On Welwitschia, a new Genus of Gnetaceae.

By J.D. Hooker. 1863.

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CONTENTS.

PART I.—1863.

I. *On* Welwitschia, *a new Genus of* Gnetaceæ. *By* JOSEPH DALTON HOOKER, *M.D.*, *F.R.S.*, *V.P.L.S.*, *F.G.S.* . . . . . page 1

2135
3

TRANSACTIONS

OF

THE LINNEAN SOCIETY.

I. *On* Welwitschia, *a new Genus of* Gnetaceæ.

By JOSEPH DALTON HOOKER, *M.D., F.R.S., V.P.L.S., F.G.S.*

(Plates I.–XIV.*)

Read January 16th, and December 18th, 1862.

Discovery and general remarks, p. 1.
Technical description, p. 6.
Trunk, p. 7. Anatomy of, p. 10. Development of, p. 16.
Leaf, p. 17. Comparison with those of Conifers, p. 19.
Inflorescence, p. 20.
Hermaphrodite cone and flowers, p. 21. Comparison with *Gnetaceæ*, p. 23.
Female cones, p. 24. Flower, &c., p. 25. Comparison of, with *Gnetaceæ*, p. 27. Ovule, p. 27. Comparison with gymnosperms, p. 28. Carpellary theory of integuments, p. 30.
Fertilization and embryogeny, p. 31. Development of embryo, p. 34. Seed, p. 37. Ovular theory, p. 37. Comparison with *Coniferæ*, *Gnetaceæ*, *Loranthaceæ*, and *Santalaceæ*, p. 38.
Summary, p. 40.

THE first notice of this singular plant that reached Europe was contained in a letter addressed by its discoverer, Dr. Frederic Welwitsch, A.L.S., to Sir William Hooker, dated St. Paul's, Loanda, August 16, 1860. This letter, which was at once communicated to the Linnean Society and published in its Journal of Proceedings (vol. v. p. 182), was shortly followed by another, announcing the intention of its finder to send the specimens to Kew for examination, and expressing his hope that the results might be published in the Linnean Society's Transactions.

Dr. Welwitsch's botanical attainments being well known and justly appreciated, his brief account sufficed to assure botanists that he had made a most remarkable discovery; and soon after the publication of his letter, inquiries respecting the plant reached Kew from several parts of Europe; indeed I have been assured by those who remember it, that, since the discovery of the *Rafflesia Arnoldii*, no vegetable production has excited so great an interest as the subject of the present memoir.

* The expense of drawing these plates on stone was defrayed by a grant from the fund for the promotion of science, placed annually by Parliament at the disposal of the President and Council of the Royal Society.

Before describing in detail the structure of this plant, and discussing its many anomalies, I shall give a brief general account of its appearance and prominent characters, partly from the descriptions of its discoverer, and partly from the specimens sent home by himself and others.

The *Welwitschia* is a woody plant, said to attain a century in duration, with an obconic trunk about 2 feet long, of which a few inches rise above the soil, presenting the appearance of a flat, two-lobed, depressed mass, sometimes (according to Dr. Welwitsch) attaining 14 feet in circumference (!), and looking like a round table. When full grown, it is dark brown, hard, and cracked over the whole surface (much like the burnt crust of a loaf of bread); the lower portion forms a stout tap-root, buried in the soil, and branching downwards at the end. From deep grooves in the circumference of the depressed mass two enormous leaves are given off, each 6 feet long when full-grown, one corresponding to each lobe: these are quite flat, linear, very leathery, and split to the base into innumerable thongs that lie curling upon the surface of the soil. Its discoverer describes these same two leaves as being present from the earliest condition of the plant, and assures me that they are in fact developed from the two cotyledons of the seed, and are persistent, being replaced by no others. From the circumference of the tabular mass, above but close to the insertion of the leaves, spring stout dichotomously branched cymes, nearly a foot high, bearing small erect scarlet cones, which eventually become oblong and attain the size of those of the common spruce fir. The scales of the cones are very closely imbricated, and contain when young and still very small, solitary flowers, which in some cones are hermaphrodite (structurally but not functionally), in others female. The hermaphrodite flower consists of a perianth of four pieces, six monadelphous stamens with globose 3-locular anthers, surrounding a central ovule, the integument of which is produced into a styliform sigmoid tube, terminated by a discoid apex. The female flower consists of a solitary erect ovule contained in a compressed utricular perianth. The mature cone is tetragonous, and contains a broadly winged fruit in each scale. Its discoverer observes that the whole plant exudes a resin, and that it is called "Tumbo" by the natives, whence he suggests that it may bear the generic name of "*Tumboa*;" but this he withdrew at my suggestion, for reasons which I shall presently give. It inhabits the elevated sandy plateau near Cape Negro (lat. 15° 40′ S.), on the S.W. coast of Africa.

In his letter to Sir William Hooker, Dr. Welwitsch says nothing definite as to the affinities of this plant, but compares the stigma (or, as I consider it, the apex of the ovular integument) to that of certain *Proteaceæ*, the cones to those of certain *Abietineæ*, the resin to that of *Coniferæ*, and the fibrous substance in the integument of the seed to that of *Casuarina*.

After his arrival in Portugal in 1861, Dr. Welwitsch addressed to M. DeCandolle at Geneva a very interesting letter on the vegetation of Benguela and the neighbouring parts of Africa, in which the "Tumbo" was again described. In this letter, which was dated Lisbon, April 20, 1861, and communicated to the 'Bibliothèque Universelle de Genève,' Dr. Welwitsch makes the following remarks:—"This is assuredly one of the most extraordinary plants that exist in intertropical Africa; and notwithstanding certain

resemblances of structure with *Coniferæ* and *Casuarineæ*, and even with *Proteaceæ*, I believe we have here the type of a new family."

During the autumn of 1861, and some months before the arrival in England of Dr. Welwitsch's specimens, Sir William Hooker received from Mr. Thomas Baines, an accomplished artist, then travelling in the Damara Country, a box containing some admirable coloured drawings illustrating the vegetation of that country, together with the cones and a sketch of a plant which I at once recognized as generically, if not specifically, identical with that discovered by Dr. Welwitsch. Unfortunately the box was not accompanied by any letter, nor the specimens and drawings by descriptions: they appear to have been collected in lat. 24° or 25° S., about 500 miles south of Cape Negro, where Dr. Welwitsch found his plant. They were gathered on the 10th of May, and were packed without being dried, along with some gigantic succulent aloe leaves and flowers; and not arriving at Kew until late in the following autumn, they were then all in a very decayed state. The cones contained ripe seeds, the albumen of which was perfectly rotten; by careful dissection of them, however, and hardening them with alcohol, I had no difficulty in proving their great similarity in development and structure with the seeds of *Cycadeæ* and *Gnetaceæ*. Mr. Baines's sketch of the plant (Plate I. fig. 2) somewhat differs from Dr. Welwitsch's description, in presenting the appearance of five leaves spreading on the ground, instead of two only; they are, however, curled, and split into thongs, though not so deeply as Dr. Welwitsch describes. Mr. Baines's sketch is, however, more artistic than scientific; the insertion of the leaves is not precisely indicated, nor are their bases separated. From the copy, it will be seen that it may represent a plant with five leaves, or two split respectively into two and three, or even one leaf split into five! The name "Tumbo" is appended by Mr. Baines to the drawing of this plant and also to that of an aloe; but on a slip of paper accompanying the specimen, he has written, "Branch of the cones of a plant called by the Hottentots 'Ghories,' and by the Damaras 'Nyanka-Hykamkop.'"

On the arrival of Mr. Baines's specimens and drawings, I immediately communicated the fact to Dr. Welwitsch, urging him to send his materials to Kew as he had proposed; and as he had done me the honour of desiring that I should publish them, I offered to do so. At the same time I directed his attention to the fact that the name of "*Tumboa*," which he had proposed, was, according to Mr. Baines, applicable to various plants, whilst other names were applied to this; and I suggested the propriety of his withdrawing it, and permitting me to replace it by that of *Welwitschia** *mirabilis*. To this Dr. Welwitsch at once consented; and two fine young specimens, together with flowers, and cones with unripe seeds, soon afterwards arrived, along with his original drawings, proving the identity of his plant with that of Mr. Baines; and I have now the pleasure of commemorating Dr. Welwitsch's indefatigable and successful botanical labours in tropical Africa by attaching his name to a discovery of his own, and one that I do not hesitate to consider the most wonderful, in a botanical point of view, that has been brought to light during the present century; for an attentive study of the structure of its vascular system, as well as of its reproductive organs, and of the evidences we have of its functional peculiarities and mode of development, will disclose in all these points very singular anomalies, which even

* *Welwitschia*, Reich. Handb. p. 94, is reduced by Bentham to *Gilia* (DC. Prodr. ix. 310).

appear in some instances subversive of theoretical axioms hitherto considered as fundamental in Botany.

After receiving Dr. Welwitsch's specimens, I wrote to my friend Joachim Monteiro, Esq., a very intelligent and successful zoologist residing at Loanda, who had sent many seeds and bulbs to the Royal Gardens of Kew, requesting him to procure some plants of *Welwitschia* for me, through any correspondent he might have in the Cape Negro district. Mr. Monteiro instantly replied to me from Cuio Bay, where he happened to be travelling, informing me that he had found the plant some weeks before the receipt of my letter, and, feeling assured that it would interest me, had already packed a box with six fine specimens, and a bottle of cones preserved in spirits. The following is a copy of Mr. Monteiro's letter :—

"Cuio Bay, February 25, 1862.

