut by the 'rocker' are not quite satisfactory, because the sudden impact on the knife-edge breaks the epithelial walls, and frequently displaces the cell-contents. It seems to the writer that the only means of satisfactorily settling this question is to imbed in celloidin and cut with a sliding microtome.

REVIEW OF TERMINOLOGY IN RELATION TO MORPHOLOGY.

As indicated in the introduction on terminology, certain of

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[1] 'Die primären Gefässe werden in Form eines Vierstrahlers im Centrum gleichzeitig angelegt, später schliessen sich daran dickwandigere, kleinere Gefässe, teilweise in secundären Strahlen.'

[2] Loc. cit., p. 390.

the older and more recent conceptions of the morphological importance of certain histological layers are being abandoned. Farmer and Hill point this out with regard to the endodermis and histogenetic layers, and Pitard[1] expresses himself as follows with regard to the pericycle: 'Cette notion du péricycle apparaît donc en définitive comme inadéquate aux faits et sans utilité pour l'expression.' The writer is quite in accord with these views, and thinks these layers should be, in many cases, abandoned as morphological criteria.

The new terms put forward tentatively have been based almost entirely on the idea of the stele as originally set forth by Van Tieghem. In view of the writer's belief in the unimportance of the endodermis, pericycle, &c. as morphological criteria, it is somewhat doubtful if the method adopted was a wise one. It would perhaps have been better to abandon the stelar theory altogether, and substitute for it the conception of a connected system of vascular strands on the one hand and non-vascular tissue on the other. At the same time the non-vascular tissue would not be considered as something essentially and fundamentally different from the vascular, for they are both differentiated from the same meristem, and what has become vascular in one case might very well be non-vascular in another or *vice versa*. To take one illustration: in most Dicotyledons the pith is simple with no vascular strands, but in some cases there are what are called 'medullary bundles.' Therefore the pith in Dicotyledons may be said to be potentially vascular. It is undesirable to apply the term stele to the suggested conception of the vascular system, but perhaps another and suitable term may be found which could be combined with the prefixes already used to distinguish the different stelar systems. They could further be appropriately dealt with as follows:—The vascular system of typical Dicotyledons would be described as *cyclodesmic*, Monocotyledons as *atactodesmic*, the vascular network of Ferns as *dictyodesmic*, and so on. These terms might even

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[1] Pitard, 'Le péricycle et la taxonomie: valeur anatomique du péricycle,' Actes de la Société Linnéenne de Bordeaux, sér. vi, t. vi, 1901, p. 43-61).

be used at the present time; in fact, 'mondesmic' has already been used by Scott in his 'Studies in Fossil Botany'[1] in the sense of possessing one strand. It would unnecessarily expand this paper to discuss the various additions to botanical knowledge which are bringing about this change of attitude. Perhaps the time is hardly yet ripe, but the day does not now seem far off when the three histogenetic layers, as well as cortex, pith, endodermis, pericycle, &c., will have lost to a great extent their present morphological connotation and be used simply as convenient descriptive terms in certain cases.

RÉSUMÉ AND CONCLUSIONS.

Development of the Vascular System of Danaea. The vascular system is developed from a simple type of stele, a haplostele. The haplostele does not pass through a medullated stage, but becomes crescentic after the successive departure of a variable number of leaf-traces. When this stage is reached the next leaf-trace passes off from the convexity of the crescent, thus causing a distinct leaf-gap. Two meristeles are left behind with what is usually considered extrastelar tissue between them. The crescent gap is closed, a leaf-trace is given off, the gap again closed, &c. By the repetition of this process, followed by branching, anastomosis, and increase in number of leaf-trace meristeles, at length a network of strands or the dictyostele is formed. At one level or another a transitory solenostelic stage intervenes owing to the closure of one leaf-gap before the next one is opened. Also at no very definite level a strand arises as a branch from the concavity of the crescent, pursues an upward spiral course anastomozing with the large gamomeristele formed to close the successive leaf-gaps, so to speak, and at the same time give rise to the root. This central commissural column, or central strand, later gives off two branches which however reunite on their upward course. In this way then the irregular stelar network of *Danaea simplicifolia* is built up, and is shortly expressed by the statement that it is an *adelosiphonic dictyo-*

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[1] l. c., p. 303.

stele developed from a non-medullated *haplostele* by an early formation of overlapping leaf-gaps accompanied by branching and anastomozing of the meristeles.

The only point in which *Danaea* differs essentially from *Angiopteris* and *Marattia* is in not passing through a medullated stage before the commencement of the formation of the dictyostele. There can be little doubt that *Kaulfussia* and *Archangiopteris* pass through a similar stage, and in a very similar manner.

Comparative Anatomy of the Marattiaceae. The result of the study of the comparative anatomy is broadly that there is a great amount of uniformity in internal structure. They are all adelosiphonous with a greater or less tendency to dorsiventrality in *Angiopteris*, *Marattia* and *Danaea*. In the last-named it is distinctly marked and practically complete in *Kaulfussia* (Kühn, and Farmer and Hill). In the young sporophyte of the three first-named the symmetry is radial.

The meristeles of the stem and leaf are practically identical in structure. The veins of the first leaf are collateral, as also the ultimate ramifications of the veins of the young and adult fronds.

The protoxylem seems to be normally endarch and mesarch in the stem, endarch in the frond. A very imperfect mesarch condition also quite exceptionally occurs in the larger leaf meristeles, and occasionally in the fine veins.

The root-structure, as already stated, is practically identical throughout the family. The aerial roots of *Angiopteris* and *Marattia* are polyarch and their subterranean portions oligarch. In *Danaea alata*, and presumably many others, the adult roots are polyarch. In *Angiopteris* there are very thick sclerotic cells sparingly present in the cortex and there is a mid-cortical ring of sclerenchyma in *Danaea*. *Danaea* also has a medullary strand of sclerenchyma fibres, which differentiate very early. The roots of *Archangiopteris* and *Kaulfussia* were not examined, but the latter are described by Kühn and are tetrarch to pentarch, but not otherwise essentially different.

For a good *résumé* of the chief literature and an excellent general account of the *Marattiaceae* the reader is referred to the article in Engler and Prantl's 'Natürlichen Pflanzenfamilien.'

Other Histological Details. Certain of these were found to be of some use for generic and specific distinction, e. g. structure of sclerenchyma, but only to a limited extent.

Finally the writer cannot express too strongly his great indebtedness to Dr. D. H. Scott for his constant interest, encouragement and advice during the course of the investigation. Mr. L. A. Boodle also gave much assistance by helpful discussion and references to literature.

EXPLANATION OF FIGURES IN PLATES XXII AND XXIII.

Illustrating Mr. Brebner's Paper on the Anatomy of *Danaea* and other Marattiaceae.

Abbreviations.

alb. albuminous cell (?); *col.* collenchyma; *cp.* cavity parenchyma; *en.* endodermis; *en.'* internal endodermis; *lt.* leaf-trace; *mc.* mucilage canal; *ms.* meristele; *mx.* xylem; *mx.'* xylem formed to inside of protoxylem; *pa.* parenchyma; *px.* pericycle; *ph.* phloem; *pph.* protophloem.

Figs. 1–10 and 19 are from microtome series of *Danaea simplicifolia* seedlings. The radial walls of the endodermis are indicated conventionally.

Figs. 1–4. From very young seedling showing formation of leaf-trace. (× 242.)

Fig. 5. Section from the same seedling showing departure of the first two leaf-trace meristeles and the approach of a root. (× 114.)

Fig. 6. Section from a seedling showing abnormal preparation for the departure of several leaf-traces almost simultaneously. (× 212.)

Fig. 7. Section from the stem of a seedling with an abnormally long internode near the base. It clearly shows the endodermis round the stele and leaf-trace meristele. The stele is preparing for the departure of the next leaf-trace. (× 182.)

Fig. 8. Section from the same seedling. It shows an almost solenostelic stage owing to the junction of a root. (× 242.)

Figs. 9 and 10. Sections from the same seedling showing departure of the next leaf-trace. (× 242.)

Figs. 11 and 12. *Marattia fraxinea.* Primary pulvinus and petiole in transverse section. (× 5.)

Fig. 13. *Marattia fraxinea.* Section of petiole just below first pair of pinnae. (× 5.)

Fig. 14. *Marattia fraxinea.* Pulvinus of secondary axis on one side. (× 5.)

Fig. 15. *Marattia fraxinea.* Pulvinus of secondary axis on the other side. (× 5.)

Figs. 16 and 17. *Marattia fraxinea.* Secondary rachis near the apex. (× 5.)

Fig. 18. *Marattia alata.* Transverse section of meristele of developing petiole to show the protophloem, *pph.* (× 318.)

Fig. 19. *Danaea simplicifolia.* Solenostelic stage from the same series as figs. 7–10. (× 238.)

Fig. 20. *Marattia attenuata.* Transverse section of meristele from secondary rachis near base. (× 131.)

Fig. 21. *Kaulfussia aesculifolia.* Transverse section of meristele from leaflet midrib. (× 131.)

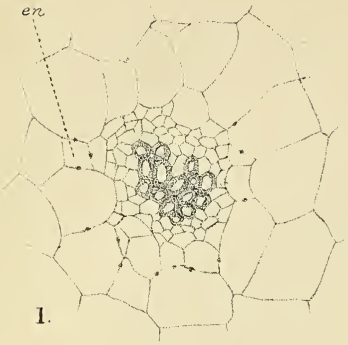
Fig. 22. *Danaea alata.* Transverse section of petiolar meristele. (× 131.)

Fig. 23. *Danaea simplicifolia.* Transverse section of lateral vein near base. (× 200.)

Fig. 24. *Marattia cicutaefolia.* Transverse section of lamina showing fine collateral vein with endarch protoxylem. (× 200.)

Fig. 25. *Marattia cicutaefolia.* Longitudinal section of similar vein. (× 200.)

Fig. 26. *Danaea simplicifolia.* Transverse section of incompletely differentiated actinostele of young root. (× 200.)



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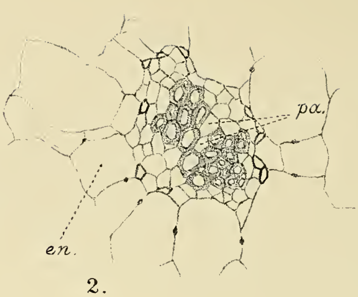

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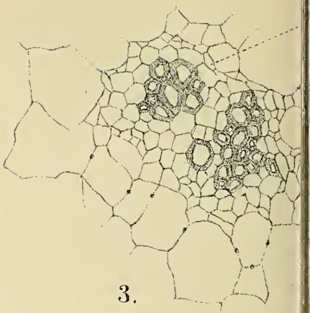

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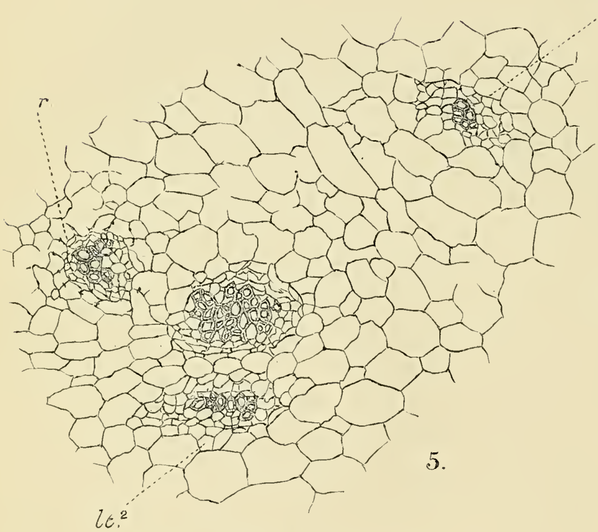

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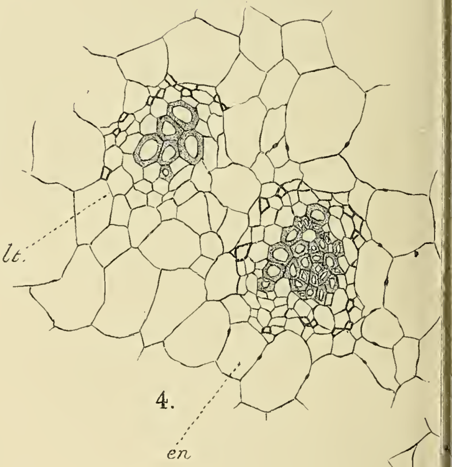

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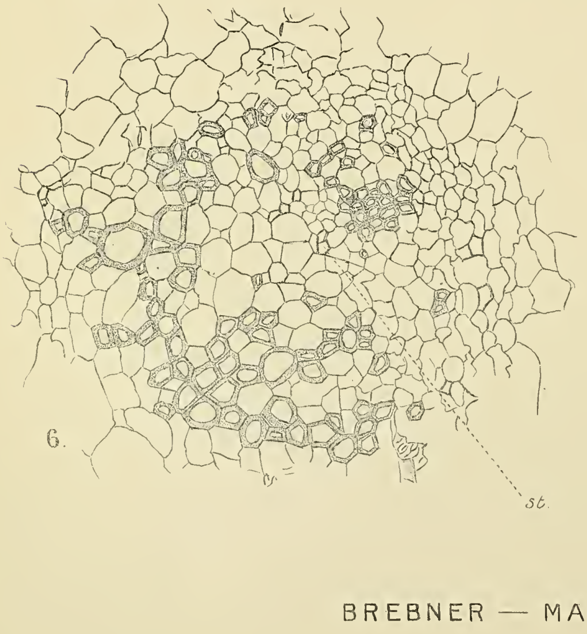

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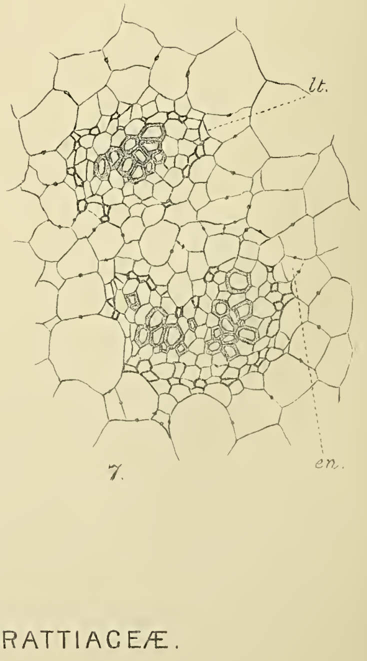

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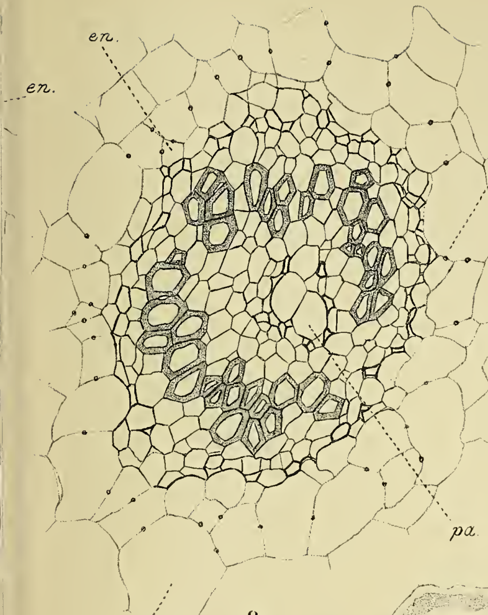

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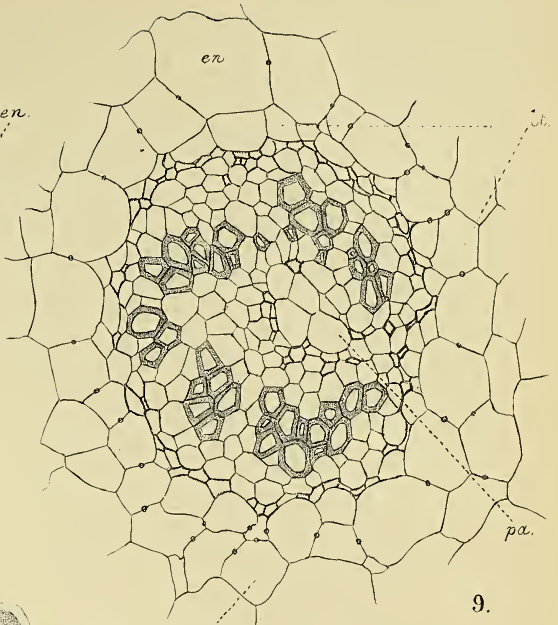

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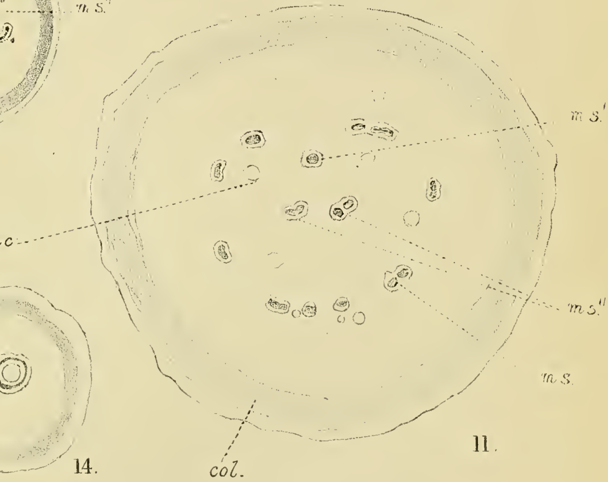

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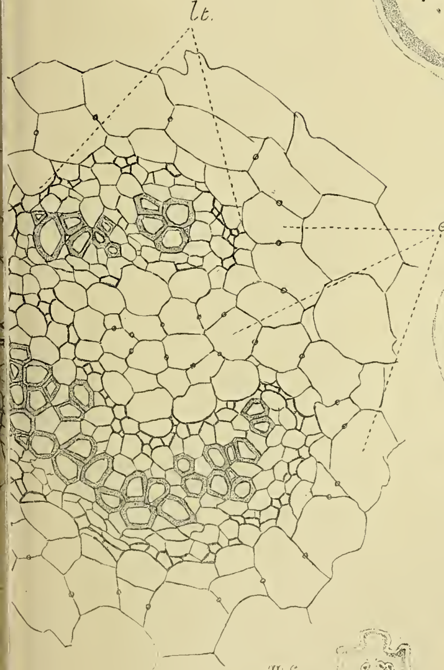

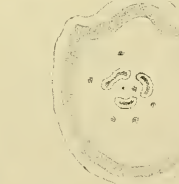

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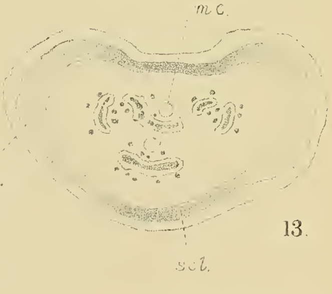

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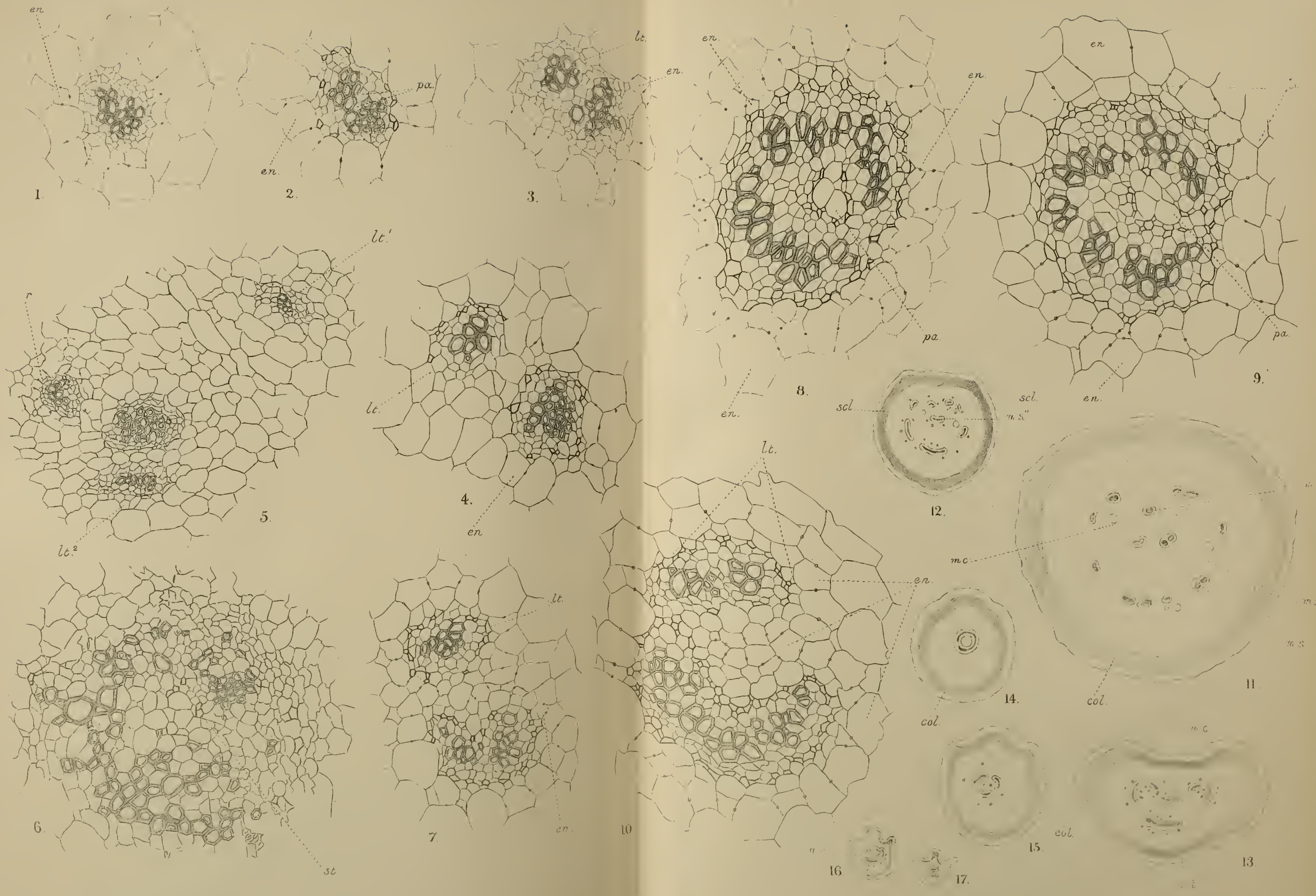

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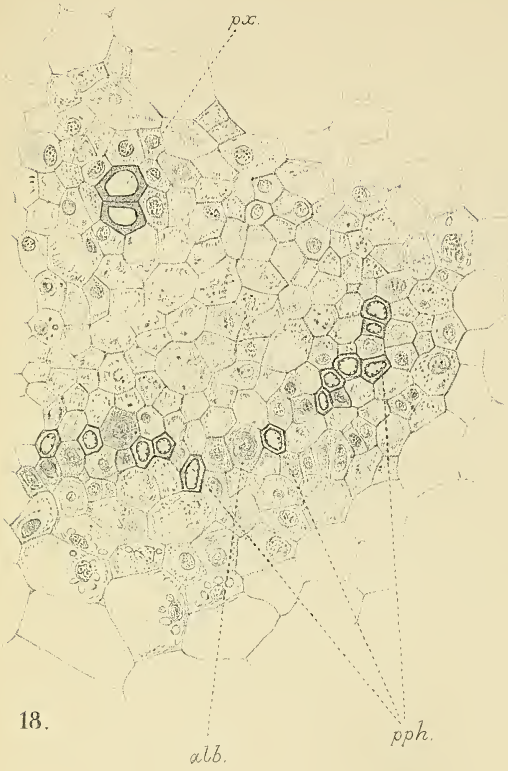

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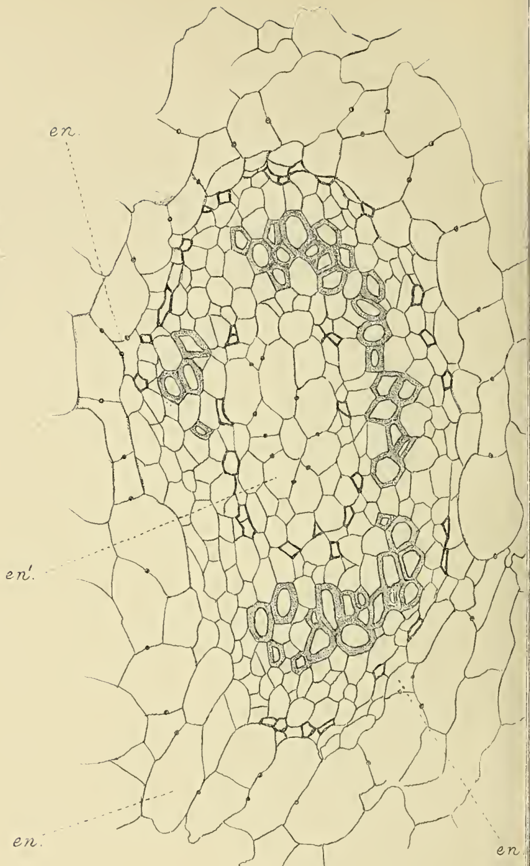

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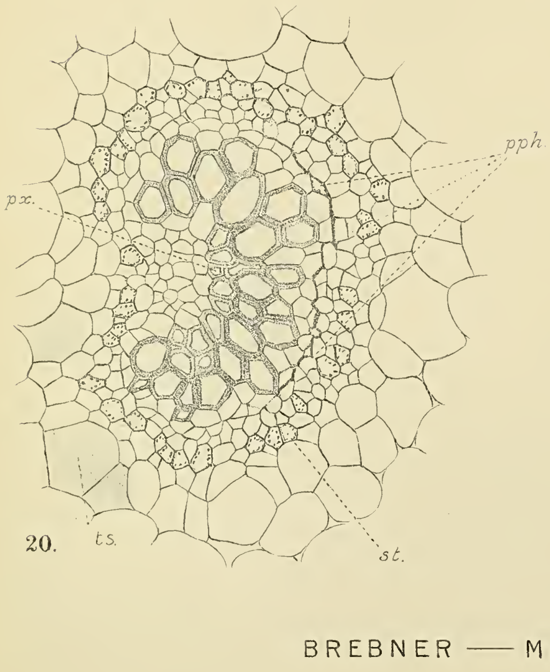

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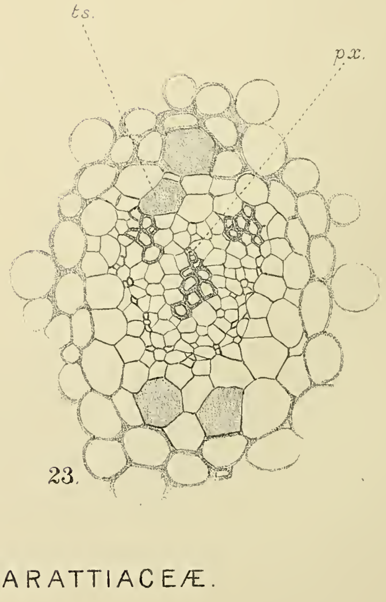

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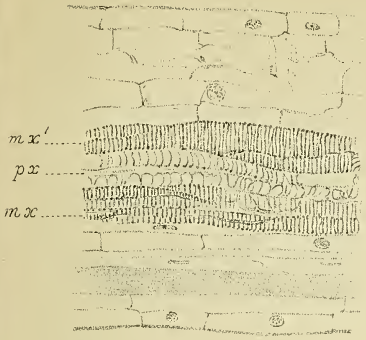

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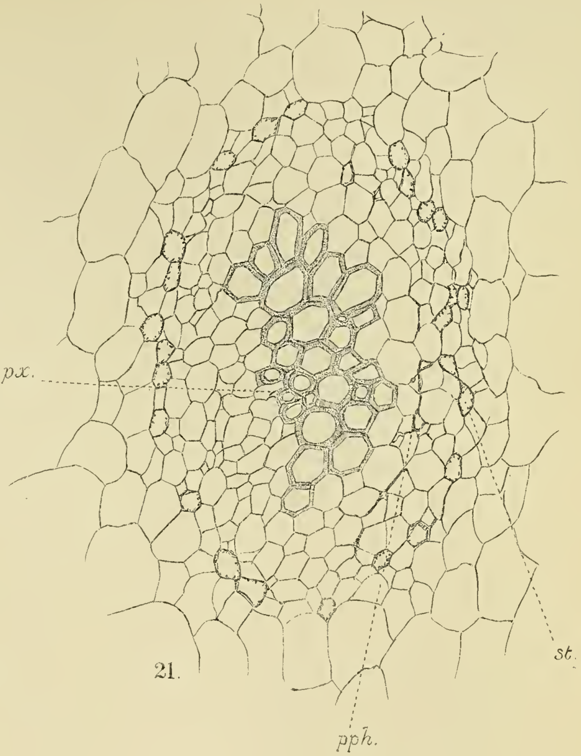

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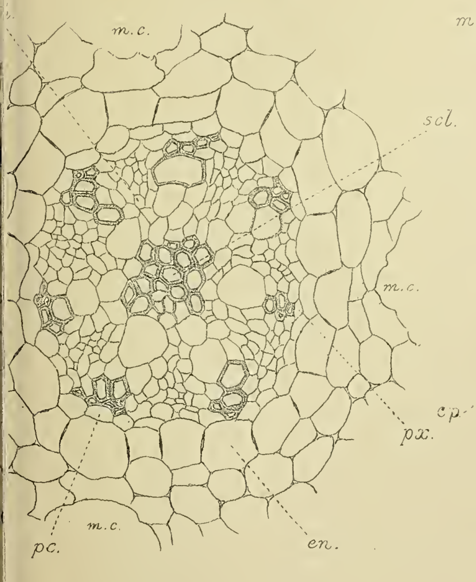

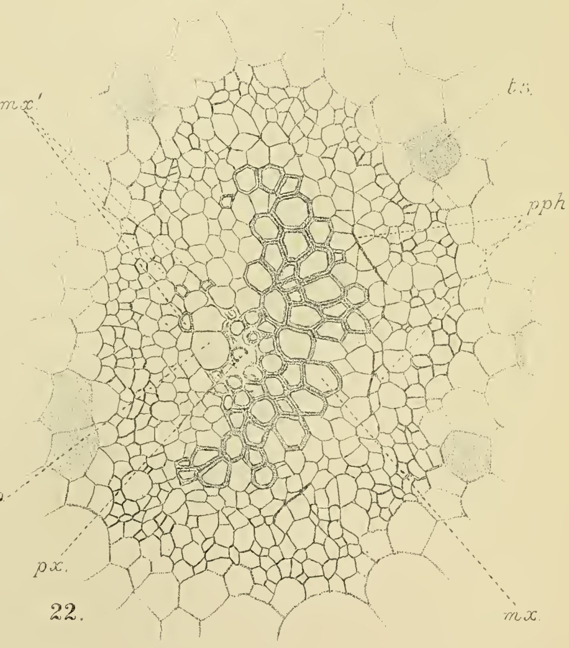

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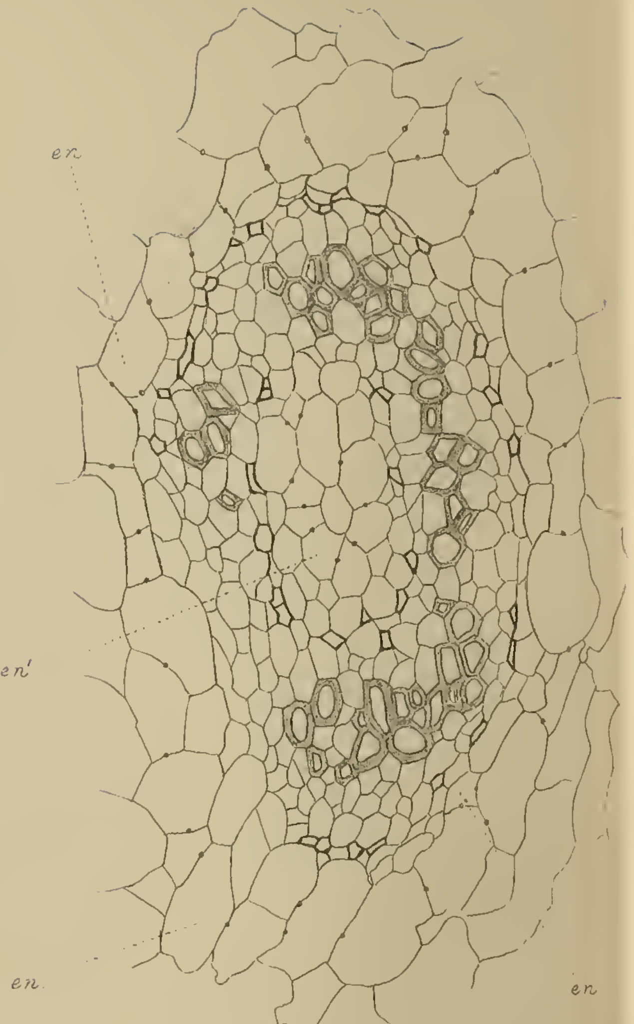

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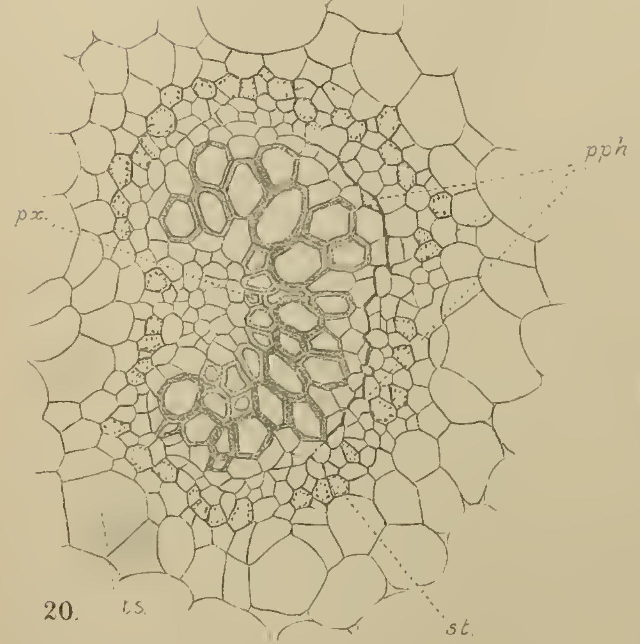

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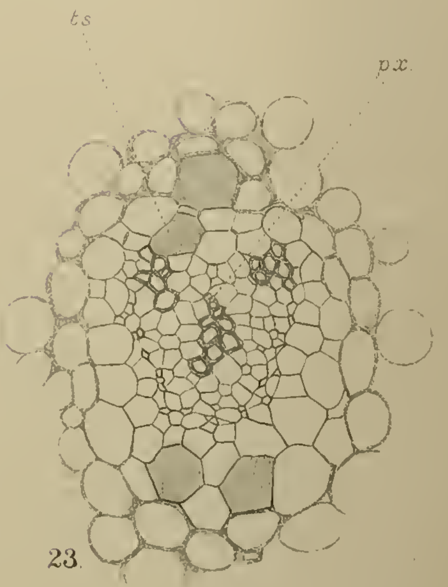

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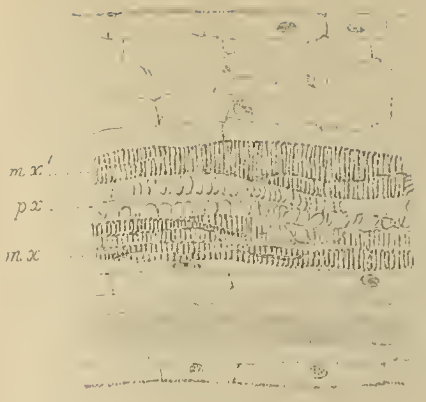