"My dear Sir,—I was delighted to receive a week ago your letter of December last, and still more so in being able to comply in part with your wishes with regard to *Welwitschia mirabilis*, as I today forward by the steamer to Lisbon a box containing one large and five small specimens of this plant. I also send you in the same box a glass bottle with the cones that I cut off the large specimen.

"These I myself collected at Mossamedes (Little Fish Bay of the English charts) in December last. For the large specimen I had to send a black with a hoe, to dig it out of the very hard soil in which it was growing; but the rascal cut the leaves off, as you will see.

"On my journey to visit a copper-mine about thirty miles distant from the coast, I passed a plain about three miles across, on which this plant was growing abundantly; that is to say, I saw about thirty specimens on my line of march. The plain was perfectly dry, and bare of other vegetation than the *Welwitschia* and a little short grass. The ground was of a hard quartzose schist. The *Welwitschia* was generally growing near the little ruts worn in the plain by running water during the rainy season. The large specimen sent was the largest that I saw; but I was careful to inquire of several Portuguese belonging to the Possession at Pinda (Cape Negro), whether Dr. Welwitsch's description to me, of these plants being found with tops measuring 6 feet across, was correct or not; and they all assured me they had seen them of that size and even larger, with the ribbon-like leaves 2 and even 3 'braças' (fathoms) long. I was told that the largest they had seen were on the banks of the River Croquis, a little to the north of Port Alexandre. The main land of this is Pinda, where there is a small Portuguese force, several fishermen, plantations, &c. A friend of mine, the principal trader at Mossamedes, is the owner of a cotton-plantation at Pinda; and I will write to him by the next steamer to procure for me the very largest specimen of the *Welwitschia* that can be found in the neighbourhood, or that can be transported to the coast.

"I know that Dr. Welwitsch desired several persons at Little Fish Bay to procure specimens of this plant for him, but it is very likely they will never do so; but I think you can depend on my friend getting one of the largest.

"All the plants I saw were growing flat on the ground; none with the top raised above the surface, as represented in your drawing; but I know not whether this may perhaps be the case with the larger ones. I was unable to obtain seeds; nor had I time to gather more specimens: I transplanted a young one into a box with earth, but it rotted. I have information that the *Welwitschia* is found growing in the vicinity of the River San Nicolau, in 14° 20′ S. lat. About here it is unknown to the natives, so that you may consider 14° S. lat. as its most northern limit.

"Yours very sincerely,

"J. J. Monteiro."*

* This letter also contains the following account of a most curious plant, not yet known to botanists :—

"I found a very extraordinary-looking plant growing rarely near Little Fish Bay, which in appearance is like a great

Again, since the receipt of the specimens mentioned in this letter, I received, only ten days ago, a further supply from the same indefatigable correspondent, consisting of four very large specimens of a much shorter obconic form than any heretofore received, and with the terminal lobes greatly dilated, much divided, and almost erect, so that the crown of the plant, with its dark rugose ridges, bears a fanciful resemblance to the open mouth and palate of some monstrous animal; these I have had figured at Plate V. figs. 1–4.

I have also to acknowledge the receipt of a very fine Damara Land specimen (Plate V. fig. 5) from Mr. C. J. Andersson, the same gentleman who forwarded the cones and drawing from Mr. Baines, and through whom Sir W. Hooker had written to Mr. Baines, begging him to procure some more specimens with as little delay as possible, and to favour him with any information about their habits and habitat. Mr. Baines being absent, this letter was answered by Mr. Andersson himself, and I have now the pleasure of laying its interesting contents before the Society.

"*To Sir William Hooker.*

"Damara Land, Otjim Cinguè, February 12th, 1862.

"Sir,—Mr. J. Logier, of Cape Town, forwarded to me lately a letter from you to Mr. Thos. Baines, artist, now travelling in the interior of these parts. As Mr. Logier correctly conjectured that his friend would not just now be within hail, he requested me to peruse the letter in question, in hopes of my being able to throw some light on the subject of your inquiries. It is on the strength of this that I now address you.

"The plant sent you by Mr. Baines from Damara Land, and which seems so much to have awakened your curiosity, is, I think, well known to me. Indeed, it is so peculiar as scarcely to be mistaken even by the rudest description. In the first instance, it is only found in one single locality—that is, as regards Damara-Land—which locality is exceedingly circumscribed. It grows moreover in sandy soil, and luxuriates when it can find a few stones where to fix its extraordinary tap-root, penetrating often several feet deep; so that it is, indeed, a work of labour and patience to extract one single plant. I have been thus occupied more than an hour, and even then I have come away with only a *portion* of the root. It has 'leaves' of a dark-green colour, of which several spring from the same stem or root, spreading and curling along the ground. They will tear into innumerable shreds, each of which is exceedingly strong and tenacious; they are straight-grained—that is, you can tear them from top to bottom without deviating a single line from a straight course; and they attain sometimes a length of several feet. A small portion towards the points, and sometimes the sides, will be found slightly withered; in other respects they might almost be considered evergreen. The plant has cones. The root is usually found flush with the surface, or just rising an inch or two above it, the *soi-disant* leaves springing immediately from it.

"Rain rarely or never falls where this plant exists*. I have crossed and recrossed Damara Land throughout its entire length and breadth, but only found the plant growing on that desperately arid flat stretching far and wide about Waalvisch Bay, or between the 22nd and 23rd degrees of S. lat. It is most

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full wine-skin. I was told that Dr. Welwitsch pronounced it to be a great curiosity: it is called by the Portuguese, from its appearance, 'Odres.' Some of them could not have weighed less than a ton. I have here with me two young plants in a flourishing condition, as well as another plant brought by a Portuguese trader from the Gambos country in the far interior, on account of the wonderful medicinal virtues of its milky juice. It bears most curious unsymmetrical little flowers. These, as well as several other botanical curiosities, I shall forward as soon as your climate allows them a warmer welcome."

* Mr. Galton informs me that, though no rain ever falls, the night dews are so heavy that a small party of men, residing on the coast, is supplied thereby with water throughout the year.

common about the lower course of the river Swakop (see Map of my work 'Lake Ngami'). But I feel my description is very inadequate to the subject, and shall therefore endeavour to procure the plant itself, and forward it at an early date to England, where I trust it will arrive in sufficiently healthy condition to enable you to identify it satisfactorily. Indeed, I would have sent a specimen years ago, had I not been under the impression that you had already specimens of it; for I assisted a Mr. Wollaston once to excavate a couple, which I thought he purposed presenting to the Kew Gardens. I know that the specimens were received at the Botanical Garden at Cape Town; for I saw them there only the other day, pitched away among some rubbish. No one seemed to take the slightest notice of them, which rather surprised me, since the plant cannot well escape even the dullest eye, it is so singular.

"I remain, Sir, your obedient Servant,

"CHAS. J. ANDERSSON."

Before proceeding to a detailed description of this plant, I have to record the great obligations I am under to Professor Oliver, who has taken equal interest with myself in its investigation, has verified most of my observations, has directed my attention to several important points which I might otherwise have overlooked, and who has made the greater part of the anatomical drawings contained in Plates XII., XIII., and XIV. But for his unremitting attention to my progress through some of the most minute and difficult points, and especially those connected with its embryogeny, confirming the views I had myself formed, I should have felt great diffidence in laying before this Society some of its most anomalous features.

WELWITSCHIA, gen. nov.

DESCR. GEN.—Dioica? *Inflorescentia* strobilacea. *Strobili* oblongo-cylindracei, 4-goni. *Squamæ* 70–90, arcte 4-fariam imbricatæ, latissime ovato-orbiculatæ, 1-flores, utrinque nervis 2–3 flabellatim ramosis aream hyalinam centralem enervem includentibus percursæ. *Flores* in axillis squamarum coriacearum strobilorum parvorum siti, sessiles, compressi. FL. HERMAPH. *Perianthium* 4-phyllum: foliola membranacea; 2 exteriora lateralia, falcata, anguste spathulata, acuta, dorso carinata v. subalata; 2 interiora late obovato-spathulata, unguibus in tubum compressum connatis, imbricata. *Stamina* 6, filamentis crassis cylindricis subulatis basi in tubum crassum connatis, post anthesin geniculatim reflexis, æstivatione inflexis; *antheræ* capitatæ, obtuse 3-gonæ, 3-loculares, vertice rima 3-cruri dehiscentes; *pollen* simplex, ellipsoideum. *Carpellum* 0. *Ovulum* in centro floris, solitarium, compressum, ovoideum, lata basi sessile; integumentum simplex, calyptræforme, apice in tubum tortum cylindricum styliformem disco papilloso stigmatiformi terminatum desinens; nucleus conicus, ima basi 2 nervis, sacculo embryonali 0. FL. FŒM. *Perianthium*: utriculus simplex, hyalinus, compressus, 2-alatus, post anthesin ampliatus. *Ovulum* solitarium, ut in flore hermaphrodito, processu tamen integumenti stricto apice lacero non dilatato, et nucleo sacculo embryonali (endospermio repleto) donato. *Fructus* siccus, e perianthio ampliato (pericarpio) orbiculari medio semen nudum fovente conflatus. *Pericarpium* orbiculare, basi subcordatum v. breviter stipitatum; pars centralis obovoidea, cava, coriacea, ala latissima hyalina eleganter undulata circumdata; loculus superne in canalem tenuem alam percurrentem et processum styliformem integumenti exsertum foventem productus. *Semen* erectum, obovoideum, compressum, sessile, ad apicem calyptra membranacea (integumento ovuli) in processum styliformem producta terminatum; testa (nuclei parietes) carnosula, utrinque ad latera 1–2 nervis, apice in conum carnosum desinens; albumen obovoideum, densum, superne in collum carnosum annulare constrictum. *Embryo* in cavitate albuminis receptus, elongatus; cotyledones parvæ, planiusculæ, compressæ; plumula 0; radicula teretiuscula, v. medio paulo incrassata, extremitate radiculari incrassata, carnosa, abrupte in filum suspensorem longissimum tortum desinente.