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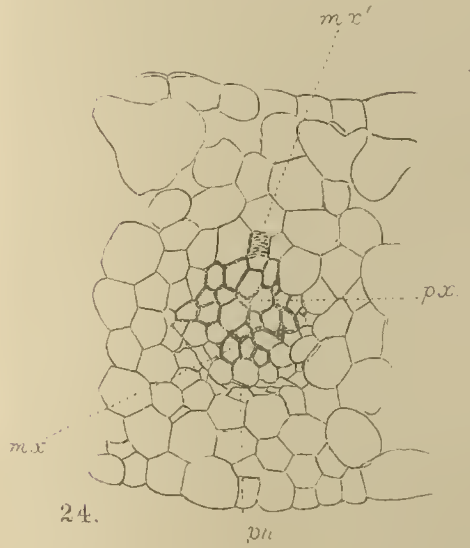

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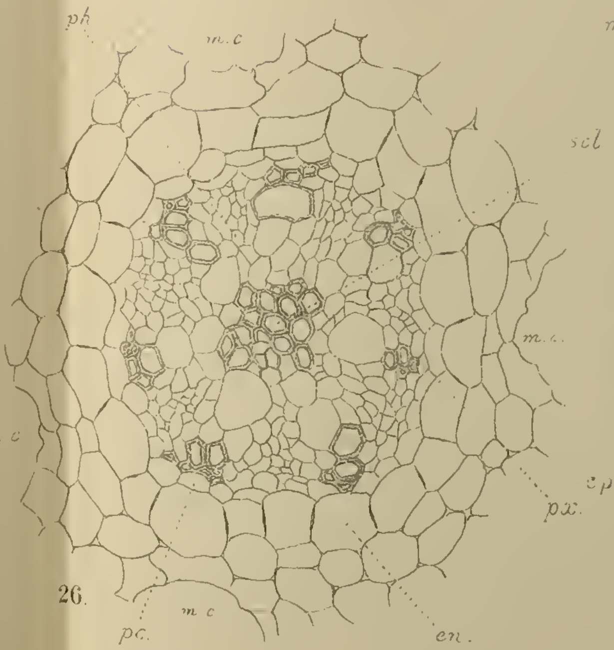

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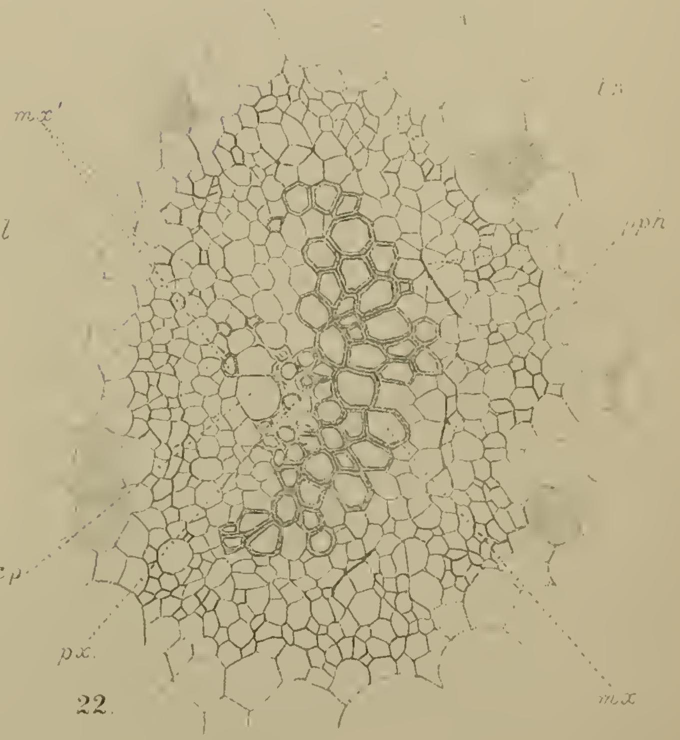

22.

BREBNER — MARATTIACEÆ.

University Press, Oxford.

Morphological Notes.

BY

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Director, Royal Botanic Gardens, Kew.

With Plates XXIV and XXV, and a Figure in the Text.

VIII. ON POLYCOTYLEDONY.

IT is the object of these notes as much to suggest problems as to solve them. In the present case I propose to tell a story of which I do not quite see to the bottom. I impose no restrictions on any one disposed to make it a subject of speculation.

My friend Professor Bayley Balfour, in the very suggestive address which he delivered from the chair of Section K. at the Glasgow Meeting of the British Association, gave a theory of the Dicotyledonous Embryo, the main points of which I will quote:—

'We ought, I think, to look upon the embryo as a protocorm of embryonic tissue adapted to a seed-life. . . . Confining ourselves to the general case, the axial portion of the protocorm of the Dicotyledon, the hypocotyl, bears a pair of lateral outgrowths, the cotyledons, and terminates in the plumular bud and in the primary root respectively. The cotyledons are its suctorial organs, and the hypocotyl does

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the work of rupturing the seed and placing the plumular bud and root by a rapid elongation which commonly brings the plumular bud above ground, protected it may be by the cotyledons. These latter may then become the first assimilating organs unlike or like to the epicotylar leaves[1].'

This, though a guarded statement, appears to imply that the cotyledons are more or less organs *sui generis*, and not homologous with ordinary or epicotylar leaves. It brought to my recollection some observations which I made some years ago, and which it now seems worth while to put on record. It is well known that the Sycomore (*Acer Pseudoplatanus*) reproduces itself spontaneously from seed with great readiness. This was the case with a tree at Kew which was ultimately, for unavoidable reasons, cut down. A notable proportion of the seedlings of this tree came up with three cotyledons. The circumstance is not, however, unusual, and similar cases are discussed in Duchartre's classical *Mémoire sur les Embryons qui ont été décrits comme Polycotyles* in the 'Annales des Sciences naturelles' (3^{e} sér., x, pp. 210–11). I quote his account:—

'*Embryons à cotylédons accidentellement partagés.*

'Sur plusieurs points des environs de Paris, notamment à Meudon et Bellevue, on remarque au printemps, le long des allées, dans le voisinage des jardins et des parcs, une quantité considérable de germinations des Érables Plane [*Acer platanoides*] et Sycomore. Leurs grandes feuilles séminales, lancéolées-oblongues, entières, y forment quelquefois une sorte de gazon: or, parmi ces nombreuses germinations il est facile de trouver tous les degrés de division médiane des feuilles séminales, depuis une simple échancrure jusqu'à une partition tellement profonde, qu'elle ferait croire, dans certains cas, à l'existence de trois cotylédons distincts et séparés. Je me borne à figurer ici deux de ces germinations, choisies entre beaucoup d'autres; dont l'une présente un

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[1] Nature, lxiv, pp. 560, 561.

cotylédon bifide, tandis que l'autre en montre un profondément biparti. Dans celle-ci, les deux lobes cotylédonaires ressemblent assez, de grandeur et de configuration générale, au cotylédon entier, pour que chacun d'eux pût facilement être regardé comme un cotylédon distinct et séparé. Mais si l'on observe que la fente qui les sépare descend un peu moins profondément que celle qui existe entre les deux vrais cotylédons; si, de plus, on fait attention à la situation des deux petites feuilles primordiales déjà développées, qui alternent avec le cotylédon biparti comme avec celui qui est resté entier, on ne pourra conserver le moindre doute sur le phénomène de division qui a valu à cette germination son apparente polycotylédonie.'

Nothing apparently could be clearer than this explanation, but unfortunately it does not meet the facts as they presented themselves at Kew. In Pl. XXIV, Fig. 2, I have figured a seedling with three perfectly distinct and normal cotyledons and three equally normal young leaves developed from the plumule. It is difficult to see how such a case is to be reduced to the ordinary type by any theory of bipartition. A number of such anomalous seedlings were carefully taken up, potted and grown on. Pl. XXV, Fig. 4, shows the result at the end of the second year. It will be seen that I obtained a young sycomore with ternary instead of opposite leaves, and I was in hopes that I had secured a new seminal variation which would be constant. These hopes were, however, frustrated, as in the third and following year the seedlings reverted to the ordinary type with opposite leaves.

Such cases of plants with opposite varying with whorled leaves are not uncommon, though in some species it is rarer than in others. Of the former *Stachys palustris*, in which I have met with three leaves in a whorl, is an example. The fact was not overlooked by Linnaeus, who observes:—'*Opposita folia* saepe evadunt Terna, seu Quaterna, et tum ex caule Quadrangulari fit caulis Polygonus' (Philosophia Botanica, 241).

I mentioned the matter in conversation to the late Professor

Decaisne, and he remarked that he thought there was a tendency in *Acer* to a ternary distribution of parts, reminding me that the sycomore occasionally develops a third samara in its fruit. This is true, but in the Kew Museum there is a series of fruits of the common maple (*Acer campestre*) in which the number of samaras varies from two to eight: it is therefore apparently fluctuating.

In Pl. XXIV, Fig. 1, I have illustrated a case similar to those which Duchartre studied. In Fig. 3 I have shown one, which he apparently did not meet with, in which three cotyledons are followed by a pair of opposite leaves, one of which is bipartite. In the former, according to Duchartre's view, the embryo started with a pair of cotyledons, one of which subsequently branched. This, however, is *a priori* an improbable supposition, as cotyledons, unlike leaves, are generally simple and, except in the somewhat rare cases now under discussion, rarely show any disposition to be otherwise.

Masters (Vegetable Teratology, p. 370) gives several instances of tricotyledonous embryos, to which I may add one in the oak for which I am indebted to a former pupil, Mr. G. Cross. Masters quotes Reinsch for a seedling beech 'associated with a union of the margins of two out of the three cotyledons, and of those of two out of the three leaves next adjacent.' Masters thinks with Duchartre that 'some of these cases may be accounted for by chorisis or by a cleavage of the original cotyledons.'

I arrive, however, at the conclusion that the simplest explanation is, that in all the cases now described, the embryo is provided with three instead of two primordial lateral outgrowths, and that these either develop completely into three normal cotyledons or that two of them sooner or later coalesce into one which is more or less deeply bifid. If this explanation is true of cotyledons it must equally apply to the similar phenomena exhibited by the epicotylar leaves.

Professor Bayley Balfour looks upon the cotyledons as 'suctorial organs,' and in cases where an endosperm is present this is no doubt true. But an inspection of the large series

Fig. 30.

of illustrations drawn from all parts of the vegetable kingdom accumulated by Lord Avebury in his work on 'Seedlings' will show that in an immense proportion of cases, cotyledons are foliaceous. Nor can they be regarded as suctorial in cases such as are present in the Leguminosae, where they have become mere reservoirs of accumulated food-material destined for the future nutriment of the young plant.

I confess that all the evidence seems to me to point to the fact that cotyledons, whether suctorial, store-organs or foliaceous, must still be regarded as foliar organs. Lord Avebury (Vol. I, pp. 9, 10) cites the opinion of Klebs, who observes that 'on the whole the forms of cotyledons are much simpler than those of leaves, and . . . that while in some cases perhaps, like the first leaves, they retain the form which characterized the species in bygone ages, we may rather, as a more generally applicable explanation, apply to them the suggestion of Goebel with reference to stipules, and regard them as simplified by arrest.' Lord Avebury adds that another suggestion has been that cotyledons are 'a survival of the universal foliage of deciduous trees in olden geological days, ere time had differentiated them into their present varied forms.'

That cotyledons preserve a more ancient and primitive type of foliage is in accordance with the general facts of embryology. The cotyledons have their own battle to fight, but it is not that of the adult plant, and adaptations suitable for the more strenuous struggle would be superfluous in the simpler conflict. This consideration is strengthened by the case reproduced in Fig 30 of a young seedling of *Libocedrus macrolepis*. In this after a time there is a complete change in the form and disposition of the foliar organs. The primitive leaves, which are not very different to the cotyledons with which they are serially continuous, no doubt represent a generalized and unmodified type of foliage.

An analogous but distinguishable phenomenon is described by Asa Gray in the case of the common pea (Botanical Text-book, p. 19):—

'The plumule . . . usually rises as a stout stem of several internodes lengthening almost simultaneously, or at least the upper strongly developing long before the latter have finished their growth; and the latter are practically leafless, having only small and scale-like and useless rudiments of leaves. . . . The abortion of the earliest leaves of the plumule is in correlation with the hypogaeous situation of the cotyledons throughout the germination.'

Finally I may suggest that the anatomy of cotyledons affords a promising field of investigation, at present almost wholly unworked, which may throw much light on their history.

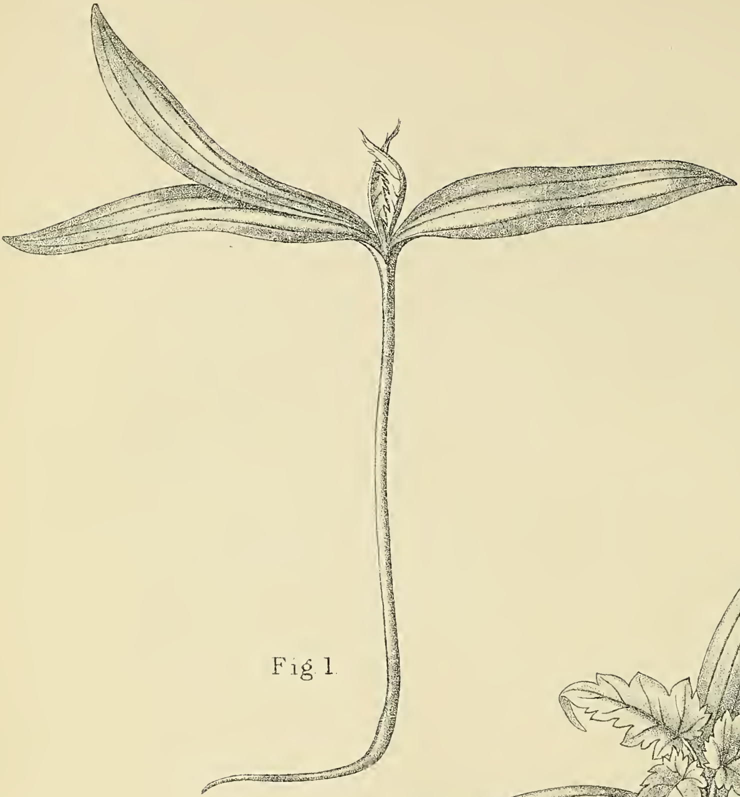

Fig. 1.

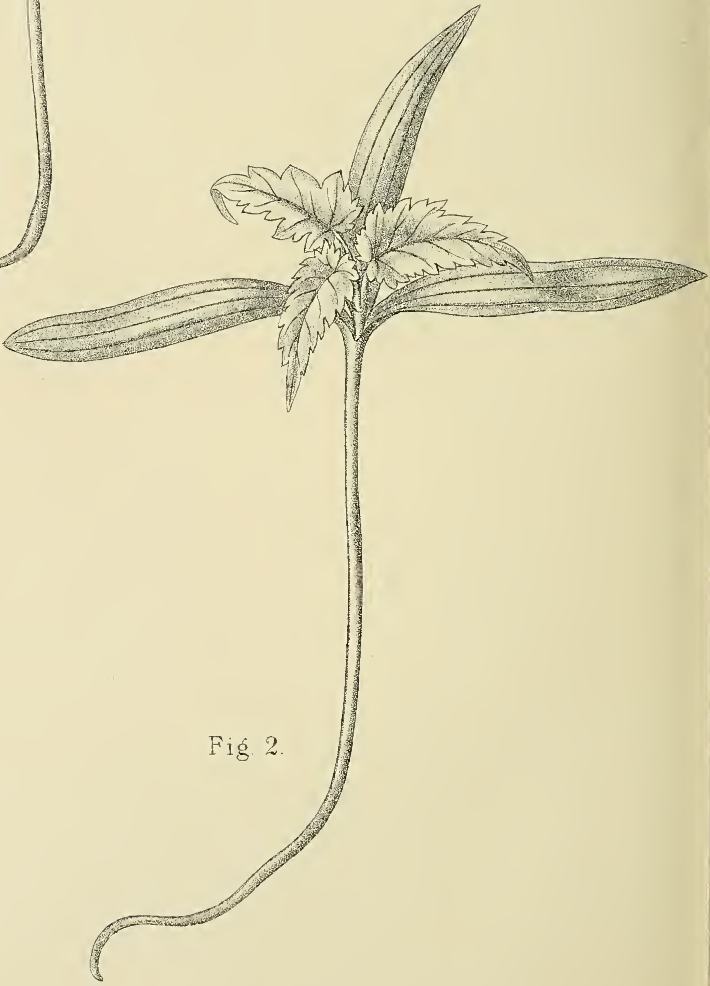

Fig. 2.

H. T. D. del.

THISELTON-DYER.— ACER PSEUDO-PLATANUS.