Planta lignosa, simplex, 2-phylla, gummi colloideum exsudans. *Truncus* crassus, obconicus v. turbinatus v. subglobosus, plus minus compressus, ambitu infra folia transverse sulcatus v. undulatus, basi in radicem fusiformem brevem v. elongatam inferne ramosam contractus, supra folia in lobos 2 amplos depressos monstrosos rugosos floriferos foliis respondentes dilatatus. *Folia* 2, opposita, longissima, lineari-ligulata, obtusa, crasse coriacea, mox valde dilacerata, et in lacinias angustissimas emarcidas basi sæpe discretas fissa, marginibus integerrimis, utrinque nervis parallelis creberrimis striata; basibus membranaceis truncum fere circumambientibus, et in fissuram horizontalem profundam trunci receptis. *Lobi floriferi* valde indurati, trunco latiores, medio depressi, integri v. multilobati, in vertice jugis concentricis rugosis foveolatis (annis totidem? floriferis respondentibus) operti. *Pedunculi strobiliferi* numerosi, ambitu loborum in jugis externis siti, dichotome ramosi, teretes, pseudo-articulati, ad nodos tumidi et 2-bracteati, bracteis oppositis persistentibus. *Strobili floriferi* parvi; *fructiferi* 2-pollicares, coccinei, squamis persistentibus. *Flores* minuti. *Fructus* amplus, membranaceus.

WELWITSCHIA MIRABILIS.

Hab. In desertis petrosis oræ occidentalis Africæ tropicæ australis prope Caput Negro (*F. Welwitsch, et J. J. Monteiro*). Damara Land prope Waalvisch Bay (*T. Baines et C. J. Andersson*).

Locus in Systemate Naturali.—Non obstantibus forma et structura trunci, dispositione systematis vascularis, floribus hermaphroditis, et evolutione anomala embryonis, planta ista inter *Gnetaceas* prope *Ephedram*, ob inflorescentiam strobilaceam, squamas 2-nervias, perianthii formam, et stamina, ovula et semina omnino cum *Gnetaceis* congruentia, sine dubio militat.

Genera tres *Gnetacearum* notis sequentibus dignoscas.

1. GNETUM. *Squamæ* strobili heterogami in discos carnosos peltatos confluentes, post anthesin immutatæ, omnes floriferæ. *Flores* conferti, unisexuales, filis articulatis immixti. FL. ♂. *Perianthium* 2-labiatum. *Stamen* solitarium, filamento 2-nervi, loculis polliniferis 2. FL. ♀. *Perianthium* ampullaceum. *Ovuli* integumenta 2. *Fructus* drupaceus.—Arbores *erectæ v.* arbusculæ *scandentes.* Folia *opposita, ampla, penninervia.*
2. EPHEDRA. *Squamæ* strobili homogami per paria connatæ, post anthesin ampliatæ v. carnosæ, inferiores vacuæ, 2 terminales majores 1-floræ. *Flores* unisexuales, filis articulatis 0. FL. ♂. *Perianthium* membranaceum, 2-labiatum. *Stamina* 2–8, monadelpha; antheræ capitatæ, 2-loculares. FL. ♀. *Perianthium* ampullaceum, 3-gonum. *Ovuli* integumentum solitarium. *Fructus* siccus, squamis amenti membranaceis v. carnosis inclusus.—Suffrutices *aphylli, rhizomate lignoso; ramis teretibus, articulatis, striatis, ad nodos squamosis.* Folia *squamæformia.*
3. WELWITSCHIA. *Squamæ* strobili homogami 4-fariam imbricatæ, perplurimæ floriferæ, fructiferæ valde auctæ. *Flores* hermaphroditi et fœminei. FL. ☿. *Perianthium* 4-phyllum, foliolis 2-seriatis, interioribus connatis. *Stamina* 6, monadelpha; antheræ 3-loculares. *Ovuli* integumentum solitarium, disco stigmatiformi terminatum. FL. ♀. *Perianthium* ampullaceum, compressissimum, 2-alatum. *Ovulum* maris, sed processu styliformi recto apice simplici lacero. *Fructus* siccus, squamis membranaceis strobili velatus.—Truncus *obconicus, lignosus.* Folia 2, *opposita, longissime linearia, dilacerata, nervis parallelis.*

Trunk.—External Characters.

The trunk of *Welwitschia* differs essentially in its mode of development from that of any other plant known to me, and indeed does not even approximate to any. It consists of three more or less distinct portions:—(1) a compressed swollen body, which I shall call the *stock*; this gives off the leaves, and is surmounted by (2) a bilobed *crown*

appropriated to the inflorescence; whilst, below, it is more or less suddenly contracted into (3) a subcylindrical *tap-root*, that branches towards its base.

All these parts, at all stages of their growth, are externally of a dark colour, and very hard woody consistence: the terminal lobed mass, from being ever exposed to the scorching rays of a tropical sun in an arid climate, is much the hardest and darkest, resembling, as I have before stated, both in colour and texture, the crust of an overbaked loaf: the stock is the lightest in colour and softest in consistence, and, as well as the root, often has pebbles imbedded in its cortical substance.

All these parts differ a good deal in relative as well as in actual form and dimensions in the several specimens (amounting to fourteen) which I have received. Dr. Welwitsch's largest (Plates III. & IV.) have a flattened turbinate stock with a lobed base, long root, and their crown is neither much dilated nor very concave. Dr. Welwitsch's smallest specimen (Plate II. fig. 1), and Mr. Andersson's very large one from Damara Land (Plate V. fig. 5) have globose stocks, in each case suddenly much contracted into a long root, and rather tumid crowns. Mr. Monteiro's last-received specimens, on the other hand (Plate V. figs. 1–4, & Plate XI. figs. 1, 5 & 7), have all of them conical stocks, gradually or rapidly tapering into the roots, and much dilated crowns, of which the lobes in the older specimens are very concave, or almost erect. The amount of lobing of the periphery of the plant also varies extremely; in Mr. Monteiro's oldest and largest, the periphery is cut into many lobes of various sizes (Plate V. figs. 1 & 2), some of which are contracted at the base, and form appendages singularly resembling in form, marking, and texture *Polyporus fomentarius*, to which a structureless fossil specimen of this part of the plant would probably be referred.

Some of these peculiarities are no doubt to be attributed to age, and others to the nature of the soil, and the depth at which moisture exists in the arid coasts of Cape Negro and Damara Land.

The following are the principal dimensions and weights of the largest specimens :—

	Length.		Girth round the crown.		Weight.
1. Mr. Monteiro's, which arrived December 13, 1862.	ft.	in.	ft.	in.	lbs.
Largest (Plate V. fig. 3)	2	0	4	7	$32\frac{3}{4}$
Second largest (Plate V. figs. 1, 2)	1	8	4	0	$20\frac{3}{4}$
Third largest (Plate V. fig. 4)	1	9	4	8	$19\frac{3}{4}$
2. Mr. Andersson's from Waalvisch Bay (Plate V. fig. 5) . .	2	5	3	5	$26\frac{1}{4}$
3. Dr. Welwitsch's largest (Plates III. & IV.)	1	4*	3	5	$15\frac{3}{4}$

Crown.—This is oblong in outline, with the longer axis parallel to the insertion of the leaves; it is at first very tumid, but as the plant grows older it gradually subsides, especially towards the centre, until in some cases (Plate V. figs. 1, 2, 4, & Plate XI. fig. 1) it becomes so concave that the base of the hollow is far below the level of the insertion of the leaves. The surface is very irregularly marked with concentric ridges that are thickly studded with circular pits, denoting the position of fallen flowering peduncles. The number of distinct ridges in the largest specimens seldom amounts to more than 8 or

* The lower part of the root is cut off.

10, and these are only distinguishable towards the periphery; the others are so indistinct and confused towards the centre that they cannot be accurately estimated. The pits are usually in one series on each ridge; but sometimes, probably from the ridges being confluent, two are seen here and there; and they amount to upwards of one hundred on the circumference of a large specimen, diminishing in numbers on the ridges towards the centre. In old crowns these pits become raised on mammillary eminences. Radiating and concentric fissures of various depths intersect these ridges as the plant grows older. The crown, according to Dr. Welwitsch, sometimes attains 12–14 feet in circumference (Bibl. Univ. Genève, July 1861), and, if Mr. Monteiro's informant be correct, even 6 feet in diameter. It is very possible that the concentric ridges rudely represent annual increments to the plant; for the soft texture of the cones and peduncles is opposed to the view that these are more than annual, as is the fact that the cones sent by Dr. Welwitsch, Mr. Baines, and Mr. Monteiro, respectively, have all advanced to the same state of development. On the other hand, though, as is seen by Mr. Baines's drawing (Plate I. fig. 2), the cones are produced in great abundance, it is very improbable that in old specimens every pit indicates the presence of a fully developed peduncle with cones; for in this case each of the large plants must have borne at one time many hundreds of cones.

The surface of the crown is sometimes hoary, and presents under the microscope scattered, minute, hair-like bodies. These are peculiar spicular cells, hereafter to be described, which are developed within the tissue of the plant, but become exposed through its superficial disintegration.

The *Stock* presents several remarkable features, especially the deep horizontal groove between it and the crown, the transverse ridging of its surface below the leaf, and the occasional presence of flower-buds, and even of the scars of fallen peduncles, on its circumference. It often presents an upper lighter and a lower darker portion, the junction of which probably indicates the depth to which the specimen was sunk in the soil: this is well shown in Dr. Welwitsch's specimen, figured at Plate I. fig. 1., and agrees with his description of the stem being only partially buried; whereas those of Mr. Monteiro, which he states were immersed in the soil up to the origin of the leaves, do not show it.

The stock either terminates more or less abruptly downwards—most conspicuously so in all Dr. Welwitsch's specimens (Plates I., II., III. & IV.),—or tapers into the root, as in Mr. Monteiro's (Plate V. figs. 1–4, & Plate XI. figs. 1, 5, 7). The deep transverse slit dividing the stock from the crown, and at the base of which the leaves originate, is a most curious feature: it is nearly an inch deep in the largest specimen which I cut open; it clasps the leaf-base throughout its extent when the plant is fresh; but as the latter dies, its walls separate, leaving half-an-inch space between the upper and lower surfaces at the widest part (Plate XI. fig. 1). Whether fresh or dry, its orifice is so contracted that there is very little external trace of its existence, and its lips clasp the leaf so tightly that the latter, even when detached at the base, cannot be withdrawn entire. The object of this arrangement is, no doubt, to protect the young growing part of the leaf from the dry atmosphere.

The compression of the stock varies much in amount, and is no doubt proximately due to the dilatation of the base of the leaf, and consequent bilateral character of the trunk.

Towards its upper part, close under the base of the leaf, the circumference of the stock is marked more or less obscurely or deeply by concentric furrows, separating convex ridges, that repeat as it were the ridges of the crown: these are best seen in Plates IV., V., & XI. fig. 1, where they extend far down the stock. On the upper or outer of these ridges of the stock a few pits occur, in which flower-buds are occasionally developed; and, as it would appear, the latter sometimes arrive at maturity; for in one specimen I find the bases of three old peduncles *in situ*. In Mr. Andersson's large specimen there are four of these pits, vertical, superimposed on the four uppermost ridges of the stock. This may be regarded as an anomaly, to which I shall again allude when treating of the development of the plant.

The texture and appearance of the surface of the stock vary at different positions and ages: in the oldest specimens (Plates III., IV., & V.), it is uniformly hard, brown, rugged, and traversed by longitudinal fissures extending through the periderm; the ridges here extend but a little way below the leaf, and the superficial tissue of the periderm is broken up into isolated, distant, angular masses (Plate III.), denoting the great increase of the subjacent tissues. The superficial tissues of the ridges are always smoother and lighter-coloured than those of the rest of the stock; and in Monteiro's and Andersson's fresh specimens these parts are some of a pale yellow-green colour, and others of a bright green, and were still in a living state on their arrival.

The gummy substance (a true collenchyma) which exudes in large tears from the stock and other parts will be noticed when describing the internal anatomy of the stock.

Root.—This varies in my specimens from 1 to 2 feet in length; it is, as I before observed, either continuous with the stock, or else the latter terminates abruptly above it; it is slightly twisted, either nearly cylindrical, or if compressed, not so much so as the stock, although parallel to it; it gives off few fibres anywhere, and branches chiefly towards the base—indicating that the upper stratum of soil is extremely dry. Superficially it is of a much darker colour than the stock, being sometimes quite black; and the periderm peels off in places as a distinct bark. Owing to the nature of its tissues, the root is somewhat flexible.

Anatomy of Trunk. (Plates XI. & XII.)

A vertical section through the axis of a plant of *Welwitschia* exposes the following structure: 1. a brown cortical layer or periderm; 2. a largely developed parenchyma, of which the mass of the plant consists; 3. a fibro-vascular system of a very anomalous character.

Periderm.—This invests almost the whole plant with a very hard layer, of variable thickness and undefined boundary; it is most developed over the crown and towards the lower part of the stock, where it attains a thickness of $\frac{1}{2}$ to $\frac{3}{4}$ of an inch in the largest specimen, becoming thinner and finally disappearing towards the insertion of the leaf; it is absent from the inner surfaces of the groove enclosing the base of the leaf. Its colour is a dark brown on the crown and stock, and almost black on the root; it is much the hardest on the crown, which is probably owing to the action of the sun's rays in the arid climate which the plant inhabits. The outer surface of this periderm cracks extensively as the plant grows, chiefly longitudinally on the stock, and radially on the

crown,—the external portion sometimes breaking up on the stock into distant angular areolæ, as seen in Plates III. & IV. There is no lamination in the substance of the periderm, nor any trace of periodic growth. The epidermal cells, as long as retained, have thicker walls than the subjacent ones; the outer of all (Plate XII. fig. 3) are very large, radially elongated, and their outer walls are excessively thick, hard, and dark brown, almost as if charred by fire. The subjacent tissue (Plate XII. fig. 2) is a transversely elongated parenchyma, full of peculiar rigid spicular cells, hereafter to be described.

This periderm is not an independent growth, but is the outer portion of the parenchyma of which the mass of the plant consists, and which, having lost its vitality, forms a durable integument, in some parts of almost stony hardness, to the tender tissues beneath. In the root, but probably only in a dried state, this periderm is often separable from the subjacent tissues; this is in part owing to the vascular bundles which traverse the root running parallel to the periderm, not more or less transversely to it, as in the stock and crown.

Within the groove that holds the base of the leaf, the periderm is replaced by an exceedingly soft and tender tissue, which in Mr. Monteiro's specimens was still fresh and living. It consisted of a bright yellow-green parenchyma, covered with a delicate membranous transparent glistening layer of epidermal cells, with walls of extreme tenuity, without stomata, and without any appreciable thickening of the outer cell-wall. The cells were loosely filled with a watery grumous endochrome.

Parenchyma.—A *cambium-layer* * of soft parenchyma occurs beneath the periderm, investing nearly the whole trunk of *Welwitschia*: it is in all respects identical in structure with the subjacent parenchyma; but the cell-walls are more delicate, abounding also in the before-mentioned rigid spicular cells. This layer is best developed on the periphery of the crown, where the flower-buds originate, and it also forms the uppermost (outermost) of the ridges of the stock just below the leaf-base, whence it passes inwards surrounding the groove. It is least developed towards the depression in the long axis of the crown, and is perhaps absent under the periderm in its disc; but it otherwise invests the whole trunk with a layer of tissue, endowed with more or less vitality.

Beneath this cambium-layer a cellular tissue, of the ordinary hexagonal form in section, forms the chief substance of the crown, stock, and root. It is most developed in young and middle-sized specimens, and becomes gradually more intruded upon by the fibro-vascular tissues. In the freshest of Mr. Monteiro's specimens, this parenchyma was quite soft, and of a pale straw-colour, due chiefly to the abundance of large yellow spicular cells; it had a faint odour, something like that of fresh-boiled meat†, and contained, scattered through its substance, small cavities full of transparent gum. The cells of this tissue (Plate XII. fig. 1) are thin-walled; they have no markings, and are apparently not nucleated; their contents are insignificant, and present nothing worthy of notice.

The cellular and vascular tissues, though soft, are so interlaced, and spicular cells

* I apply this term here to the stratum of thin-walled cells, capable of multiplication by division, such as is to be found in *Dracæna*, and which is wholly distinct from the closed cambium of the vascular bundles. It is a persistent layer of the "meristem" of Nägeli (Beitr. z. wiss. Bot. i. 3).

† This I have not perceived in other equally fresh specimens; and it may be attributable to decay.

are so abundant in the former, that in a full-grown specimen the tissue cannot be cut smoothly with the sharpest knife, and a saw works through it with considerable difficulty, leaving very ragged surfaces. The root especially, owing to the masses of liber in the wood-wedges, and their waving courses, can scarcely be either cut or sawn, but may be riven if sufficient force be applied.