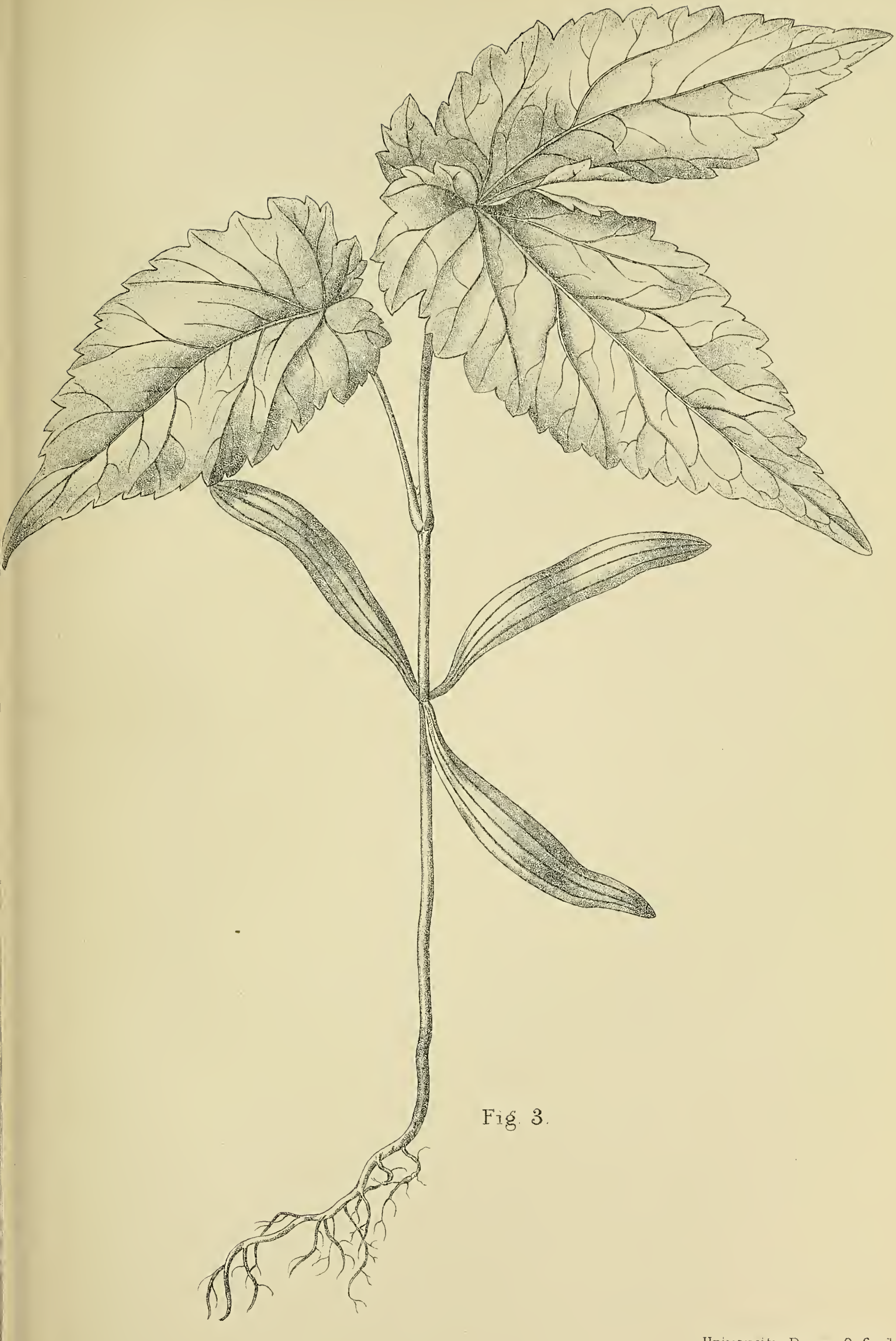

Fig. 3.

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Fig. 4.

H. T. D. del.

University Press, Oxford.

THISELTON-DYER.— ACER PSEUDO-PLATANUS.

The Vascular Branches of Stigmarian Rootlets.

BY

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With Plate XXVI.

IN his 'Cours de botanique fossile [1],' and also in his 'Étude sur les Stigmaria [2]' in the Annales des Sciences géologiques, Renault has described and figured rootlets of *Stigmaria* from the neighbourhood of Manchester, in which a very delicate vascular branch was given off from the stele. Such branches were given off according to Renault from each of the three protoxylem-groups of what he considered the triarch rootlet of *Stigmaria* and went to supply lateral rootlets (*radicelles*). The importance of this observation will be recognized by the following conclusion which Renault drew from it: 'Ce caractère important éloigne toute idée de rapprochement entre les organes qui nous occupent maintenant et les racines des plantes cryptogames.'

Williamson ('87) in his criticism of this statement [3] points out that the rootlets of *Stigmaria* branch invariably by dichotomy, and states that he has seen nothing like the branching figured by Renault in any of the innumerable rootlets in his cabinet.

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[1] Renault, B., Cours de botanique fossile, Pl. XX, Fig. 4.

[2] Renault, B., Annales des sciences géologiques, 1882, Pl. II, Fig. 8.

[3] Williamson, W. C. ('87), p. 32, note 1.

[Annals of Botany, Vol. XVI. No. LXIII. September, 1902.]

Solms-Laubach ('91) in his description of the rootlets of *Stigmaria*, in which he reproduces Renault's figure[1], expresses some doubt as to the existence of such tracheal branches from the central cylinder of the rootlets, and does not support Renault's view as to their mode of branching.

In a previous publication (Weiss, 1902) I have pointed out that the vascular branches described by Renault do actually occur in Stigmarian rootlets, and have figured such a branch in a rootlet[2], which was characterized by its well-preserved middle cortex. I was unable in the case of that specimen to do more than confirm Renault's observation, which up to that time had not met with confirmation. On the publication of my paper, Dr. D. H. Scott kindly sent me some notes which he had made on Stigmarian rootlets in preparation for his 'Studies in Fossil Botany.' From these it appears that Dr. Scott had no doubt as to the correctness of Renault's observation, as he himself had repeatedly come across such delicate vascular branches, and had 'been able in some cases to trace them to the cortex.' He was, however, unable to accept Renault's conclusion that they supplied lateral rootlets.

Since my first observation of these vascular branches I have examined a large number of Stigmarian rootlets from the Cash, Hick, and Wild Collections of the Manchester Museum at the Owens College, with the result that I not only found numerous specimens showing such vascular branches, but was able to trace them to their termination in the cortex, as I mentioned at the end of my earlier paper ('02). From the relatively large number of rootlets, I have chosen four to illustrate the structure, the origin, the course and termination of these vascular strands. Figures 1 and 2 (Pl. XXVI) are taken from rootlets of a different type from that which I have previously figured ('02), but of the same type as the one represented by Renault ('82). The middle cortex appears in these to be entirely absent, as is the case, indeed, in the majority of

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[1] Solms-Laubach ('91), Fig. 35, p. 27.

[2] Slide, No. 109 in the Hick Collection in the Manchester Museum, Owens College.

Stigmarian rootlets. In the rootlet represented in Fig. 1[1], as in some other rootlets which are cut longitudinally, there can be seen running obliquely between the parenchymatous sheath of the inner cortex (*i. c.*), which surrounds the stele, and the outer cortex (*o. c.*) a delicate strand of tracheids (*tr.*) surrounded by a layer of parenchymatous cells. Though its origin from the central stele is not seen, there can, I think, be no doubt as to the identity of this delicate strand with the vascular branch described by Renault. In confirmation of this view, it may be mentioned that the position of this strand of tracheids is on that side of the rootlet which lies nearest to the protoxylem. Hence it would not be wrong to assume that it was probably connected with the protoxylem elements in the same way as in the rootlet figured by Renault.

Another point of agreement with Renault's figure is the small process (*p.*) passing off from the parenchymatous sheath which would seem to have connected it with other parenchymatous cells of a delicate character, forming lacunar or trabecular tissue, remnants of which can be seen near the upper end of this strand, as also in Renault's figure.

For all these reasons we are I think justified in assuming that the isolated vascular branch seen in Fig. 1 is similar to that which Renault figures as connected with the protoxylem of the stele, and which in a very different type of rootlet I also found connected with the protoxylem elements.

Both Renault's figure and my previous one were taken from transverse sections, and the fact that in the latter the vascular branch ran only for a short distance transversely into the middle cortex may be taken to indicate that after leaving the stele its course must have been more or less oblique, a supposition which is borne out by the longitudinal section as represented in Fig. 1.

But while the inner connexion of these vascular branches with the protoxylem of the central cylinder was established by Renault, very little has been known about their termination. Renault, rather naturally, was inclined to regard them

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[1] Hick Collection, No. 107.

as supplying lateral rootlets, but he did not figure the latter, and he stated that owing to the minuteness of these strands, which do not exceed $\frac{1}{10}$ of a millimetre, 'ce n'est donc que dans des cas assez rares que les empreints pourront reproduire les cicatrices laissées par des radicelles.'

Such slender evidence, especially as the Stigmarian rootlets exhibit well-marked dichotomy, justified Williamson's and Solms-Laubach's refusal to accept Renault's conclusions. Dr. Scott, though he has been able to observe these strands, states in his manuscript notes referred to above, with reference to a well-marked strand in one of his preparations (slide, No. 113), that 'there is no sign of branching.' In one of these rootlets he observed 'an oblique strand of xylem running from the stele to the inner edge of the cortex.' And indeed, as we shall see presently, that is as far as the strand generally goes. In the rootlet represented in Fig. 2[1] the termination of a vascular branch in the outer cortex is reproduced. Here the cortex will be seen to contain a number of curiously wide and short tracheids with delicate spiral or reticulate markings, resembling very closely the spirally-marked cells which form the termination of the finest ramifications of the veins in leaves. A characteristic feature of these cortical tracheids is the wide interval between two successive turns of the spiral thickening.

These cells are seen in Fig. 2 at (*a*) on the inner side of the outer cortex. At (*c*) where we obtain a tangential view of this portion of the cortex it will be seen that these cells form a fairly broad patch. At (*b*) the cells become narrower in diameter and somewhat more closely set, and this is evidently the point at which a connexion existed with the vascular strand of fine and closely-marked tracheids running out from the protoxylem group. This connexion is not observable in this section, but I was fortunately able to discover a longitudinal section in which this connexion was preserved.

Fig. 5[2] is a drawing made from a section in which we have not only the connexion of the spiral tracheids of the cortex

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[1] Hick Collection, No. 107.

[2] Cash Collection, No. 401.

with the vascular strand, but also the continuity of the latter with the stele of the rootlet.

This rootlet is unfortunately somewhat compressed, so that the space between the stele and the outer cortex is very much reduced, and the vascular strand is thrown into a fold. It will be seen that in this rootlet the strand on passing out from the protoxylem elements takes a very oblique direction, and would not in transverse section have had the appearance of the vascular strand figured by Renault. In structure, however, it shows the same features, and is surrounded by a sheath of parenchymatous cells, from which trabecular tissue (*trb.*) runs to the parenchyma of the stele. On reaching the outer cortex the vascular branch communicates at first with some closely-set tracheids very similar to those at (*b*) in Fig. 2, and these are in their turn connected with wider spirally-marked tracheids (*sp. tr.*). From a comparison of Figs. 2 and 5 I have no hesitation in considering (*b*) in Fig. 2 as the point of entrance of the vascular strand into the outer cortex of that rootlet. Another feature shown by the longitudinal section represented in Fig. 5 is that the vascular strand seems to have been in some cases continued for a considerable distance beyond its entry into the outer cortex, and connected with several groups of spiral tracheids. Indeed, a branch (*v. br.*) is given off from the vascular strand close to its entry into the outer cortex, and this branch was in all probability connected with another patch of spiral tracheids at some other part of the root. It is difficult to ascertain what was the size and distribution of these patches of spirally-marked cells of the outer cortex. As will be seen from Fig. 2, and as is apparent from other preparations, it was of some breadth. In one longitudinal section, indeed, such cells seem to have extended almost halfway round the root. In other cases, however, as can be seen in Fig. 4, the spiral tracheids extended only a little way on either side of the entrance of the vascular strand. No doubt there was considerable variation in this respect in the different types of rootlets, which belonged probably to different Lepidodendroid plants.

It will be seen that in the two rootlets in which the spirally-marked elements are described in the cortex they are found in the innermost layers of the cortex, and therefore within the very dark cells which are so often found, forming a more or less continuous ring in the outer cortex. It is hardly possible to say whether the darkness of the cell-walls in this layer, which was no doubt due to the cell-walls and not to the contents, marks them out as an impervious or protective sheath; or whether the cell-walls, though differing in constitution, and probably also in thickness, may not have been as readily permeable as those of the other cells of the cortex. Even if they were less permeable, or actually impervious, there may have been at intervals thin-walled elements similar to those of a thick-walled endodermis, and through such thin-walled cells the water taken in at the periphery might have reached the spiral tracheids on the inside of the cortex.

In his memoir on *Stigmaria*, Williamson figures a transverse section of a rootlet[1] in which there appear, in close proximity to the protoxylem group, two other groups of spirally-marked tracheids in the parenchymatous sheath of the stele. These isolated groups of tracheids, together with the small tracheids immediately adjoining the metaxylem, Williamson considers to 'constitute the monarch point, to which the remaining vessels of the bundle were added centripetally.' A similar condition had been previously figured by Williamson[2] in Part XI of his Organization of the Fossil Plants of the Coal Measure, and the same explanation given of its occurrence. Dr. Scott, in his manuscript notes, dissents from this interpretation because 'the elements at (f''') are too big and too remote from the protoxylem to form part of it.' He considers that we have here another case of a tracheidal strand being given off from the protoxylem. This conclusion is undoubtedly correct, the difference in appearance between Williamson's figure and that of Renault being due to the fact that the strand of tracheids runs very nearly parallel to the

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[1] Williamson, W. C. ('87), Pl. XI, Fig. 59.

[2] Id. ('81), Pl. LIII, Fig. 19.

central cylinder as it does in Fig. 5 of the present communication, and not at right angles as was the case with the rootlet figured by Renault and that figured previously by me ('02). The correctness of Dr. Scott's view is further borne out by several rootlets in the Manchester Museum, one of which is represented in Figs. 3 and 4[1]. This rootlet is one of a type not uncommon among Stigmarian rootlets, but differing both from the one first described by me with a vascular branch ('02), and also from the three rootlets described above. It will be seen that in this third type of rootlet the stele does not lie freely in the space left between the inner and outer cortex, but is definitely connected with the latter by a strand of parenchymatous cells, reminding one of the similar connecting strand in the roots of *Isoetes*. Such rootlets have been figured before, but no special attention has been drawn to this feature, which might from Williamson's Fig. 16[2] be thought to be an attribute of very young roots only. A careful examination of a large number of rootlets of this type, many of them evidently fully developed, convinces me that it is a somewhat different type of rootlet. In the one represented in Fig. 3 it will be seen that this parenchymatous connexion between the stele and the outer cortex is traversed by three strands of tracheids (tr', tr'', tr''') similar to those figured by Williamson, and rightly interpreted by Dr. Scott as vascular branches similar to those described by Renault. From the number of these isolated groups of tracheids it would appear that such branches were given off at short intervals in the rootlets of his type, and that they ran very obliquely towards the cortex, so that two or three strands are cut across in transverse section. Their oblique path is evident from the enlarged drawing of a portion of this rootlet (Fig. 4), in which the lateral markings of the tracheids are visible in a transverse section. It is, of course, possible that these strands were not all of independent origin, but that the appearance may be due to some branching of the strand similar to that of Fig. 5

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[1] Hick Collection, No. 75.

[2] Williamson, W. C. ('81), Pl. LIII, Fig. 16.

but of a more complex character, so that more numerous branches appear in the transverse section. Of this, however, I have not been able to see any trace in such longitudinal sections of this type of rootlet as I have been able to examine. Unfortunately they were mostly too oblique to allow any very definite statement to be made. It will be noticed that in Fig. 3, as in the case referred to by Dr. Scott, the tracheids increase somewhat in size soon after they are given off from the protoxylem, a feature which is not noticeable in the other types of rootlets, where the dilated tracheids are only observable after the strand has reached the outer cortex. In all cases, however, we have that sequence of narrower tracheal elements to which Strasburger draws attention ('91)[1]. He points out that in all cases the narrower absorb water from the wider elements. In both categories of Stigmarian rootlets, therefore, the flow of water would take place from the wider tracheids of the cortex to the narrower protoxylem elements of the central cylinder. The rootlet represented in Figs. 3 and 4 shows very clearly the wider spiral tracheids of the cortex, similar in general features to those of the rootlets in Figs. 2 and 5. These tracheids appear, however, in the second type of rootlet to be differentiated into narrow ones running longitudinally in the rootlet and wider transverse ones. This arrangement reminds one forcibly of the terminal ramifications of the vascular bundles in a Monocotyledonous leaf as figured by De Bary for *Zea Mais*[2].

The position of the spiral tracheids is also different in this last rootlet from that described for the other rootlets. It will be seen in Figs. 3 and 4 that the tracheidal elements of the cortex are here found externally to the cells with dark cell-walls. Whether these were in all cases thick walls, or whether their constitution caused a discolouration of the cell-wall substance, it would be difficult to say; but the presence of the tracheids on the outside of this layer of cells would suggest that in this rootlet they might be less permeable

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[1] Strasburger, E., Leitungsbahnen, p. 873.

[2] De Bary, A. ('84), Fig. 175, p. 371.

than the lighter external parenchyma. It is a noticeable feature of these rootlets, too, that the thin-walled cells of the outer cortex are considerably larger where they adjoin the tracheidal patch than in any other part of the circumference, and present therefore a specialized appearance, and one suggestive of very active absorption at this point. This larger-celled portion of the outer cortex does not run continuously along the rootlet, but, as can be seen from longitudinal sections, is confined to those regions where a vascular branch terminates in the cortex in wide spiral tracheids.

We are in the case of fossil plants at a great disadvantage in endeavouring to explain the function of unknown organs, as we cannot adduce any experimental evidence, and must base our conclusions on inferences drawn from anatomical facts only. In the present case the specialized cells of the cortex just referred to may be taken to give an important clue to the function of these peculiar vascular strands of the Stigmarian rootlets. It would appear from Figs. 3 and 4 that the rootlets were more particularly active as absorbent organs at those points at which the large-celled parenchyma occurred beneath the epidermis. Not only are these cells marked out as likely to maintain active osmosis, but they were in the most advantageous position to pass on the water they had absorbed to the central cylinder across the parenchymatous bridge which joins the outer cortex at this same point. The passage of water might be considerably accelerated by the presence of the vascular strands described above. As in the leaves, so in the rootlets, there was no direct connexion between the turgid parenchyma and the narrow spiral tracheids, but an intermediate tissue of wide spiral tracheids was interpolated.

In the case of the leaves of Monocotyledons and Dicotyledons, these tracheids, through which the outward diffusion of water takes place, are generally spirally-marked and of a very angular appearance[1]—due, as De Bary states, to the end surfaces bordering on the parenchyma being usually 'cut off sharply either transversely or obliquely.' The same description

[1] Cp. Sachs, J. ('87), Fig. 196.

might be given of some of the tracheids in the outer cortex of the Stigmarian rootlet. Comparison might also be made with those plants which possess a more definite and restricted 'transfusion tissue,' as defined by Mohl ('71). De Bary ('87) describes this transfusion tissue in the Conifers as 'attached to the xylem by means of one or two longitudinal rows of tracheids,' and as consisting of tracheids which 'are on the average shorter and wider, and have terminal surfaces which are but little oblique, and may even be horizontal.' This, too, would very fitly describe the tracheidal elements seen in Figs. 2 and 5 of the present paper. This comparison with the 'transfusion tissue,' in the restricted sense, receives additional weight from the fact that the leaves of the Lepidodendraceae possessed a considerable amount of transfusion tissue[1], the cells of which resemble very closely the spiral tracheids in the rootlets of *Stigmaria*. A clear functional difference must, of course, have existed between these two very similarly constituted cells of the root and leaf of the Lepidodendraceae. The latter must have facilitated the outward passage of water in the leaf, whereas the former, if my interpretation is correct, must have accelerated the inward passage of water in the root.

This would not be the only instance of similarly constituted organs acting in opposite ways in different parts of a plant. Indeed, the same organ may act both as a water-secreting or absorbing structure, as has been shown by Haberlandt ('95) and Von Minden ('99) in the case of the hydathodes of many leaves. The 'digestive glands' of insectivorous plants may be taken as a special instance of the double function of modified hydathodes.

A further support for the view I have advanced as to the probable function of the tracheidal patches of the outer cortex is gained from an interesting instance to which Professor F. W. Oliver has drawn my attention. Jönsson ('02), in his account of the germination of *Agave*[2], refers to the occurrence in the

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[1] Cf. Scott, D. H. ('00), Studies in Fossil Botany, p. 148.

[2] Cp. Jönsson, B. ('02), Pl. III, Fig. 10.

top of the cotyledon, which forms the absorbing organ of the seedling, of a considerable development of fibrous cells. These spirally-marked cells are 'short and parenchymatous,' and remind him of the tracheids found under the epidermis of the glands of *Drosera.* In the latter the tracheids are no doubt to a great extent excretory as well as absorptive, but in this 'Saugorgan' of *Agave* the function of these tracheids must be exclusively absorptive, and they would therefore readily compare with the cortical tracheids in the Stigmarian rootlet.

The only roots which offer any counterpart to the vascular strands with tracheidal terminations in Stigmarian rootlets are the highly modified roots of certain parasitic Phanerogams. Here, as Solms ('68) has shown, the haustoria are often traversed by vascular strands quite similar in structure to the ends of bundles in the foliar expansions. We have, therefore, here an instance of roots becoming modified for special reasons very much in the same way as the Stigmarian rootlets were adapted to their peculiar conditions.

That the roots of *Stigmaria* should require some special provision for facilitating the absorption of water might be expected from a consideration of their general structure. In some cases, as in the rootlet reproduced in Fig. 3, a thin band of parenchyma was the only connexion between the stele and the outer cortex, and through it alone could a passage of water take place from the peripheral to the central portion of the rootlet. In other cases there appears to have been only a delicate trabecular tissue constituting the middle cortex, and in some there was possibly no definite connexion between the stele and the outer cortex, except by such vascular strands as are described above. In all cases there seems sufficient reason for the existence of special vascular communication between the central cylinder and the peripheral tissues to ensure an adequate supply of water.

It should be remembered that in the roots of Calamites, which probably existed in similar conditions of climate and habitat, the roots were not monarch, and had numerous stout rays of parenchymatous cells running from the epidermal tissue to the various protoxylem groups. The same may be said of most recent aquatics. The only existing type of aquatic with a monarch root, *Isoetes*, has as a submerged plant a much smaller requirement for root-absorption, and is apparently able to dispense with this additional method of conduction shown to be characteristic of the various types of Stigmarian rootlets.

GENERAL CONCLUSIONS.

In the various types of Stigmarian rootlets fine strands of spiral tracheids, like those described by Renault, may be seen leaving the protoxylem elements.

These strands do not pass out to lateral rootlets as suggested by Renault, but terminate in the outer cortex, sometimes in connexion with distinct groups of large parenchymatous cells.

The vascular strands are not directly connected with the parenchyma of the outer cortex, but pass out into short and wide spirally-marked cells resembling the transfusion cells of leaves.

The vascular strand and the transfusion cells in which it terminates form a special means of conducting water from the peripheral to the central tissues of the rootlet, a means which is rendered necessary by the development of the middle cortex into an air-conducting tissue or space.

The existence in the cortex of Stigmarian rootlets of spiral tracheids comparable with the transfusion-cells of Lepidodendroid leaves may possibly be taken by some palaeobotanists as a further argument in favour of Schimper's view of the homology of these two sets of organs[1].

In making the above comparison, however, I desired merely to refer to them as organs of similar structure and analogous to some extent even in function, in so far as they establish a passage between the parenchymatous and vascular tissues. I have searched in vain in Lepidodendroid leaves for the fine vascular strand which traverses the middle cortex of the

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[1] Schimper, W. Ph., Paléontologie végétale, 1872, vol. ii, p. 111.

rootlet, and I regard both this conducting strand and the tracheids of the outer cortex as a highly specialized adaptation of the rootlet, and not as the survival or transformation of transfusion-cells of a leaf-like organ. Except in their position, the rootlets and leaves of the Lepidodendraceae seem to be as different from one another and quite as highly specialized as those of *Isoetes*. In this latter plant, too, the rootlets have a fairly regular arrangement on the basal part of the stem, which may readily be compared with the dilated base of *Pleuromeia*. It is quite possible also to conceive the latter to be morphologically equivalent to the 'rhizome' or 'rhizophore' of *Stigmaria*, and possibly of both, as a special development of the protocorm of the ancestral sporophyte. Such a protocorm would not have borne any leaves at its base, but its rootlets may have had the same position as the leaves on the stem.

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EXPLANATION OF PLATE XXVI.

Illustrating Professor Weiss's paper on Stigmarian Rootlets.

Figs. 1, 2, and 3, from photographs taken by Mr. Abraham Flatters.

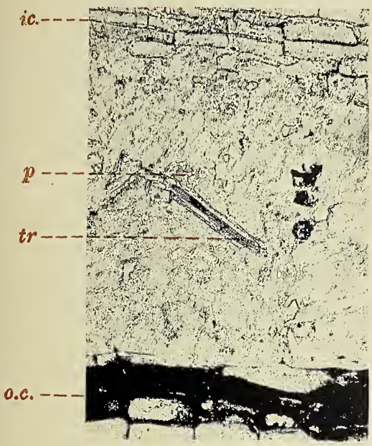
Fig. 1. Photograph of a rootlet cut in longitudinal direction from slide, No. 107 of the 'Hick Collection' in the Manchester Museum. × 60. *i.c.* = inner cortex; *o.c.* = outer cortex; *p.* = process from parenchymatous sheath indicating the trabecular nature of middle cortex; *tr.* = tracheids of vascular branch.

Fig. 2. Photograph of another rootlet from slide, No. 107 in the 'Hick Collection.' × 60. This section is cut rather obliquely so that the right-hand portion passes tangentially through the outer cortex. The central cylinder is not seen in this section. *o.c.* = outer cortex; *sp.tr.* = spiral tracheids of the outer cortex.

Fig. 3. Photograph of a rootlet from slide, No. 75 in the Hick Collection. × 30. This rootlet shows the stele connected with the outer cortex by a definite strand of parenchymatous tissue. In this parenchymatous strand will be seen traces of spiral tracheids cut slightly obliquely.

Fig. 4. A more enlarged drawing of a portion of Fig. 3 showing, *i.c.* = inner cortical sheath; *px.* = protoxylem; tr', tr'', tr''' = three portions of vascular strands running to outer cortex; *sp. tr.* = spiral tracheids of outer cortex; *par.* = patch of large-celled parenchyma of outer cortex.

Fig. 5. Enlarged drawing of a portion of a longitudinal section of a rootlet from slide, No. 401 in the 'Cash Collection' of the Manchester Museum. In this rootlet the vascular strand is seen in connexion both with the protoxylem of the central cylinder, and also with the spiral tracheids of the outer cortex. Owing to compression of rootlet the vascular branch is thrown into a fold; *st.* = stele with inner cortical sheath *i.c.*; *tr.b.* = trabecular tissue connecting the vascular strand; *v.br.* = branch from original vascular branch; *st.* = outer cortex with spiral tracheids *sp.tr.*



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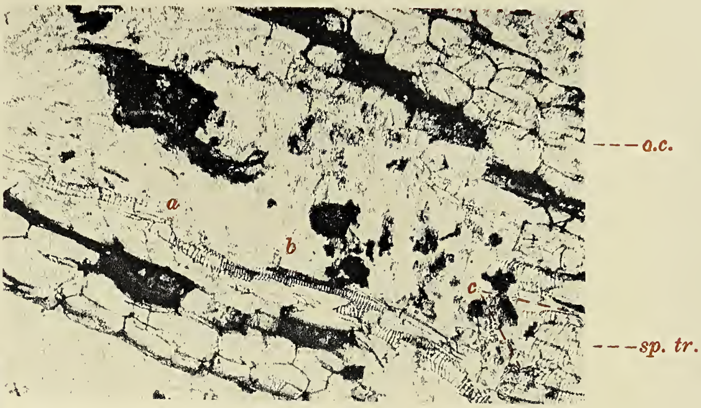

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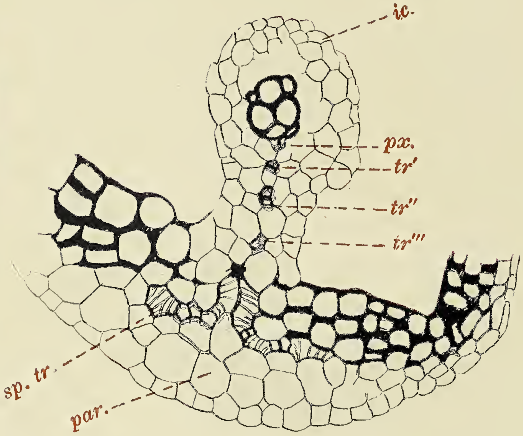

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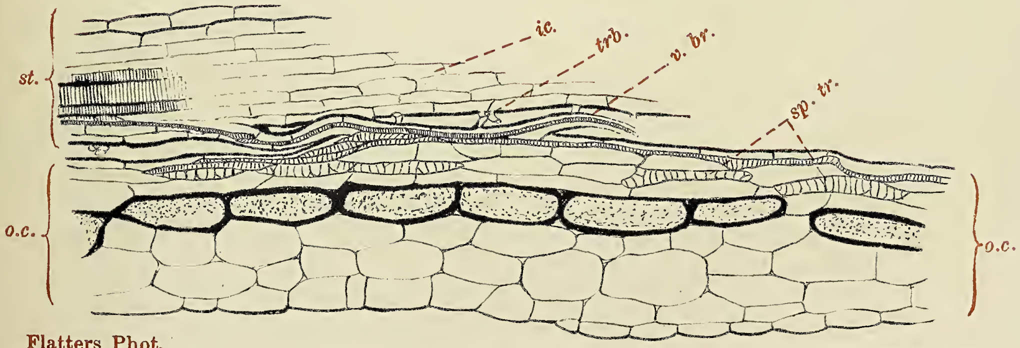

Flatters Phot.

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Weiss Del.

WEISS.—STIGMARIA.

NOTES.

THE FRUCTIFICATION OF LYGINODENDRON OLDHAMIUM.—In many of the slides recently prepared by Mr. Lomax from a large Dulesgate block, I have detected sporangia which seem to have every mark of belonging to *Lyginodendron,* short of direct continuity with the petiole. In five of the slides the sporangia are aggregated together in clusters of eight, being coherent at the base, though free at the apex. They are about 4 mm. in length and 1 mm. in width, and they taper to the apex and slightly to the base. Transverse sections of clusters at three different levels show that the periphery of the cluster is surrounded with tissue of the characteristic structure of the *Lyginodendron* pinna. The epidermis, hypoderm and lacunar tissue are all present at the base of the cluster, while the two former continue to the apices of the sporangia. Thus each sporange has the exposed part of its wall thicker than that towards the centre of the cluster. These clusters are associated in all five slides with small petioles of Lyginodendron.

FIG. 31. Tracing of photograph of a longitudinal section (×12).

The form and size of these clusters strongly suggest the *Calymmatotheca* type of fructification, which has been made familar to all in the frontispiece to Dr. Scott's 'Studies in Fossil Botany.' The arguments in favour of this being the fructification of *Lyginodendron* are clearly stated in this work.

[Annals of Botany, Vol. XVI. No. LXIII. September, 1902.]

Hence for the two reasons, (1) association both in impressions and in petrifactions with Lyginodendron, (2) the structure of the tissue in which the sporangia are embedded, the claim of these clusters to be the fructifications of *Lyginodendron* is overwhelmingly strong.

My thanks are due to Professor F. W. Oliver for the loan of several confirmatory slides.

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ALGOLOGICAL NOTES.—

III. PRELIMINARY REPORT ON THE PHYTOPLANKTON OF THE THAMES.—Freshwater Plankton-investigations, so vigorously prosecuted on the continent, have received little or no attention in England. As far as the writer is aware no paper on this subject has ever been published in this country. The Plankton of the sea has occupied English botanists since some years, and systematic work in this direction is being done at some of our marine stations; but we possess nothing whatever comparable to the inland biological stations established on the continent; take for example Plön in Schleswig-Holstein, which is practically devoted solely to research on the Plankton of the numerous small lakes of this part of the German Empire. This special line of research has here become so proficient and prolific, as to admit of the publication of a separate journal[1] to embody its results.

It was with the intention of drawing attention to this kind of work in our country that I commenced to investigate the Plankton of the Thames—the more as the Plankton of the artificial waters at Kew, which are fed more or less directly from the river, seemed to promise good results. And indeed a little over a month's investigation has given such interesting results that I venture now to publish a general account of the Plankton without being able to say anything as to its periodicity.

Investigations of the Plankton of rivers have not been often carried out as yet. Lauterborn[2] in 1893 published the results of some collecting, performed on the Rhine near Ludwigshafen; his list consists chiefly of animals, two Diatoms being the sole representatives of the vegetable kingdom. It is really Bruno Schröder who first gives

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[1] Forschungsberichte aus der biologischen Station zu Plön, edited by the Director Dr. O. Zacharias. Stuttgart. Appeared first in 1893.

[2] Beiträge zur Rotatorienfauna des Rheins und seiner Altwasser. Zoolog. Jahrbücher, 1893.

a clear account of the Plankton-life of a river, the Oder. His first paper on this subject was published in 1897 [1], to be followed in 1899 by a fuller account [2]. In the interval which elapsed between these two papers of Schröder's, Zacharias [3] published a brief general account of the Plankton of rivers (so-called Potamoplankton). This paper gives the results of Plankton-collecting in a number of rivers (Pleisse, Schlei, Trave, Oder, &c.), and terminates with a discussion of the probable origin of the Potamoplankton. Quite recently Brunnthaler [4] has published a short communication on the Plankton of the Danube near Vienna, whilst Zykoff [5] and Bolohoncew [6] have described that of the Volga near Saratow.

Brunnthaler also discusses the possibilities of an independent existence of Plankton-organisms in flowing water, and maintains that in the swift Danube all the Plankton found has been carried down from quiet portions of the stream's course. This view seems very probable, and can also, without doubt, be extended to rivers of less rapid current. Thus in a river like the Thames many of the organisms found floating freely in the main-water of the river have probably been derived from higher and almost stationary parts of its course. Schütt [7] opposes the idea of an independent existence of Plankton in streams, and maintains that all the individuals present have been derived from its stagnant backwaters and slow-flowing tributaries. In rivers which flow as slowly as the Thames, however, reproduction of the Plankton-organisms even in mid-stream undoubtedly goes on. *Pediastrum* and *Eudorina*, two of the commonest among the chlorophyceous Plankton of the Thames, were again and again met with in every stage of reproduction, and I am quite certain that the other organisms reproduce in the same way, but perhaps less frequently. Diatoms were often seen in a state of reproduction,

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[1] Ueber das Plankton der Oder. Ber. Deut. Bot. Ges. xv, 1897, p. 482. See here for further literature.

[2] Das pflanzliche Plankton der Oder. Forschungsber., Plön, 1899. Teil vii, p. 16. Recent literature mentioned.

[3] Das Potamoplankton. Zoologischer Anzeiger, No. 550, 1898, p. 41.

[4] Das Phytoplankton des Donaustromes bei Wien. Verhandl. der k. k. zoolog.-botan. Gesellsch. in Wien, Jahrg. 1900, Heft 6, pp. 308–11.

[5] Zykoff, V. Das pflanzliche Plankton der Volga bei Saratow. Biol. Centralbl., Bd. xxii. No. 2, 1902.

[6] Bolohoncew, E. Materialien zur Kenntnis des Phytoplanktons der Volga (bei Saratow). Moscow, 1901. (Russian.)