The spicular cells above alluded to are the most singular feature in the tissues of the plant, and, whether in their size, form, or surface, are quite unlike anything I have seen elsewhere. They are often $\frac{1}{8}$th of an inch long, extremely rigid, fusiform or acicular, acute (even pungent), or more rarely obtuse, at both ends, straight or branched, often more or less angled, curved, or hooked, and more or less thickly covered with minute crystals (Plate XII. figs. 5–8). They are found entangled in the parenchyma of all parts of the plant; but their walls become at a very early period free from the surrounding cell-walls. Their average diameter is that of four or five of the parenchyma-cells. The oldest ones are yellow. In a transverse section their walls appear concentrically laminated, the central cavity becoming all but obliterated with age: in the younger tissues they are smaller, paler, have thinner walls, and the crystals also are smaller and more remote (Plate XII. fig. 8); and, as I shall hereafter show, in the more membranous tissues of the plant (hermaphrodite perianth, &c.) they remain permanently thin-walled, are wholly void of crystals, and resemble the corresponding acicular cells in *Gnetum*, *Balanophoræ*, and other plants (Plate VI. fig. 9; Plate VII. fig. 8; Plate VIII. figs. 26, 27).

The crystals are flat, and applied to the surface of the cell by their broad faces; they are either rhomboidal or short six-sided prisms, always thin, of various sizes, $\frac{1}{1000}$th of an inch being the average of the larger, though some reach $\frac{1}{800}$th; they often assume irregular forms, as if they were broken, but are always flat and angular; they are often so thickly crowded as entirely to cover the surface of the cell. They are soluble in strong nitric acid, at least when heated. Dr. Frankland, who has attempted to analyse them, informs me that they are neither phosphates nor oxalates, but that after incineration they become soluble in acids, which indicates silica; but there is no test for silica sufficiently delicate to deal with a microscopic substance procurable in such very minute quantities.

As to the use of these spicular cells, they may be supposed to give solidity to the cellular mass of the plant: their abundance in the periderm, great size, curved and angular and often branched forms, surfaces roughened with crystals, and irregular arrangement suggest that this is the purpose they are intended to serve. In the leaf they brace together the several layers of parenchyma; and in the perianth, under a modified form, they give strength to the cellular tissue, acting in this respect like vascular bundles. Under this view they are analogous to the siliceous spicula of sponges, though formed on a totally different plan.

The gum which exudes from the trunk, peduncles, and various parts of the inflorescence, and which is also found abundantly in small cavities of the parenchyma of the leaf and trunk, is formed by the collenchymatous swelling and subsequent deliquescence of the cellular tissue, as is shown at Plate XII. figs. 14, 15. Occasionally the spicular cells are involved in the forming collenchyma, and, being similarly acted upon, their superficial coat of crystals becomes mixed up with the mass. The gum is dry, transparent, pale yellow-brown, inodorous, and insipid.

Fibro-vascular system.—This consists primarily of a thin, elongated or cup-shaped stratum, crossing the axis of the stock (to the surface of which it is parallel), just beneath the crown, and uniting the bases of the leaves. This gives origin to, secondly, an ascending system of definite isolated vascular bundles, which traverse the crown, and terminate in its ridges; and, thirdly, to a descending system of bundles, which in the axis of the stock and root are collected into wedges, but elsewhere in the stock are for the most part definite and isolated, and lose themselves in its cambium-layer.

Owing to the depression of the centre of the crown, or, more strictly speaking, to the upward growth of the lobes of the stock, the vascular stratum, which always keeps at a uniform distance from the periderm of the crown, is never horizontal, but becomes more and more cup-shaped as the plant grows older; the concavity varies, however, extremely in depth in different individuals (Plate XI. figs. 1, 5, 6). The circumference of this stratum (being coincident with the bases of the leaves) is the focus of greatest vitality in the plant; from it the innumerable fibro-vascular bundles which traverse the leaf are given off, and through it that stimulus to growth which is set up by the leaves is transmitted (so to speak) to the living tissues throughout the crown, stock, and root. At the margin of this stratum the cambium-layers of both the stock and crown meet, and having formed the soft walls of the leaf-groove, are continuous with the parenchyma of the leaves. This, then, is the point of greatest vitality in the whole plant; and, as we have seen, the delicate and important tissues here concentrated are protected from external influences by the tightly compressed lips of the groove, described at p. 9.

The vascular stratum itself forms neither a very conspicuous nor well-defined system, though necessarily rendered evident in the sections figured in Plate XI.; but it is sufficiently distinguishable when once understood. The bundles that compose it do not arrange themselves in groups, nor unite into a compact mass, but are arranged side by side, forming a fibrous layer not more than 3–4 lines thick in the largest specimens (Plate XI. fig. 2). They contain more vessels and comparatively less liber than the bundles in the root. In young and middle-aged specimens they run with great regularity; in old ones they sometimes branch, and present many anomalies in their course and arrangement.

This fibro-vascular stratum consists of two very ill-defined parts, in which the bundles are somewhat differently arranged, viz., a central and a circumferential portion. Of these the central is much the smallest; it occupies in the largest specimen a circular area of about 2 inches diameter, and consists of a matted fibro-vascular plexus, in which bundles of liber, barred vessels, spirals, &c., are all confusedly mixed. In a vertical section of the stock through the base of both leaves (*i. e.* at right angles to the lobes) (Plate XI. fig. 1), this central system is very manifest, though merging into the better-defined circumferential portion; and in a vertical section taken in a line exactly parallel to the lobes, and between them (fig. 5), it is hardly apparent. The circumferential portion consists of innumerable, very closely set, laterally compressed bundles, radiating outwards from the central portion to the entire semicircular base of each leaf. The structure of this portion is best seen in a vertical section through one of the lobes, halfway between the leaf-base and medial depression of the crown, and parallel to its long axis (Plate XI. figs. 2 & 6), which section intersects transversely all the bundles.

Each of the bundles forming the stratum consists of the same elements as those seen in the leaf (Plate XIV. figs. 1, 2, 3); but whereas in the leaf they increase only at the base, and give off no branches, in the stock their component elements are continually added to, and they give off bundles upwards to the crown and downwards to the stock. They increase, in short, from mere oblong dots, represented in fig. 6, to the linear bundles seen in fig. 2.

The plexus of the central portion, on the other hand, gives off to the root vascular bundles, which, unlike those of the crown and stock, coalesce into indefinite wedges (Plate XI. figs. 8 & 9).

The ascending vascular bundles which run to the ridges of the crown, and some of which enter the peduncles, are given off in vast abundance from all parts of the vascular stratum. These are very slender, isolated, but crowded, and in a transverse section of the crown, above the stratum (Plate XI. fig. 4, lower left-hand quadrant), appear to run in not very defined concentric lines, answering to the ridges of the crown. Many enter each peduncle, but without manifest order, though after entering they arrange themselves in groups having a relation to the bracts, as hereafter to be described.

The direction of the descending fibro-vascular bundles varies much more than that of the ascending, owing to their having to conform to the requirements, both of the stock, in which the increase of tissue is mainly centrifugal, and of the root, in which it is vertical; and, further, owing to the previously described concavity of this stratum, the outer series of these bundles actually ascends instead of descending. To explain this, it is necessary to refer to Plate XI. fig. 1. Commencing with the last-formed bundles in the stock: these start from the vascular stratum just beneath the base of the leaf, arch outwards and upwards, and, running parallel with and near to the floor of the groove, lose themselves in the cambium of the periphery. Those which are given off from points successively further from the leaf-base follow first a similar course, but successively arch downwards instead of upwards, till the innermost of all, which reach the periphery of the tumid base of the stock, run parallel to its periderm. All these bundles in the stock are usually very slender; they neither anastomose nor collect into bundles nor wedges, except sometimes along the medial line between the lobes of the crown (Plate XI. fig. 3), where the bundles from the contiguous leaf-bases become extremely confused, tortuous, and anastomose, forming very irregular, ill-defined plates. In old specimens, however, many deviations occur.

Those bundles which descend from the central part of the stratum, through the axis of the stock, and traverse the root, are more or less collected into several irregularly concentric series of wood-wedges, surrounding one or two medullary centres, and are separated by wide and interrupted medullary rays and very broad parenchymatous rings. The parenchyma of the axis and root is further traversed by many isolated bundles, scattered between the wood-wedges (Plate XI. figs. 8, 9; Plate XIII. fig. 12).

The wood-wedges are collected into groups of 3 to 6 or more, which are parallel to one another, but often placed obliquely to the radius and to other groups. Those nearest

the axis are always larger than those towards the circumference, the outermost of all being extremely small. The individual wedges are radially very much elongated, taper outwards, and are often waved, and split from the centre nearly to the tip by intruded parenchymatous wedges; they are, for the most part, formed of liber, which, in a transverse section of youngish specimens, presents a dense, somewhat horny, pale brown mass; this is succeeded, towards the axis of the root, by a very inconspicuous cambium-layer, and this by a bundle of slit-marked vessels. In old specimens the liber preponderates so inordinately over the parenchymatous and other tissues, that, when riven open, the interior of the axis and root presents the appearance of tangled hemp-yarn, the masses of which, when torn out, are as thick as the little finger, and are matted together with dry parenchyma, full of yellow spicular cells and fragments of vessels. The whole forms a tissue so loose and tough, that an old root can neither be sawn nor cut clean across.

In some specimens, the wood-wedges of the root are obviously arranged round two centres (Plate XI. figs. 8 & 9), a vertical plane passing through both corresponding with the depression between the bases of the leaves.