[7] Das Pflanzenleben der Hochsee. Kiel, 1893, pp. 9–11.

although I must say that the extremely abundant *Melosira* was only found with reproductive organs in a quiet, almost stationary backwater. Undoubtedly it is from these backwaters and tributaries of the upper part of a stream's course that the initial mass of the Plankton is derived; they act, so to say, as reservoirs[1], from which by means of currents or incidentally during storms new supplies are continually being dealt out. It is, however, just as certain that these organisms do afterwards multiply still more, and that a great part (quantitatively) of the Plankton of the Thames is formed when the individuals have already reached the flowing stream. Zacharias holds the same view of the matter and adduces the river Schlei as evidence[2]; each year it becomes covered with a dense stratum of *Clathrocystis*, and it is impossible that this can all have been derived from the few backwaters of the river. Zimmer[3] places the Plankton of rivers in three classes:—

(1) The *eupotamic* Plankton which flourishes and reproduces either in the flowing water of the stream or in stationary water (e. g. *Pediastrum*, *Eudorina*, *&c.*).

(2) The *tychopotamic* Plankton which only reproduces in stationary water, and when swept into the main water of the river continues to live, but not to reproduce (probably many Diatoms).

(3) The *autopotamic* Plankton which has become adapted to life in flowing water (e. g. *Actinastrum Hantzschii*, Lagerh., var. *fluviatile*, Schröd., and *Synedra Ulna* (Nitzsch), Ehrb., var. *actinastroides*, Lemm.[4]).

What then becomes of the Plankton as it gets nearer and nearer to the river's mouth? On most of the Plankton-organisms, found higher up the river, the increasing brackishness of the water[5] will act fatally. In the Thames, in which the tide extends to Richmond or further, this action is noticeable already at Kew. The quantity of Plankton-organisms decreases steadily as we approach the river's mouth. Plankton-hauls from the Thames at Kew showed that many of the Desmids and Pediastrums are either dead or in a dying state, and many of the Diatoms merely consist of the empty frustules. These after some time sink to the bottom of the water, and in this

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[1] Cp. Zimmer, Das thierische Plankton der Oder. Forschungsber., Plön, 1899. Teil vii, p. 4.

[2] Zacharias, loc. cit., p. 47.

[3] Zimmer, loc. cit., p. 5.

[4] Cf. Schröder, loc. cit. I have not found either of these varieties in the Thames as yet.

[5] Cp. foot-note on p. 581.

way large numbers of Diatoms are to be found in the mud of the river's bed. These were described as far back as 1854 by Roper[1], who having examined the mud from Hammersmith and from spots lower down the river remarks on the large number of marine species present. Even at Kew a few truly marine species (e. g. *Coscinodiscus radiatus*, *Surirella ovata*, *Rhaphoneis Rhombus*) were found, and had my observations extended over a greater length of time more would probably have been discovered. I do not think that many of the freshwater forms found in the upper reaches of the river will be met with much further down than Kew, although Hensen[2] and Brandt[3] found a number of freshwater Plankton-species, present in some cases in quite considerable quantity, in the slightly brackish water of the Stettiner Haff.

My collecting was performed between Kew and Cookham on six separate days during a period of a little more than a month. The dates, together with the temperature of the water and the nature of the weather, may be mentioned at once so as to save repetition:—

(1) Kew–Richmond: August 14; 18° C; bright, with a few clouds at intervals.

(2) Richmond–Teddington: July 11; 20° C; slightly cloudy.

(3) Hampton Court–Sunbury: July 16; 23° C; overcast.

(4) Shepperton–Weybridge: July 26; 18½° C; cloudy, water very much disturbed.

(5) Datchet–Windsor: August 8; 18½° C; rainy.

(6) Maidenhead–Cookham; August 19; 18° C; bright, with a few clouds at intervals.

All the samples were collected from a rowing-boat with the help of an ordinary funnel-shaped net of fine gauze, the lower narrow end being attached to a glass tube. Samples were collected from the surface of the water, and in some cases from deeper strata, the net being maintained below the surface at a depth of 1–2 feet. The net was usually allowed to remain in the water for a period of about three minutes, during which the boat was rowed at a medium rate. The samples were examined the same day or the day after they were

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[1] On the Diatomaceae of the Thames. Trans. Microscop. Soc. of London. New Series, vol. ii, 1854.

[2] Das Plankton der östlichen Ostsee und des Stettiner Haffs. Sechster Ber. der Commission zur wissenschaftl. Unters. deutscher Meere, 1890.

[3] Ueber das Stettiner Haff. Same periodical, vol. ii, 1895 (new series).

collected. In considering the table on pp. 582 and 583 it is necessary to remember that this year has been an abnormal one, that the months July and August have been very rainy, whereas the temperature of the air and therefore of the water also has been considerably below the average. The quantity and quality of the Plankton will therefore in all probability be different from that of a normal summer.

The accompanying table may indicate the distribution and relative number of individuals of the various species found. [i. = isolated; vr. = very rare; r. = rare; rc. = rather common; c. = common; vc. = very common; a. = abundant; — = wanting.]

A few words may now be said on the constitution of the Thames Plankton, and on the distribution of the various species. As in all rivers, as yet investigated, Diatoms play an important part, generally exceeding the other forms in quantity to a great extent. In the neighbourhood of Kew this is not so noticeable, there being perhaps two or three Diatoms to one individual of the other groups, but as we go farther up the stream the former increase rapidly in number, so that at Windsor or Maidenhead the ratio has become about 20·1. Diatoms are especially abundant in the backwaters, although the number of different species is frequently less here than in the main stream. I am only able to account for the great decrease in the number of Diatoms at Kew by the above-mentioned hypothesis—the fresh-water species are dying off, whereas the marine species are not yet common at this point. The samples from Kew and even from Teddington altogether present a very different appearance to those collected higher up; at Kew the stream is full of mud, and when a sample is examined under the microscope nothing but organic and inorganic detritus is found in the field of view, the few living forms being very widely scattered in between these particles[1]. The samples from higher up, on the contrary, are practically free from mud, and the field of view is full of Diatoms, &c. Possibly this mud, occurring in the lower parts of the stream, is partly accountable for the decrease in number of the Diatomaceae.

Fragilaria virescens is very common in all parts of the river examined; the other species, *Fr. mutabilis*, is far less abundant. Next, as regards abundance to the first-mentioned species comes *Melosira varians*; *M. moniliformis* is found very commonly in some parts. *Pleurosigma attenuatum* is another very common form, especially

[1] Zimmer, loc. cit., p. 4.

in the surface layers. The species of *Surirella* are very typical of the Thames Plankton; one or other of them will always be found in the field of view, when a sample is placed under the microscope. *Campylodiscus noricus* is common in many parts. Forms like *Coscinodiscus radiatus*, *Melosira angulata*, *Rhaphoneis Rhombus*, *Synedra Acus* var. *delicatissima*, &c., become rarer as we go higher up stream.

Amongst the green Algae the two species of *Pediastrum* were common in nearly all parts of the river. After that *Closterium moniliferum*, *Cosmarium margaritiferum* and *Scenedesmus quadricauda* are most abundant. *Eudorina elegans* is common higher up, and is probably one of those forms which dies off early when the water becomes brackish. *Pandorina morum* is found sparingly everywhere. The other species of *Scenedesmus* is much rarer than the first, and this is also the case with the other species of Desmids. Most probably the Thames water is too calcareous[1] to admit of a proper Desmid vegetation. This is also the case with the artificial waters at Kew, which yield very few Desmids.

The blue-green forms are commoner in the lower parts of the river. Only the two species of *Microcystis* are present in any quantity. The others are isolated and local. Rather commoner are some of the Flagellates, especially *Euglena viridis*; *Phacus pleuronectes* was also frequently found. *Dinobryon* is rare, but I think it probable that early in the year this and other Flagellates are much more abundant than they are now. No Peridiniaceae were observed, which is worthy of note.

As to the difference between the samples taken from the surface and those taken from deeper layers, I have found that the green forms are less common in the deeper strata, and consequently the Diatoms preponderate the more. Some of these latter, however, are also much rarer, e.g. *Pleurosigma* (cp. table).

The backwaters always present a much more flourishing and

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[1] My friend, Mr. L. Guttmann, was kind enough to analyse two samples of Thames water, for which I desire to express my sincerest thanks. The results were as follows:—

First sample from Kew:—
3·0 parts of Cl in 100,000 (most of this is due to Sodium Chloride).
11·70 parts of $CaCO_3$ in 100,000. (Total hardness = 19·13.)
Second sample, from Maidenhead:—
2·20 parts of Cl in 100,000.
16·20 parts of $CaCO_3$ in 100,000. (Total hardness = 22·02.)

	1. Kew–Richmond; surface layers; t=18°C; bright; 14, viii.[1]	2. Kew–Richmond; deeper layers; t=18°C.	3. Backwater near Brentford; surface layers; t=18°C; bright; 14, viii.	4. Richmond–Teddington; surface layers; t=20° C; slightly cloudy; 11, vii.	5. Hampton Court–Sunbury; surface layers; t=23°C overcast; 16, vii.	6. Shepperton–Weybridge; surface layers; t=18½°C; cloudy, water much disturbed; 16, vii.	7. As in 6; deeper layers.	8. Backwater near Weybridge; surface layers; t=15°C; sun; 26, vii.	9. Datchet–Windsor; surface layers; t=18½°C; cloudy; 8, viii.	10. As in 9; deeper layers.	11. Maidenhead–Cookham; surface layers; t=18°C; sunny; 19, viii.	12. As in 11; deeper layers.	13. Taplow Backwater; t=18°C; cloudy; 19, viii.	14. Backwater near Cookham; t=18½°C; sunny; 19, viii.
I. *Chlorophyceae.*														
1. *Scenedesmus quadricauda* (Turp.), Bréb.	vr.	r.	r.	rc.	c.	c.	rc.	vr.	r.	r.	r.	vr.	—	vr.
2. ,, *quadricauda*, var. *horridus*, Kirch.	—	—	—	—	—	—	—	—	—	r.	—	—	—	—
3. ,, *acutus*, Meyen.	r.	r.	r.	—	—	—	—	rc.	—	—	—	—	—	—
4. ,, *acutus*, var. *obliquus*, Rab.	r.	r.	—	—	—	—	—	—	—	—	—	—	—	—
5. ,, *acutus*, var. *dimorphus*, Rab.	—	—	—	—	r.	—	—	—	—	—	—	—	—	—
6. *Pediastrum Boryanum* (Turp.), Men.	rc.	rc.	rc.	c.	c.	c.	rc.	—	c.	rc.	c.	rc.	c.	rc.
7. ,, *pertusum*, Ktz.	rc.	c.	c.	c.	c.	c.	rc.	—	r.	r.	r.	—	rc.	—
8. ,, *pertusum*, var. *clathratum*, Braun.	—	rc.	rc.	—	rc.	—	—	—	—	—	—	—	—	—
9. *Botryococcus Braunii*, Kütz.	r.	rc.	r.	—	—	rc.	—	—	—	—	—	—	—	—
10. *Ophiocytium circinatum*, Wolle.	—	—	—	—	—	—	—	rc.	—	—	—	—	—	—
11. *Rhaphidium pyrenogerum*, Chod. var. *falciforme*	i*	—	—	—	—	—	—	—	—	—	—	—	—	—
12. *Kirchneriella lunaris* (Kirch.), Moeb.	i*	—	—	—	—	—	—	—	—	—	—	—	—	—
13. *Actinastrum Hantzschii*, Lag.	—	i*	—	—	—	—	—	—	—	—	—	—	—	—
14. *Chlamydomonas*, spec.	—	—	—	—	—	—	—	—	—	—	vr.	—	—	—
15. *Eudorina elegans*, Ehrb.	—	—	—	r.	rc.	r.	—	—	r.	r.	c.	vr.	c.	rc.
16. *Pandorina morum*, Ehrb.	vr.	—	—	rc.	r.	rc.	rc.	—	r.	—	r.	vr.	rc.	r.
II. *Conjugatae.*														
17. *Closterium acerosum* (Schrank.), Ehrb.	—	vr.	—	vr.	r.	r.	—	—	—	r.	—	—	—	—
18. ,, *moniliferum*, Ehrb.	vr.	—	r.	—	c.	c.	rc.	—	c.	rc.	c.	—	c.	rc.
19. ,, *Leibleinii*, Kütz.	—	—	—	—	—	i.	—	—	—	—	—	—	—	—
20. *Cosmarium margaritiferum*, Men.	vr.	—	r.	—	rc.	rc.	rc.	—	r.	rc.	rc.	—	r.	rc.
21. ,, *ornatum*, Ralfs.	—	—	—	—	—	—	—	—	—	rc.	—	—	—	—
III. *Bacillariales.*														
22. *Coscinodiscus radiatus*, Ehrb.	r.	r.	r.	rc.	—	—	—	—	—	—	—	—	—	—
23. *Melosira angulata*, Rabenh.	r.	rc.	—	—	—	—	—	—	—	—	—	—	—	—
24. ,, *moniliformis* (Müll.), Ag.	r.	r.	r.	rc.	c.	rc.	r.	—	rc.	rc.	c.	c.	c.	c.

25. *Melosira varians*, Ag.	rc.	rc.	rc.	c.	vc.	c.	c.	a.[1]	c.	vc.	vc.	vc.	a.	a.
26. *Campylodiscus noricus*, Ehrb.	—	r.	—	rc.	c.	rc.	r.	—	rc.	r.	r.	r.	—	r.
27. *Surirella biseriata*, Bréb.	rc.	r.	r.	rc.	rc.	rc.	rc.	—	rc.	rc.	—	r.	rc.	rc.
28. " *ovalis*, Bréb.	r.	r.	—	c.	c.	c.	c.	—	rc.	c.	rc.	rc.	rc.	rc.
29. " *ovata*, Ktz.	—	—	—	vr.	r.	—	—	—	—	—	—	—	—	—
30. " *splendida* (Ehrb.), Ktz.	r.	r.	—	r.	r.	rc.	r.	—	rc.	rc.	r.	—	rc.	rc.
31. *Cymatopleura Solea* (Bréb.), Sm.	—	r.	r.	r.	r.	rc.	r.	r.	rc.	rc.	rc.	—	—	—
32. *Himantidium faba*, Ehrb.	—	—	—	—	—	—	—	—	rc.	rc.	r.	—	—	—
33. *Cymbella gastroides*, Ktz.	—	—	r.	rc.	rc.	c.	c.	rc.	c.	c.	c.	rc.	r.	c.
34. *Amphora ovalis*, Ktz.	rc.	—	—	rc.	rc.	rc.	rc.	rc.	r.	c.	rc.	rc.	r.	rc.
35. *Encyonema prostratum*, Ralfs.	—	—	—	—	r.	—	r.	—	—	—	—	—	—	—
36. *Cocconeis Placentula*, Ehrb.	—	r.	—	rc.	rc.	rc.	rc.	—	c.	c.	rc.	rc.	rc.	rc.
37. *Fragilaria virescens*, Ralfs.	c.	c.	c.	c.	vc.	vc.	c.	a.	c.	rc.	vc.	vc.	a.	c.
38. " *mutabilis* (Sm.), Grun.	r.	rc.	r.	rc.	rc.	r.	r.	a.	r.	rc.	rc.	r.	—	—
39. *Rhaphoneis Rhombus*, Ehrb.	rc.	r.	r.	rc.	—	—	—	—	—	—	—	—	—	—
40. *Synedra Acus*, Ktz.	r.	rc.	r.	—	—	—	—	—	r.	—	r.	r.	r.	—
41. " *Acus*, var. *delicatissima*, Sm.	—	rc.	r.	—	—	—	—	—	—	—	—	—	—	—
42. " *Ulna*, Ehrb.	r.	—	—	rc.	c.	c.	rc.	c.	rc.	rc.	rc.	rc.	rc.	rc.
43. *Asterionella gracillima*, Heib.	—	—	i*	—	—	—	—	—	—	—	—	—	—	—
44. *Nitzschia sigmoidea* (Nitzsch.), Sm.	rc.	r.	r.	rc.	rc.	rc.	r.	—	rc.	rc.	rc.	rc.	r.	r.
45. *Navicula amphisbaena*, Bory.	rc.	rc.	c.	r.	r.	—	—	—	r.	r.	—	—	—	—
46. " *gracilis*, Ehrb.	—	—	—	rc.	rc.	rc.	r.	rc.	c.	c.	rc.	rc.	rc.	rc.
47. *Pinnularia viridis* (Ehrb.), Rab.	—	vr.	—	—	rc.	rc.	rc.	rc.	r.	r.	r.	—	r.	—
48. *Pleurosigma attenuatum* (Ktz.), Sm.	r.	—	r.	rc.	c.	vc.	rc.	—	c.	c.	c.	r.	c.	c.
49. *Stauroneis Phoenicenteron*, Ehrb.	—	—	—	—	r.	r.	r.	—	—	—	—	rc.	—	r.
50. *Tabellaria fenestrata*, Ktz.	—	—	—	—	—	r.	—	—	rc.	rc.	rc.	—	r.	r.
IV. *Schizophyceae.*														
51. *Coelosphaerium Kützingianum*, Näg.	—	—	—	—	—	—	r.	—	—	—	—	—	—	—
52. *Microcystis protogenita*, Rabenh.	rc.	rc.	c.	—	—	rc.	—	—	—	—	—	—	—	—
53. " *marginata* (Men.), Kirch.	r.	—	r.	—	r.	—	—	—	—	r.	—	—	—	—
54. *Clathrocystis aeruginosa*, Henfrey.	—	—	i.	—	—	—	—	—	—	—	—	—	—	—
55. *Merismopedia glauca*, Näg.	—	—	—	—	—	—	—	c.	—	—	—	—	—	—
V. *Flagellatae.*														
56. *Euglena viridis*, Ehrb.	rc.	c.	rc.	rc.	rc.	—	—	—	rc.	—	rc.	—	—	—
57. *Phacus pleuronectes*, Nitzsch.	—	—	r.	r.	rc.	—	—	rc.	—	—	—	—	—	—
58. *Dinobryon Sertularia*, Ehrb.	vr.	—	—	rc.	—	—	—	—	—	—	—	—	—	—
59. *Synura Volvox*, Ehrb.	—	vr	—	r.	—	—	—	—	—	—	r.	—	—	rc.

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* Species marked thus were only met with once.

[1] With auxospores.

abundant Plankton than does the main stream, and the species found are sometimes different. They also differ in that animal life is much commoner than in the main stream, which at some points is almost destitute of Zooplankton. These backwaters thus form a kind of transition from the typical Potamoplankton of the flowing river to the Heleoplankton of the ponds of the Thames valley. Thus, if we compare the Thames Plankton with that of the stationary Plankton of the artificial waters at Kew, we find that in the latter the animals and also the green organisms far exceed the Diatoms in number, whereas the latter are far the most abundant in the river. It has been shown[1] that the Potamoplankton approaches in its character more to the Heleoplankton of a pond the slower the stream flows.

One backwater somewhat above Shepperton gave very interesting results. The samples were crowded with *Melosira varians*, *Fragilaria virescens* and *mutabilis*, whereas forms like *Pleurosigma attenuatum* and the three species of *Surirella*, so common in the samples collected in the main river on that day, were quite absent. *Pediastrum* was wanting, the green and blue-green forms being represented by *Scenedesmus quadricauda*, *Scen. acutus*, *Ophiocytium circinatum*, Wolle, and *Merismopedia glauca*, which except for the first were not found in the main stream. The chief reason for this difference in the Plankton is undoubtedly to be found in the fact that the temperature of the water in this backwater was only 15° C., whereas in the main river it was $18\frac{1}{2}$° C. Diatoms flourish well in cold water!

The results embodied in the present note are, of course, of a preliminary nature. The number of species to be found in the Plankton of the Thames is undoubtedly considerably greater than that mentioned in the table. My present object has been to obtain some idea of the distribution of the commoner species, and time was only rarely expended on the determination of isolated forms or on possible new species and varieties. Such observations as have been made in this direction have been retained for future publication after the investigations of Thames Plankton shall have been extended over a year's time and the periodicity of the flora has been determined.

F. E. FRITSCH.

JODRELL LABORATORY, KEW,
August, 1902.

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[1] Cp. Zacharias, loc. cit., p. 46; Zimmer, loc. cit., p. 7.

ERRATA.

P. 383. The sentence beginning on line seven from bottom *should read:* 'Sometimes the protoxylem directly abuts upon the endodermis, but it may also be separated from it by a layer of parenchymatous (pericyclic) cells,' &c.

P. 391. The clause beginning on line six from bottom *should read:* 'nevertheless it may exhibit a variation which recalls that already described for the primary and first-formed lateral roots, namely, that the protoxylem of many or even all of the rays may abut immediately upon the endodermis (which is sharply marked from the first) whilst in others it is separated from it by one or more layers of pericyclic parenchyma.'

NOTES.

ON LUMINOUS BACTERIA[1].—Many instances of light production occur in Nature amongst plants and animals. This luminosity is most strikingly exhibited by marine animals and by minute vegetable cells belonging to the group of the Bacteria. Light-production by living protoplasm is a process intimately bound up with the life of the organism, as in the case of the luminous Bacteria. The luminosity of mineral and other inert bodies is dependent on an extraneous light source.

Amongst light-producing organisms our knowledge of the process is most exact in the case of the Bacteria. Their simple semicellular structure, and the fact that modern bacteriological methods enable us to isolate and study particular organisms, renders it somewhat more easy to study the conditions under which light-production can best occur. The observations which are embodied in this paper were made on luminous Bacteria. These organisms are to be found mainly in sea-water and on dead marine animals. They are widely distributed in this respect. We have obtained and studied the most important types. About twenty-five varieties have been described, but it is probable that some of these are very closely related, if not identical. A hitherto undescribed form has been isolated from sea-water in the course of investigations made by one of us at Plymouth. It belongs, like most of the other species, to the group of the Bacilli. The temperature-conditions as regards growth vary considerably, and range from zero to 37° C.

The luminosity of the sea is mainly due to higher forms of marine life and not to Bacteria, at any rate in northern latitudes. On the other hand the phosphorescence of dead objects, such as fish, &c., is due to bacterial forms of life.

We have not been able to confirm the statements that luminous

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

[Annals of Botany, Vol. XVI. No. LXIV. December, 1902.]

Bacteria have direct infective properties as regards crabs and other marine animals.

These organisms require particular and exact conditions in order to exhibit their luminous properties. They must have a suitable nutrient soil containing such proportions of salts as shall render the medium isotonic. For example, sodic chloride, if present to the extent of 3 per cent., will render the organisms luminous and ensure their remaining so for some time. In this manner they can be readily cultivated and studied in the laboratory.

The luminosity appears to be a function of the living cell and can be disturbed by any process which interferes with the vitality of the cell itself. The dead cell is non-luminous, whilst antiseptics which kill the cells inhibit at the same time their luminosity.

A supply of free oxygen is essential; in the absence of oxygen the organisms live but are non-luminous. There is no evidence of a bacterial product as the source of the light. The process appears to be the result of an active oxidation occurring within the cell. The light produced is confined to a small portion of the visible spectrum, and invisible radiations have not been detected. As the spectrum of none of these luminous organisms extends even to the red, it may safely be assumed that no heat radiations are emitted. The light is produced without heat. No invisible radiations allied to the X-rays were detected. Photographs have been obtained by the aid of the light emitted by these organisms. The time-exposure required is, however, considerable.

An exposure to the temperature of liquid air does not destroy the luminosity of the organisms. It has been found possible to triturate Bacteria at the temperature of liquid air by means of special methods devised at the Jenner Institute of Preventive Medicine. The luminous Bacteria mechanically broken up in this manner ceased to phosphoresce. The luminosity, therefore, is due to the vital processes of the cell, and essentially depends for its origin on the *intact* organization of the cell.

We have brought these results forward because this interesting group of organisms have not hitherto been studied in this country so far as we can trace.

J. E. BARNARD.
ALLAN MACFADYEN.

JENNER INSTITUTE.

ON THE SUSPENSION OF LIFE AT LOW TEMPERATURES[1].—Our first experiments were made with organisms possessing varying degrees of resistance, the extremes in this respect being represented by the sensitive *Spirillum* of cholera asiatica and the resistent spores of *Bacillus anthracis*. Ten organisms altogether were used and cooled down to −190° C., in the first instance for twenty hours, and eventually for seven days. These exposures did not produce any appreciable impairment in the vitality of the organisms, either as regards their growth or their characteristic physiological properties, such as pigment and gas-production, pathogenicity, &c. Amongst the organisms tested were photogenic Bacteria, and these likewise preserved their normal luminous properties; and we were able, through the kindness of Professor Dewar, to apply a still severer test—namely an exposure to the temperature of liquid hydrogen (about −252° C.), a temperature which is as far removed from that of liquid air as is that of liquid air from the average summer temperature. Ten hours' exposure to this temperature had no appreciable effect on the vitality of the micro-organisms tested. At such temperatures it must be assumed that the chemical metabolism of the cell ceases, in the absence of heat and moisture. At the same time it appeared to us advisable to test the influence of a *prolonged* exposure to low temperatures on the vitality of cells. The experiments were conducted with the aid of the liquid air plant at the Jenner Institute of Preventive Medicine. The organisms employed were the *Bacillus typhosus*, *B. coli communis*, *Staphylococcus pyogenes aureus*, and a *Saccharomyces*. The Bacteria were suspended in small loops of platinum wire or on cotton-wool swabs, and directly immersed in the liquid air. The yeast, washed and pressed, was wrapped in rice-paper, and likewise directly immersed in the liquid air. Samples were taken and tested at intervals for a total period of six months. In no instance could any impairment of the vitality of the organisms be detected. The yeast gave a good growth, and exhibited its fermentative powers unaltered; the typhoid *Bacillus* retained its pathogenic and other properties; the *Staphylococcus aureus* gave a characteristic pigment growth, and the colon *Bacillus* responded to all the typical tests that were applied to it. Judging by the results, the experiments might have been prolonged for a much longer period

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

than six months without appreciable influence on the vitality of the organisms in question.

The ordinary manifestations of life cease at zero, but at —190° C. we have every reason to suppose that intra-cellular metabolism must also cease, as a result of the withdrawal of two of its cardinal physical conditions, heat and moisture.

It is difficult to form a conception of living matter under this new condition, which is neither life nor death, or to select a term which will accurately describe it.

It is a new and hitherto unobtained state of living matter—a veritable condition of *suspended animation.*

ALLAN MACFADYEN.
JENNER INSTITUTE. SYDNEY ROWLAND.

RESISTANCE OF SEEDS TO HIGH TEMPERATURES[1].—Various experimenters have investigated the limits of temperature which spores of the lower plants and animals can withstand. The results they have obtained show that these spores, if dry, can germinate after exposure to the lowest temperatures obtainable, while the upper limit for similarly dried spores lies between 100° C. and 130° C.

For seeds of the higher plants also it has been more recently shown that the lowest temperatures available are without harmful effects. This note contains an account of some experiments on the maximum temperatures which seeds can withstand and after which they will retain their germinative power.

Before exposure to the high temperatures the seeds were either desiccated over sulphuric acid, or dried in an oven the temperature of which was gradually raised to 90° C. After desiccation the seeds were exposed for at least one hour to the higher temperature. After exposure the seeds were sown on moist sand. The following temperatures were obtained as the highest after exposure to which the seeds of the species mentioned could germinate:—

Mimulus moschatus	105° C.	*Medicago sativa*	121° C.
M. luteus	112°	*Avena sativa*	118°
Papaver somniferum	100°	*Hordeum distichum*	118°
P. nudicaule	100°	*Cucurbita Pepo*	112°

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

Meconopsis cambrica	100° C.	*Helianthus annuus*	112° C.
Schizopetalon Walkeri	105°	*Pisum sativum*	112°
Brassica Rapa	110°	*Trigonella Fenum-graecum*	90°
Eschscholtzia californica	110°	*Lotus tetragonolobus*	110°
Lactuca sativa	114°	*Convolvulus tricolor*	120°
Helianthus argophyllus	110°	*Nicotiana Tabacum*	112°
Lolium perenne	110°	*Galtonia candicans*	105°

Seeds of *Lagenaria vulgaris* and *Heracleum giganteum* were unable to germinate after exposure to a temperature of 90° C.

The seeds of any one species show considerable individual differences in their power of resisting high temperatures. Thus a large percentage of a sample of seeds, say of *Avena sativa*, will germinate after exposure to a temperature of 100°–105° C., while only a very small percentage will germinate if exposed to 118° C.

The time needed for germination is increased by exposure to temperatures near the maximum. In a general way the higher the temperature to which the seeds are exposed the longer will be the period of germination.

Long exposure to a comparatively low temperature may prove more fatal than a short exposure to a high temperature. Thus seeds which will germinate successfully after one hour's exposure to 110°–120° C. will not germinate after twelve days' exposure to a temperature of 95°–97° C.

HENRY H. DIXON.

TRINITY COLLEGE,
DUBLIN.

THE EFFECT OF TEMPERATURE ON CARBON DIOXIDE ASSIMILATION[1].—This investigation differs from any which have preceded it on the same subject in the attention paid to uniformity in the environment of the leaves *before* the experiment. Recent work has shown that both the assimilation and the respiration of a leaf depend on its previous nutrition and temperature. For this reason a separate leaf was used for each temperature, care being taken to keep them for some time under exactly similar conditions.

Leaves of the Cherry Laurel (*Prunus Laurocerasus*) were employed throughout.

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

Since allowance had to be made for the respiration, this was taken for each temperature under exactly similar conditions to those existing in the corresponding assimilation experiments. A good curve showing the gradual increase of the respiration with the temperature was obtained.

The lowest temperature at which assimilation could be detected was −6° C. This is the first well-established case of assimilation below 0° C.

For temperatures between −6° C. and 33° C. it was found that assimilation is affected in exactly the same way as is respiration. Provided the illumination is sufficient, the assimilation increases with the temperature. At any given temperature the leaf is only capable of a limited absolute amount of assimilation, and increase of illumination beyond the amount requisite for this maximal amount produces no further effect at all. A greater assimilation can only be obtained by increasing the temperature. Thus the fundamental condition regulating the assimilation is the temperature, the intensity of the light occupying a secondary position similar to that of the percentage of carbon dioxide. This simple conception of the relation between temperatures and assimilation stands quite apart from all previous views.

For temperatures above 33° C. the result is complicated by the injurious effects of the temperature. The fatal temperature for Cherry Laurel leaves is in the region of 41–45° C., but the specific resistance of the individual leaves is very variable. Death is shown by a rapid decrease in the respiration, but it may be several hours before this ceases entirely. Exposure to light has a most marked effect in increasing the resistance of leaves to the effect of high temperatures.

Most interesting results were obtained from the prolonged exposure of leaves to high temperatures. It was found that the respiration of a leaf in the dark falls off much more rapidly than that of a leaf in the light, and the former can in no case be taken as a measure of the latter. At first assimilation and respiration are equally and similarly affected by the temperature, but later the assimilation ceases, while respiration is still active.

GABRIELLE L. C. MATTHAEI.

CAMBRIDGE.

ON THE DORSIVENTRALITY OF THE PODOSTEMACEAE, WITH REFERENCE TO CURRENT VIEWS ON EVOLUTION [1].—The paper read is an extract from a forthcoming paper in the Annals of the Royal Botanic Gardens, Peradeniya, upon the Morphology and Ecology of the Podostemaceae. This order shows a very far-reaching dorsiventrality of structure, both vegetative and floral. Two lines of argument are followed—one morphological, the other ecological. Commencing with the less modified types found in the order, which show a slight amount of dorsiventrality in the vegetative system and none in the floral, a series is traced through the more modified types, showing the progressive increase in dorsiventrality of the vegetative system followed throughout by an increase in that of the floral, showing first in the spathe and bracts, then in the androeceum, next in the gynaeceum, and lastly in the interior of the ovary. In the next place, the same series, regarded ecologically, shows that though the flowers are steadily more and more zygomorphic—a condition usually regarded as an adaptation to insect visits and accompanied by a horizontal position of the open flower—they at the same time stand stiffly erect, and are more and more anemophilous and autogamous.

The most reasonable explanation of these facts seems to be that the dorsiventrality of the flowers has been forced upon them, without reference to any advantage or disadvantage in the performance of their special functions, by the steadily increasing dorsiventrality of the vegetative system, the latter being due to the general effect of the total conditions of life acting on the hereditary peculiarities of the ancestral forms, whether directly or indirectly. Now the dorsiventrality of the floral organs is a character of high taxonomic value, and upon the various degrees of it the grouping of the Podostemaceae is chiefly founded, while it is always regarded as important in other families. The conclusion drawn is supported by the facts of dorsiventrality in other families, and if admitted as probable opens up a number of new points of view, and raises questions which must be settled one way or the other.

If one character of importance may thus be forced upon an organ or organs without reference to any advantage to that organ in the

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

performance of its functions, it seems only likely that others may; and consequently, that the study of adaptation must enter upon a new phase in connexion with the study of comparative and experimental morphology and of variation and correlation.

Another question raised is the insecurity of our conceptions of genera and other taxonomic groups, and the need of some more quantitative and phylogenetic basis. We divide the Podostemaceae, for example, into genera and sub-orders largely upon the degree of dorsiventrality displayed in the flowers and fruits, but we do not know the real quantitative or phylogenetic value of the distinctions. It also follows from the above conclusion that it is highly probable that many genera, species, sub-orders, or even larger groups, may be polyphyletic. We can easily imagine a group of allied or similar species, for example, all becoming more dorsiventral in their vegetative systems, and at last all of them showing the effect in the floral organs. As the effects in the latter seem to follow very definite rules, all these species may presently form a polyphyletic genus, there being no ancestor which has the generic characters. The same reasoning applies to higher groups, and in the very largest groups we are already beginning to perceive clearly that many, if not most, are more or less polyphyletic. It is evident that this view, if it prove true even in part, will help in clearing up the darkness which surrounds many of the problems of evolution, geographical distribution, &c.

JOHN C. WILLIS.

PERADENIYA.

FOLIAR PERIODICITY IN CEYLON[1].—The high temperature and humidity of the air in most parts of Ceylon allow almost continuous growth of the arborescent vegetation. There are, however, nearly two hundred species which become leafless at different times of the year.

External and internal factors affect the phenomena of defoliation and foliar renewal. The climatic effect is obvious from the fact that the majority of our deciduous species become leafless during our hottest and driest months. The deciduous trees respond only to one hot dry period of three or four months, and not to the dry part of each monsoon. Some species undergo complete defoliation twice per

[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

year; others exhibit periodic increase in foliar activity several times per year, in addition to a complete annual renewal, and many introduced species show great variation during their phase of acclimatization. In the northern districts, where the rains of the south-west monsoon are very feeble as compared with those at Peradeniya, the defoliation is considerably delayed. The climatic conditions in Ceylon are not equable enough to allow continued development along personal lines, and botanists desiring to study the personal equation in plant life should select a more equable area.

Internal forces are, however, obviously at work, as evidenced by the following facts:—

(*a*) Species retain full possession of their foliage or put forth new leaves when the temperature and dryness of the air is at the maximum.

(*b*) Some species drop their leaves and remain bare during our wet, cool months, when transpiration is at the minimum.

(*c*) Plants of the same species, on the same plots, are deciduous at periods varying by many weeks and months.

(*d*) The same species may undergo defoliation at approximately the same time of the year, though under the dissimilar climates of Peradeniya, Colombo, and Mannar.

The irregularity of foliar periodicity is very pronounced. There is not a month when all the trees are in full leaf.

The foliar periodicity of the evergreens is as complex as that of the deciduous trees, the foliar renewal taking place annually, semi-annually, or at other periods, all being subject to individual variations.

Complete defoliation and foliar renewal in temperate and tropical zones often results in the differentiation of rings of growth in the secondary xylem. The variation in our tropical species is so great that an exact knowledge of foliar activity must be at hand before the time-value of the rings of growth can be determined. Saplings may undergo foliar renewal in the first year, or several years may elapse before this occurs; mature plants may be characterized by annual, semi-annual, or periodic intervals of leaf production; further, many trees are repeatedly defoliated by the ravages of insects, bats, and Fungi.