The elements of the vascular bundles above described are singularly uniform throughout all parts of the plant, and consist of:—First, a great proportion of filiform liber-cells; these are very slender, terete, white, 1 to 2 or more inches long; their cavity is all but obliterated, and their surface marked with very fine transverse striæ (Plates VII. figs. 11, 12; VIII. fig. 25; XII. fig. 14; XIII. fig. 14); they sometimes, but very rarely, are unequal in diameter and branched (Plate XII. fig. 12). Second, slit-marked vessels, or pitted vessels, with thick walls (Plate XIII. figs. 10, 15; Plate XIV. figs. 14, 15): in some of these the whole interior is filled with secondary deposit, except opposite the slits or pits, giving rise to various modifications (Plate XIV. fig. 14); in others the pits seem united by a faint spiral line traversing the interior of the tube (Plate XIV. figs. 14 & 15). These pass into—Third, tubular vessels, with more or less thickened walls, in which the deposits are spirally arranged (Plate XII. fig. 4; Plate XIII. fig. 10). The peculiar disc-bearing tissue which abounds in all other gymnospermous plants seems to be totally absent in this.

On a comparison of the stem of *Welwitschia* with that of other vascular plants, its development seems to be referable to the exogenous plan, of which it is a remarkable and hitherto unique modification. Except, indeed, in the fact of so many of the descending bundles of the stock and root remaining isolated and closed, and in those of the stock losing themselves in the periphery, I do not see any analogy with an endogenous mode of development. The first of these characters is very common in many Orders of Exogens with anomalous wood; and the second is accounted for by the exigencies of the growth of the stock. Nor should I have expected it to be otherwise: the embryo being dicotyledonous, and giving origin (it is to be assumed) to a primary root continuous with its radicle, lays the foundation, as it were, for an exogenous arrangement of the vascular tissues within it, cellular tissue in all cases preceding and regulating the time of appearance, amount, and disposition of the vascular, which is formed as

required. Had the embryo presented any monocotyledonous character, as the development of adventitious roots from its radicle, or had it possessed but one cotyledon, then it is to be assumed that the future plant would have been unsymmetrical, and either a further deviation from the exogenous plan or a decided transition to the endogenous might have been expected.

Its discoverer affirms (see p. 2), but on what grounds he does not state, that the two leaves of *Welwitschia* are the developed cotyledons of the embryo: of this there is no absolute proof forthcoming; nor can there be any, short of watching the process of germination. But much may be inferred from the anatomy of the trunk; and all that has been there observed is entirely in favour of Dr. Welwitsch's statement. For, firstly, there is the obvious fact, that the leaves of the youngest specimens as well as those of the oldest all occupy precisely the same position in relation to the axis and cambium-layer; secondly, there is the difficulty of accounting, under any other supposition, for the single transverse vascular stratum, whose bundles are continuous with those of the leaf at every period of growth; thirdly, the absence of anything like an internode in the axis; lastly, the uniformity with which the definite bundles are given off to the crown and stock, and the condition of the tissues within the lips of the transverse groove, both indicate one continuous leaf-formation from the very earliest epoch in the plant's life.

Nor is such a development wholly without its counterpart; for a very analogous case is presented by another Dicotyledonous South African genus, though occupying a widely different position in the natural system. I allude to the cases of *Streptocarpus polyanthus* (Hook. Bot. Mag. t. 4850), *S. biflorus*, and *S. Rexii*, whose germination has been observed by Mr. Crocker at Kew, and his account of which was read before this Society, and published, with illustrations, in our Journal (vol. v. p. 65, t. iv.)*. In these plants the minute, terete, exalbuminous embryo has two short cotyledons, of which one becomes developed in germination into the great oblong penniveined leaf of the future plant, which, like those of *Welwitschia*, lies along the ground; the other cotyledon soon disappears, and the radicle developes a short caulicle terminated by rootlets. The inflorescence of *Streptocarpus* is adnate to the petiole and base of the midrib of the leaf, and consists of a depressed axis, giving off a succession of many-flowered scapes from its upper surface. Here the caulicle answers to the stock of *Welwitschia*, the adnate portion of the inflorescence to the crown, and the scapes to the peduncles. But whereas *Welwitschia* is a perennial symmetrical (bilateral) plant, of which both cotyledons are developed, *Streptocarpus* is an annual (or biennial) unsymmetrical (unilateral) plant, of which but one of the cotyledons is developed.

It is perhaps a fanciful idea, but worth recording, that the mode of growth of both these plants may have originated in a conformity to conditions, inasmuch as *Wel-*

* Some months after the publication of Mr. Crocker's paper, it was found, from a statement in the 'Revue Bibliographique' of the Botanical Society of Paris (vol. vi. p. 148), that the same fact had previously been recorded of *S. polyanthus* and *S. Rexii* by Dr. Caspary, who published it, in 1858, in the 'Verhandlungen des naturhistorischen Vereins d. Preuss. Rheinlandes u. Westphalens,' xv. Jahrg., pp. 74, 75.

witschia, growing in open flat plains, scorched by a powerful sun, and seldom visited by rain, is very slowly and symmetrically developed, while *Streptocarpus*, growing rapidly, in moist localities, out of chinks in vertical rocks, where the two sides of the embryo and of the future plant may be exposed to very different conditions, is unsymmetrically developed.

The last point to which I shall allude in connexion with the axis of *Welwitschia* is the origin of the parts I have called the stock and crown.

The stock I assume to be what is termed the caulicle (tigellum) in germinating Dicotyledons, and to be in fact the radicle of the embryo*; but whereas in most perennial dicotyledonous plants the caulicle becomes obliterated or not apparent after the first year, in this, owing to its assuming the functions of the trunk of the plant, it becomes the most important and bulky of its vegetative organs. Though I know of no exact counterpart to its vascular system in any other plant, such may exist; for M. Clos has pointed out, in his excellent papers on the structure of the tigellum (Ann. des Sc. Nat. sér. 3. t. xiii. p. 1, t. xviii. p. 321, t. xvi. and xvii.), that this part of the axis differs both from the stem and root in the disposition and number of its vascular bundles.

The question of the theoretical origin of the crown is not so easily disposed of; nor can I say whether its ridges should be regarded as plumulary, or as being wholly made up of confluent axillary flower-branches. There being no other vertical axes developed in *Welwitschia*, these ridges, if flowering branches, can scarcely be considered as truly axillary; on the other hand, any development of the embryo from between the bases of the cotyledons must be considered as more or less plumulary; it is therefore easier to conceive the successive ridges of the crown to consist of arrested plumulary axes, with which the flower-buds coalesce, than to suppose them to be wholly plumulary or wholly floral. I am not acquainted with the anatomy of the depressed flowering axis of *Streptocarpus*, which may probably throw some light upon that of this plant. The disposition of the vascular bundles in mature plants of *Welwitschia* is too vague to throw much light on the subject.

It would be most interesting to pursue this inquiry into the structure and development of the axis of *Welwitschia* much further, and especially to follow up the points of affinity between its tissues and the trunk of its allies the *Cycadeæ* and *Gnetaceæ*, on the one hand, and, on the other, the analogous forms of wood presented by *Menispermaceæ* and many other plants; but this would carry me far beyond the limits of the present essay.

Leaf. (Plate XIV.)

The youngest leaves I have seen are those of the specimen figured at Plate II. fig. 1;

* In Jussieu's 'Cours Elémentaire,' § 488, I find it expressly stated that the radicle of Dicotyledons consists almost entirely of tigellum, and becomes the tigellum of the young plant. In Henfrey's 'Elementary Course of Botany' (1857), § 35, 301, &c., the radicle is called the root; in Asa Gray's 'Introduction to Botany' (1858), § 158, 159, the radicle is rightly regarded as an axis, and not a root, but is further considered to be an internode. Of these views I adopt the first, and the first part of the last.

these are four inches long, and about one inch at the broadest diameter: the largest I have seen are those of the specimens sent by Mr. Monteiro, which are two feet broad at the base. Dr. Welwitsch states, in his letter to Sir William Hooker, that the leaves attain a length of six feet; and according to Mr. Monteiro's letter (p. 4) they may attain even a larger size. I have no evidence of the plant ever bearing more than two leaves: there is, however, no reason why more than this number should not be developed; for the embryo may occasionally be tri- or poly-cotyledonous, as is the case with so many other Gymnosperms, including its near ally *Ephedra*. In all my specimens, however, the appearance of more leaves than two arises from the splitting of one or both, and from subsequent interstitial growth of the tissues of the crown and stock completely sundering these portions at their bases. These disruptions may always easily be recognized, from their adjacent margins being ragged, and deprived of cuticle at a greater or less distance from the base, though as the severed portions grow outwards their newer parts acquire a rounded edge, covered with epidermis.

The base of the leaf, which is retained within the groove between the crown and stock, is, in the dried specimens, excessively thin and almost membranous; that this is not entirely, if at all, due to the shrinking of its substance is evident from an examination of the tissues, of which the parenchymatous is almost suppressed, and the fibro-vascular reduced to very narrow cords. The exposed portion of the leaf is of a hard leathery consistence, greenish and glaucous on the upper surface, paler green, suffused with red-brown, on the under; it is $\frac{1}{10}$th of an inch in thickness, quite entire along the rounded margins, longitudinally striated on both surfaces, the striæ answering to innumerable slender, close-set, narrow grooves. The nervation, which is parallel throughout, is scarcely distinguishable on the surface.

The internal structure of the leaf (Plate XIV.) is beautiful and singularly complicated, well supporting the other evidence of its perennial duration. The outer walls of the epidermal cells (Plate XIV. figs. 1 & 2 *a*) are horny and thickened, and their cavities have few contents. Beneath the epidermis of both surfaces is a thick layer of very lax, soft, cellular tissue (figs. 1 & 2 *b*), traversed longitudinally by bundles of liber (figs. 1 & 2 *c*), and strengthened, as it were, by a confused mass of the rigid spicular cells (figs. 1, 2 *d*, & 4) covered with crystals, that have been described as abounding in the parenchyma of the trunk. These spicula are in this part of the leaf of a rather more definite shape, and are in a far more definite position relatively to the other tissues, than in the trunk; they do not either cross or intrude upon the liber-bundles, are placed perpendicularly to the surfaces of the leaf, and are often bent at a right angle at one or the other or even at both ends. The tissue they traverse is so soft that its cellular nature is not very evident; and the effect of the spicula in holding this together is rendered obvious by pulling one with a pair of fine-pointed forceps under the microscope, when, owing to its curved form, rigid texture, and rough surface, it resists withdrawal without complete laceration of the surrounding tissues, at the same time often dragging other spicula with it, these being entangled together by their hooked or branched ends.

Towards the middle of the leaf is a thicker layer of ordinary parenchyma

(figs. 1 & 2 *e*) having cell-walls without markings, and almost empty cavities, with a few spicula, and occasionally groups of cells transformed into amorphous gum (collenchyma).

The strong fibro-vascular bundles of the leaf traverse this tissue parallel to one another, and continuously throughout the whole length of the leaf in its medial plane. The vascular bundles (fig. 2*f* & fig. 3) are of the same character as those of the stock, but more symmetrically developed: in a transverse section they are oval or cuneate, with the broad end upwards. They are surrounded by a single layer of thick-walled pitted cells (fig. 3 *a*), and consist of, superiorly, a large crescent-shaped bundle of liber-cells (fig. 3 *b*), which, like those in the stock and root, have thick walls, narrow or no cavities, and delicate transverse striæ; beneath this is a thick crescent-shaped cambium-layer (fig. 3 *c*), marked in a transverse section with radiating lines (fig. 1), due to an obscurely radiating arrangement of the cells; beneath this, again, is a bundle of slender vessels, of which the uppermost (fig. 3 *d*) are thick-walled, with slit-shaped markings, the next (fig. 3 *e*) thinner-walled, with close-set spirals, gradually passing into loose spirals. Another crescentic layer of liber-cells, like that above the cambium, but with its concavity upwards, closes the vascular bundle below. This second liber-bundle is, no doubt, developed from a second narrower belt of cambium-cells, on the lower side of the vessels.

The stomata (Plate XIV. figs. 5–13) are situated in parallel lines on both surfaces of the leaf, and occupy the striæ, thus overlying the soft cellular tissue (figs. 1 & 2 *b*). They do not differ in any essential point from the usual form of these organs; their guard-cells lie between the bases of epidermal cells which leave a funnel-shaped depression between their contiguous walls. The guard-cells have much-thickened walls, continuous with the equally thickened outer walls of the epidermal cells, and, in a transverse section (figs. 11 & 12), present interruptions of continuity which are not easily explained, except on the supposition that their walls are either perforated or much thinner at those points.

There is much in the permanent character, parallel nervation, and anatomy of the leaf of *Welwitschia* that recalls the foliage of *Dammara*, *Podocarpus*, and many parallel-nerved *Cycadeæ*, and especially of those South African species of the latter Order in which a layer of liber-cells underlies the epidermis. After a cursory examination of the leaf-structure in many species of these families, I find none of which the anatomy, in point of complexity or beauty, approaches that of *Welwitschia*; nor do I know of any plant that is in this respect to be compared with it. It is further to be observed, that in all these plants the vascular bundles of the leaf, unlike those of most Monocotyledons, nowhere anastomose nor communicate by lateral branches; whence each nerve represents a single independent vascular axis, extending from the base to the apex of the leaf, or, in *Welwitschia*, from the axis of the trunk to the apex of the leaf. Such leaves resemble more closely a series of parallel uninerved leaves united by cellular tissue, than a foliar expansion of parenchyma traversed by one system of inosculating vessels; and the frequent presence of many linear cotyledons in these plants seems to favour this view,

as does the mixed character of the foliage of *Podocarpus*, of which some species have uninerved and others many-nerved leaves. The numerous flower-buds along the periphery of the crown also further favour this view. The development of the vascular tissue in the early condition of the leaf of *Welwitschia* may be expected to throw some light upon this point.

Considering the origin of the leaf, its permanent duration, and the mode of growth of the trunk to which it is attached, the strictly horizontal and parallel arrangement of its vascular bundles ceases to be suggestive of a monocotyledonous affinity. Here the main increase of the trunk is horizontally outwards (centrifugal); and as the leaf increases in width by the addition of cellular tissue to either side of its base, it follows that the vascular bundles which originate independently in that tissue must occupy the same plane as those previously formed, and be carried outwards parallel to these, by the longitudinal extension of the leaf.

The nervation of the leaf of *Welwitschia* appears at first sight to be singularly unsuited to the requirements of the plant, promoting, as it evidently does, the early splitting-up of the bladé into innumerable narrow withered-looking thongs—except, indeed, we suppose that this early splitting is a special contrivance for exposing the cellular tissue surrounding the vascular bundles to the action of the atmosphere when damp, and thus supplementing the function of the stomata in a climate where rain is all but unknown.

Inflorescence.

The floriferous disc, or receptacle of the peduncles, is, as already explained, the lobed crown of the plant, the exact relation of which to a plumule on the one hand, and to a mass of axillary coalesced flower-buds on the other, is not clear, and has been already alluded to.

The flower-buds are developed in deep ovoid cavities in the periphery of the crown, about $\frac{1}{4}$–$\frac{1}{3}$ inch deep, just above the insertion of the leaf. These cavities open by a vertical slit (Plate XI. fig. 1), with prominent lips, and disclose an ovoid bud, enclosed in rigid coriaceous imbricating scales, the two outer of which are opposite, relatively very large (as long as the rest), and placed right and left of the lips of the cavity.

Flower-buds are also occasionally developed in the upper ridges of the stock, beneath the insertion of the leaf,—a very remarkable fact, analogous to the occurrence of shoots proceeding from the caulicle of various plants, and described by Bernardi in *Linaria arenaria* (Linnæa, vii. p. 561, tab. xiv. fig. 1).*

When fully developed, each branch of the inflorescence is essentially a dichotomous cyme, with persistent opposite bracts at the nodes; this cyme is, however, much interrupted by the irregular suppression of some of the internodes, so that the nodes often

* I am indebted to my friend Dr. Maxwell Masters for indicating this analogy, and for the reference to it. The same botanist also informs me that he has observed similar shoots on the caulicle of *Euphorbia Peplus*, and frequently on that of *Anagallis arvensis*.

present tumid masses (Plate VII. fig. 1), from which branches are given off in a more or less umbellate manner.

The internodes are stout, tetere, bright green and even on the surface, somewhat contracted as if articulated at the base, but not easily separating there.

The anatomy of the peduncle presents nothing remarkable, further than the monocotyledonous character of its isolated bundles. The green epidermis is studded with stomata similar to those on the leaf and described under that organ. In a longitudinal section through the centre of an internode (Plate XIII. fig. 6), a cellular axis is seen, with one or more bundles on either side, running parallel to and within the margin, and up to the base of the terminal cone. From a transverse section (fig. 8), these are found to be very numerous indeed; and the largest are placed towards the interior. A tangential section (fig. 7) shows how these bundles anastomose in the periphery of the nodes, at the base of the cone. The parenchyma of the peduncle (Plate XIII. figs. 9 & 10) is a loose tissue of vertically elongated hexagonal cells, with pitted walls, enclosing thick isolated liber-cells, and very rarely a few spicular cells.

The vascular bundles (Plate XIII. fig. 10) are of the same tissues as have been described in the trunk, viz., liber externally, then cambium, then (internally) spiral and slit-marked vessels.

The inflorescence of *Welwitschia* closely resembles that of *Gnetum*, and especially the American species of that genus, both as regards its dichotomous division, the suppression of the internodes, and the often arrested development of the cones themselves. The anatomy of the peduncle of *Gnetum* is, however, quite different, presenting a very elegant system of symmetrical wood-wedges surrounding a medullary axis.

Hermaphrodite Cone and Flowers. (Plate VI.)

I have seen several cymes of cones bearing these, some *in situ* on the specimen figured at Plate V. fig. 3; and one, which was sent by Dr. Welwitsch, is figured at Plate VI. fig. 1. The strobili are $\frac{1}{2}$–1 inch long, ovoid or cylindrical, bluntly tetragonous, and $\frac{1}{4}$–$\frac{1}{2}$ inch in diameter. I find no female cones on the same plants with the male, nor any female flowers in the hermaphrodite cones; but there are in the cymes of both sexes many imperfect cones in the axils of the permanent bracts. The scales are coriaceous, of the same form and general structure as those of the female cones (which will be particularly described), but only $\frac{1}{8}$th to $\frac{1}{6}$th of an inch long: they have two remote vascular bundles, one on each side of the middle, which branch in a fan-shaped manner. The lower are empty and connate in pairs at the base; the upper are rudimentary; the remainder subtend solitary flowers.