Foliar periodicity is the most potent factor in determining the number and significance of the rings of growth, but for the complete interpretation of these a further knowledge of the rate of cambial activity and the independent effect of a hot dry season is necessary.

The rate of cambial activity is of especial value in determining the varying significance of the xylem differentiations in slow-growing deciduous or quick-growing evergreen trees.

HERBERT WRIGHT.

PERADENIYA.

THE MORPHOLOGY OF SPORANGIAL INTEGUMENTS[1].

Angiosperms.

Theories on the nature of the integuments of the *ovule*:—

1. *Foliar-appendage* theory: The integuments are the foliar appendages of the nucellus, which is a stem structure. Supporters of this view: Alex. Braun, Aug. St. Hilaire, Schleiden, Payer, Schmitz.

2. *Sui generis* theory: The integuments are special protective outgrowths of the sporangium, this latter being an organ *sui generis*. Evidence for this view is afforded solely by facts of ontogeny: Strasburger, Goebel, Eichler.

3. *Foliolar* theory: chiefly elaborated by last of undermentioned authors. Based entirely on the evidence of the abnormal metamorphoses of the ovule; these are of a very constant character, subject to control of very definite laws; the two integuments tend to proliferate into a three-lobed marginal leaflet or segment of the carpel, of which the terminal lobe, bearing the nucellus (when present) on its upper surface, represents the inner, while the two lateral lobes represent the outer integument; this is the extreme proliferated form. Between this and the normal ovule *every intermediate transitional form has been observed*, the extent of proliferation depending on the stage of development of ovule at which the tendency thereto sets in. Cases where proliferated outer integument appears as a simple lamina bearing normal cup-shaped inner integument containing nucellus on its *lower* surface; this structure arises morphologically by fusion of the inner margins of the two lateral lobes of the leaflet in the extreme proliferated form across the face of the latter, the terminal lobe at the same time becoming inrolled. The whole structure and mutual relationship of the parts is well shown by means of certain abnormal forms of foliage-leaf in *Syringa*. Hence the ovular integuments are the morphological homo-

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

logues of a three-lobed segment of the carpel. In the normal ovule the upper surface of the inner integument is directed inwards to the nucellus, this latter being morphologically an *emergence* from that surface, while the upper surface of the outer integument is directed outwards and away from the inner integument. This applies to all cases: Brongniart, Warming, Cramer, Čelakovský.

Gnetaceae.

Gnetum has normally three envelopes surrounding the nucellus. Theories as to their nature:—

Some regard outer integument as an ovary, others as a perianth, others again as a third integument. View maintained here that it is a perianth, as two integuments occur uniformly throughout Gymnosperms.

Ephedra and *Welwitschia* each possess two integuments. Theory as to nature of outer envelope in former: perianth.

Coniferae.

Views as to nature of the sporangial appurtenances:—

Baillon, Parlatore, Sperk, and others regarded the single envelope as the ovary; almost all other botanists agree as to its integumental nature. Seminiferous scale: Schleiden, Baillon, Strasburger, Masters, regard it as an *axial* structure; Sachs and Eichler as a *ligular placenta*; Delpino and Penzig as the *two lateral lobes of the bract*; R. Brown as a *carpel*; Van Tieghem as *the first and only leaf of an axillary bud*; Braun, Caspary, Von Mohl, Stenzel, Čelakovský, and several others as homologous with *the two first leaves* (*or their ovular representatives*) *of an axillary bud.* Čelakovský holds further that throughout Coniferae the ovule has two integuments; in Abietineae, Taxodineae, Cupressineae, Araucarieae, the outer integument is normally proliferated as a seminiferous scale, this being the exact counterpart of certain stages in the abnormal proliferation of the ovule of Angiosperms; in *Podocarpus*, *Cephalotaxus*, *Torreya* and *Ginkgo* it is the outer fleshy coat of the seed; in *Taxus*, *Microcachrys*, *Dacrydium*, it is the fleshy aril.

Cycadaceae.

Most authors regard ovule as possessing a single integument. Čelakovský considers it, along with *Cephalotaxus*, &c., as being *holochlamydeous*, i.e., having the two integuments intimately united, the outer fleshy and the inner woody.

Filicineae.

Homosporous Leptosporangiates.

Čelakovský's view here maintained that *soriferous segment of pinnule*, bearing as a rule sporangia on its lower (dorsal) surface, is the homologue of the outer integument of the ovule in Angiosperms, and *indusium* that of the inner integument. Evolutionary series can be traced beginning with—(1) *Thyrsopteris* and *Hymenophyllaceae*, where indusium, enclosing sorus, is *terminal* to leaf-segment = most primitive type. (2) *Dicksonia, Cibotium, Davallia, Lygodium*: the indusium, along with sorus, is displaced on to lower surface by outgrowth of leaf-segment. (3) *Cystopteris, Cyathea*, &c.: sorus arises from earliest stage onward on lower surface. (4) *Polypodium, Pteris cretica*: indusium completely disappeared; all these conditions have their homologues in stages of the proliferated ovule.

Heterosporous Leptosporangiates.

In Salviniaceae the fruit is equivalent to an ovule with one integument; indusium = inner integument, and leaf-lobe bearing sorus is probably homologous with outer integument. Striking resemblance between monangic sorus of *Azolla* and an ovule. In Marsiliaceae fruit = compound fruit of Salviniaceae. In *Pilularia* it is homologous with the pinnately 4-foliolate leaf of *Marsilia*; in *Marsilia* with a pinnately multifoliolate leaf. Outer wall of sporocarp is homologous with *upper* surface of outer integument of ovule; indusium, enclosing *many sori*, with inner integument of latter.

In most Filicineae sorus is polyangic: in Schizaeaceae and *Azolla* it is monangic, as in most Phanerogams. In the latter polysorous character occurs abnormally in *Hesperis* and normally in *Cupressus*, where outer integument bears on its dorsal surface several inner integuments containing nucelli.

Lycopodiaceae.

Isoëtes: View of Čelakovský held that *velum* is equivalent to indusium of Ferns, and *ligule* to soriferous leaf-segment of latter; hence sporangium along with these two organs = ovule with its two integuments.

Lepidocarpon: 'Integument' is probably equivalent to velum of *Isoëtes*, but better developed, and thus to inner integument of ovule. Ligule is regarded as really situated outside the 'integument'; the latter is merely a special modification of velum, which is here open at its distal end.

In other genera either velum or both this and ligule have either quite aborted or never been developed, which is probably result of efficient protection of sporangia by peltate ends of sporophylls, as in *Lepidodendron* and *Spencerites.*

In Equisetaceae peltate sporophylls afford necessary protection.

W. C. WORSDELL.

KEW.

THE NATURE OF THE VASCULAR SYSTEM OF THE STEM IN CERTAIN DICOTYLEDONOUS ORDERS [1]. — The object of the present thesis is to show, from anatomical data, that no hard-and-fast line exists between the two classes of Dicotyledons and Monocotyledons. The hollow vascular cylinder of the stem of a great number of dicotyledonous orders, if not of all, has been derived from a system of scattered bundles such as is characteristic of the stem of almost all Monocotyledons. The flowering-stem and peduncle, as being those parts of the caulome which have undergone least modification owing to the necessities of adaptation to external conditions, exhibit, as a rule, most clearly the primitive structure which in the vegetative parts has become obscured. The axial organs of the seedling, owing to their limited diameter and the small number of leaf-traces concerned in the building-up of the vascular system, cannot as a rule possibly exhibit the primitive scattered arrangement of the bundles.

As the stem increased in height and became more woody, and the leaves smaller and more numerous, the scattered arrangement of bundles in the stem (chiefly a result of the latter being mainly built up of large leaf-bases from which great numbers of pluriseriate bundles entered the axis) gradually became modified into that of a hollow cylinder, which was necessary both to support the bending-strains from a tall stem, and to facilitate the continuous centrifugal addition of new conducting-tissues by means of a secondary meristem. The stems of plants possessing scattered bundles support bending-strains by means of a sub-peripheral sclerotic band, and, in those cases where a secondary meristem is present, increase their conducting-tissue by the continuous centrifugal formation of new scattered bundles accompanied by interfascicular tissue.

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

As far as the investigation has gone, the primitive scattered arrangement of bundles can be traced in the stem of about thirty dicotyledonous orders, viz., Ranunculaceae, Nymphaeaceae, Berberidaceae, Calycanthaceae, Magnoliaceae, Anonaceae, Cruciferae, Fumariaceae, Papaveraceae, Geraniaceae, Umbelliferae, Compositae, Plumbaginaceae, Acanthaceae, Campanulaceae, Solanaceae, Cucurbitaceae, Begoniaceae, Polygonaceae, Amaranthaceae, Chenopodiaceae, Nyctaginaceae, Phytolaccaceae, Melastomaceae, Cactaceae, Ficoideae, Orobanchaceae, Piperaceae, Balanophoraceae, Araliaceae, and no doubt many more will reveal it.

Other characters very frequently accompanying the above feature in dicotyledonous stems are :—

(*a*) V-shaped xylem ; (*b*) reticulate and circular phloem ; (*c*) bundle often concentric, with central circular phloem, and when collateral often with irregular orientation ; (*d*) few, large vessels in xylem ; (*e*) bundle rounded or elliptic and enclosed in sclerotic sheath ; (*f*) very small development of cambium ; (*g*) largest bundles occur nearest centre of stem, the smallest nearest the periphery ; (*h*) rudimentary character of many bundles, representing those members of the vanishing scattered system which are not destined to form part of the functional cylinder ; (*i*) limit between cortex and cylinder marked by a sclerotic zone ; (*j*) cortical system of bundles which are often concentric in structure ; (*k*) trimerous character of some or all of the floral whorls ; (*l*) several orders exhibit 5-merous single perianth-whorl in flowers, which, as Čelakovský has shown, is derived from two trimerous whorls by conversion of lowermost perianth-member into a bract.

In some Monocotyledons the scattered bundles have become very peripheral, and even reduced to a single series or row of bundles.

In some cases amongst Dicotyledons where the scattered arrangement has vanished from the stem it can still be found in the less modified foliage-leaf, especially where the petiole is cylindric in contour or possesses a considerable diameter.

In view of the above facts the author cannot agree with those writers who maintain that the vascular structure of the seedling stem of Dicotyledons generally proves it to be primitively tubular in character. The same will, for reasons above set forth, apply to the case of Monocotyledons.

W. C. WORSDELL.

KEW.

ON SOME NEW FEATURES IN RELATION TO LYGINODENDRON OLDHAMIUM[1].—Since the year 1872, when the late Dr. W. C. Williamson published his memoir, part iv, in the 'Phil. Trans. Roy. Soc.' on *Dictyoxylon*, *Lyginodendron* and *Heterangium*, this genus of fossil plants has undergone a good many alterations or modifications at the hands of the palaeobotanist.

In the memoir above quoted *Lyginodendron oldhamium* is described as an unbifurcating stem, but giving off very small branches (see p. 387, Figs. 14 and 16, Pl. XXV, loc. cit.), and in some respects similar to a Lepidodendroid stem.

In his memoir, part vi, 1874, he describes fully a stem to which he originally gave the name of *Edraxylon*, but to which he now gave the name of *Rachiopteris aspera.* (See Figs. 1 to 13, 'Phil. Trans. Roy. Soc.,' 1874, part vi. Fig. 13 he describes as a petiole with pinnules and leaflets.)

In memoir, part vii, 1875, he describes a series of specimens under the name of *Kaloxylon Hookeri.* (See Figs. 23 to 38, Pl. 5, 6, and 7, loc. cit.)

The small branches which Williamson described in 1872 under the name of *Kaloxylon* have since been proved to be the roots of *Lyginodendron.*

In the case of *Rachiopteris aspera*, it is now well known that it is the leaf-stalk or petiole of *Lyginodendron*, whilst the fossils known as *Sphenopteris Höninghausi* and *Sphenopteris distans* are the foliage of *Lyginodendron.* (See Williamson's memoir, 1890, part xvii; also Williamson's and Scott's memoir, Phil. Trans. Roy. Soc. 1895, part iii).

In most cases when this stem has been described it is as an unbifurcating or unbranching stem.

In Dr. D. H. Scott's 'Studies in Fossil Botany,' p. 321, he says that 'No stem has ever been observed to branch; it does not follow that it never did so, but branching must have been very rare.' For some time back I have had various specimens in my possession which I have collected from Dulesgate, near Todmorden, Lancashire, which to me have had the appearance of giving off a branch; but during the last few months I have discovered two specimens which

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

have set all doubt on this point at rest. Both specimens are in a first-class state of preservation.

The first of the two specimens was collected in March last, and is now in the possession of Dr. D. H. Scott; it shows a series of twenty-four sections cut transversely. The series runs through two internodes; the first shows the leaf-trace just about to leave the periderm, and the stele is commencing to take a crescent-like form on the opposite side to that of the leaf-stalk which is being given off, and so on till the stele of the branch and stem are completely separated, and till the second leaf-stalk is given off. There are also several roots given off, which dichotomize immediately after leaving the cortex.

In the above stem there are a series of four double leaf-trace bundles. The entire diameter of the stem is three-quarters of an inch, and it was about three inches long.

The last specimen I have discovered is also from Dulesgate, from a mass of small nodules, one part of which contained a quantity of foliage, broken pieces of Sigillarian bark, *Rachiopteris bibractensis*, and various other fragments.

In this there is a series of five leaf-trace bundles. This was about $1\frac{1}{8}$ inch in diameter and about four inches long.

The stem is not quite whole; a portion of one side is missing, but the development of the branch is seen quite perfectly.

The above two specimens show that *Lyginodendron* had a branching stem; also that the branch was given off in the one case between two leaf-stalks and in close proximity to several roots. This shows that it has been a plant of considerable growth.

The position of the roots also shows they must have been aerial roots, and not, as generally accepted, basal or confined to the basal regions of the stem.

There is one other point we want to make clear, and that is the generative organs of the plant. So far they have escaped our notice, but I expect that we may before very long be in a position to state definitely what were the fructificative or the regenerative organs of these most interesting fossil plants.

The detailed description of the above specimen is left in the hands of Dr. D. H. Scott.

JAMES LOMAX.

BOLTON.

ON THE OCCURRENCE OF THE NODULAR CONCRETIONS (COAL BALLS) IN THE LOWER COAL MEASURES [1].—During the last fourteen or fifteen years that I have worked amongst fossil coal plants, I have been struck with the diversity of ways in which the different genera and species of plants occur in the different calcified nodular masses which we find so plentiful in the several localities where they are found embedded in the coal.

At the meeting at Bradford in 1900 there was a joint discussion between the Geological and Botanical Sections as to whether the plants which entered into the composition of the different coal seams grew *in situ* or not, and from that discussion I gathered that the opinions were evenly balanced. Consequently, from that time to the present I have taken a very great interest in the position in which I have found the nodules embedded in the coal seam. As we all know, there is only one seam of coal in which we find these nodular concretions, and which is given different names in the different districts where it is worked. In the Yorkshire district it has the name of the Halifax Hard Bed; in Oldham, the Upper Foot Mine; Bacup, the Mountain and Union Mine; Todmorden, which includes Dulesgate, the Union Mine; Sheffield, the Gannister Mine; and so on. But, where it is found, in nearly all cases the roof contains similar concretions, with this exception—that the fossil remains contained therein are of marine origin, while those found in the coal underneath are always of vegetable origin. Sometimes, but not very often, we may find a stray stem in the nodular concretions from the roof, such as *Dadoxylon*, *Calamites*, *Lepidodendron Harcourtii*; and the best specimens of *Rachiopteris Grayii* that have ever been found in the English Coal Measures I found in one of these nodules from the roof.

It is not my intention to enter into the chemical composition of these concretions, only so far as to state that in most cases they consist of calcium carbonate and iron pyrites in varying proportions; and in a few places we find that there is a mixture of silica with the carbonate of lime. I have obtained from three localities portions of the seam with these concretions of various sizes embedded in the coal. Some of the pieces I have obtained have been over two feet long and one foot in diameter. I have cut these in various directions to show

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[1] Abstract of paper read before Section K of the British Association, Belfast, 1902.

the plant tissues—how they ran, whether one nodule was coincident with its neighbour (that is, if the tissues in the one nodule ran on into the next), and if the tissues of one nodule ran parallel with those of a succeeding nodule either higher or lower in the seam. In that object I have been very successful, as the specimens will show.

During these investigations it has been gradually forced on me that, at least in this case, these plant remains have not grown on the spot where we now find them, and for the following reasons:—In one nodule out of a number which were joined together by the surrounding coal we have a portion of a transverse section of *Stigmaria*, about one-half the whole section; and in the nodule adjoining to the right there is no portion of this *Stigmaria* whatever, but a fragment of a longitudinal section of *Amyelon radicans* and Stigmarian rootlets. In the one to the right above it there is still no part of it, and in the one to the left we have no part of it either. It is so with the various masses I have examined. Some we have which have contained nothing but Stigmarian rootlets; their neighbours would contain *Lyginodendron*, *Rachiopteris bibractensis*, and so on, in short pieces; another, Stigmarian rootlets, with a short piece of *Lepidodendron fuliginosum*, which could not be seen from the outside of the nodule, but was totally enveloped by the rootlets; and so on.

If these plants had grown on the spot where we now find them, and been petrified, we should have certainly found, where we had an abundance of nodules, that these stems would have been continued from nodule to nodule; but that is not so. What we find is a quantity of fragments of short pieces of stems, &c., some with the cortex, some without, some split in fragments, and so on. The natural conclusion is that the various portions of plants have been carried into their present position after being broken in fragments, and before petrifaction, or they have been carried from a parent bed after petrifaction.

JAMES LOMAX.

BOLTON.

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