In its earliest stage the hermaphrodite flower is a minute papilla, consisting of the naked conical nucleus of the ovule, seated on a broad compressed base, which rises on each side into shoulders; these shoulders represent the earliest condition of the two outer leaflets of the perianth. The outer leaflets grow laterally, and soon exceed in length the nucleus, when two swellings, an anterior and a posterior, appear between the

lateral lobes, and gradually develope into the two inner leaflets. These are succeeded by two other rings, formed at the base of the nucleus—the outer being the staminal tube, the inner the coat of the ovule: I cannot satisfy myself which of these two is developed first; but both the nucleus of the ovule and its coat, which is open and truncated, project far beyond the staminal ring for a considerable time; and it is some time longer before either are wholly included in the perianth.

The fully formed flowers (Plate VI. figs. 5, 6, & 7) are sessile and much compressed, broadly obovoid-spathulate, shorter than the scale ($\frac{3}{20}$ths of an inch), plane towards the axis of the cone (on the inner side), convex on the outer face.

Perianth.—The two outer perianth-leaves are strictly lateral, very narrow, spathulate, falcate, acute, and keeled or almost winged at the back; their bases are connate or very closely approximated on the inner side of the flower (Plate VI. fig. 5), and more widely separated on the side opposite to the scale (fig. 6). The two inner segments of the perianth (which are not present in the female flower) are antero-posterior, confluent into a compressed tube below, spreading into two orbicular concave lobes above, of which the inner overlaps the other by its margins all round (Plate VI. figs. 7 & 8).

These four leaflets of the perianth are very thin and transparent, formed of two layers of epidermis (figs. 8 & 9), enclosing slender thin-walled spicular cells, which are so placed as to present the appearance of radiating nerves; these cells have uniform or very obscurely dotted walls and a conspicuous cavity, and they are quite colourless and transparent. There is no vascular tissue in the perianth of the specimens which I have examined, though the two vascular bundles running up to the ovule are evident within the solid base of the flower (fig. 14).

A comparison of the perianth of the hermaphrodite flower with that of the female will be found appended to the description of the latter. In some respects it resembles that of the male flower of *Casuarina* more than any other plant I know; but the comparison cannot be carried far. The two outer leaflets of the perianth may perhaps more properly be considered bracts; but there is no evidence of consequence in favour of this view.

Stamens.—The six stamens (Plate VI. figs. 7, 10, 11, 12) are united halfway up into a fleshy tube, which is adnate at the base to the inner leaflets of the perianth; the filaments above this are fleshy, terete, and irregularly inflexed in æstivation, reflexed and exserted after anthesis. The anthers are capitate, obscurely 3-lobed, 3-celled, and dehisce at the apex by a tricrural slit (fig. 12); the three posterior are much smaller than the others. The pollen (fig. 13) is very minute, ellipsoidal, transparent, and yellow; each pollen-grain is $\frac{1}{800}$th to $\frac{1}{700}$th of an inch long, and consists of a delicate hyaline extine, which is (when preserved in alcohol) longitudinally wrinkled, and encloses grumous contents. I have not been able to determine the nature of the contents of the pollen-grain, nor whether cell-division takes place before the tube is protruded. I have never found pollen-grains on any part of the ovule of the hermaphrodite flower.

In being hexandrous, this staminal whorl presents the only marked exception to the binary arrangement that prevails throughout this plant; the only other apparent exception is in the rachis of the cone, which is traversed by four triplets of vascular bundles, of which triplets the two outer bundles alone seem to supply the scale and flower. I

cannot trace any direct connexion between these three bundles of vessels in the rachis and the six stamens, but it is conceivable that they have some relation to one another.

Ovule.—The ovule (figs. 11, 14) occupies the axis of the flower, and is connate, at its base, with the base of the staminal tube; it is conical, and its integument is narrowed upwards into a flexuose tubular styliform body, which terminates in a very broad expanded papillose stigma-like disc, depressed in the centre; the depression communicates with the tube of the styliform body, and thus downwards with the cavity enclosing the nucleus. There is no other integument to the ovule but this; it consists of elongated cellular tissue (fig. 15), and contains a conical, fleshy erect, nucleus (fig. 14), in which I find no trace of embryo-sac, nor other contents, except an opaque line in the centre (fig. 16). Two vascular bundles (fig. 14) proceed to the outer base of the nucleus (one on each side), where they abruptly terminate.

Not only is there a total absence of an embryo-sac in this ovule, but the whole body turns brown and withers after flowering; these circumstances, and a reference to my description of the ovule and development of the embryo in the female flower, will show how far it may safely be assumed that this organ in the hermaphrodite flower, though furnished with an apparently perfect stigmatic summit, is in reality constantly functionless. And if (as I shall hereafter attempt to show when treating of the female flower) impregnation takes place by the direct application of the pollen to the nucleus of the ovule before its integument is produced into a tube, it is a further argument in favour of its sterility in the hermaphrodite flower, that I have never yet found a pollen-grain within or on the ovule.

The hermaphrodite cones and their flowers, here described, accord singularly with the male cones of *Ephedra** in many essential respects. In both the scales are quadrifariously arranged, identical in nervation, single-flowered, and formed of the same tissues and on the same plan. The outer leaflets of the perianth of *Welwitschia* are absent in *Ephedra*; but the two inner are identical in both genera, in structure and appearance. The six stamens united by their filaments, with capitate anthers opening by short terminal slits, and the pollen, correspond in every respect, except that the stamens of *Ephedra* vary in number from two to eight, that its anthers are usually 2-celled, and the staminal column is solid. Lastly, the ovule of the hermaphrodite *Welwitschia*, with its tortuous styliform process and stigma-like apex, is the same in structure and appearance with the ovule of *Ephedra*, differing only in wanting the embryo-sac, and in the stigma-like disc of the latter being narrow-oblong, and not papillose. With *Gnetum* the affinity through the male flower is less obvious, and as, in so far as I can see, it is only traceable through *Ephedra*, it would be out of place to discuss it here.

The most analogous case known to me of an apparently highly perfected stigmatic organ being absolutely functionless, is that of the curious genus *Cardiopteris*, which abounds in the eastern provinces of India, and which I have examined in a living state. In this plant the ovary is unilocular and has two stigmata—one large, globular, and

* In one species of *Ephedra* I have found tristichous female cones, the scales being connate at the base in threes.

papillose, borne on a flexuous style, the other a low mamilla, in no respect resembling a stigma in outward appearance. Mr. Brown has shown* that this fully-formed stigma is, in all probability, functionless and withers away without sphacelation, but that impregnation takes place through the mamilla, which, after performing its function, becomes remarkably developed.

It is difficult to regard this remarkable ovule without speculating on the possibility of *Welwitschia* being the only known representative of an existing or extinct race of plants, in which such a stigma-like organ was really capable of performing the function of a stigma; and when we see this organ occurring in a hermaphrodite flower, it is easy to suppose that we have in *Welwitschia* a transition in function, as well as in structure, between the gymnospermous and angiospermous Dicotyledons, and that the ideal race consisted of hermaphrodite-flowered plants in which the office of the stigma of the carpellary leaf was performed by a stigmatic dilatation of the ovular coat itself. Nor is it difficult to trace the successive variations from this imaginary type which, in the course of many generations, would result, on the one hand, in the obliteration of the embryo-sac and suspension of the functions of the ovule in the flowers of certain individuals, and on the other in the obliteration of the stamens and stigmatic apex of the ovule in the flowers of other individuals,—the once bisexual plants thus becoming unisexual. Singularly enough, *Ephedra* presents one step in advance of *Welwitschia*, in the total disappearance of the ovule in its male flower, and is one step behind it in the retention of a functionless stigmatiform disc in its perfect ovule.

Female Cones. (Plates VII. & VIII.)

The female cones are $1\frac{1}{2}$ to $2\frac{1}{2}$ inches long, tetrastichous, of a bright scarlet colour when fresh. They present 40 to 50 decussating pairs of scales, which are more membranous than coriaceous; the seven or eight lowest pairs are empty; and the uppermost six to ten pairs, in the specimens examined, contained unimpregnated flowers only. The two or three lowest pairs of scales are connate at the base, very small; and the uccessive ones rapidly enlarge up to the floriferous ones (Plate VIII. figs. 28 & 29).

Each scale (figs. 19 & 20) presents a broad central hyaline area of extreme tenuity, on each side of which, but far removed from the margins, two to five vascular bundles ascend, diverge, and branch excessively towards the margin. Structurally, the scales consist of two layers of delicate epidermal cells, enclosing a layer of tortuous filiform liber-cells, which radiate outwards towards the margin, and terminate in rounded apices within its edge (Plate VIII. figs. 21 & 22). These liber-cells are quite free, unbranched, and vary in length. They are much more densely packed nearer the vascular bundles, and are of precisely the same nature as those which occur in the wings of the perianth surrounding the female fruit, but are far less tortuous. The vascular bundles present nothing remarkable. Towards the thickest part of the scale are found short spicular

* In Bennett's 'Plant. Jav. rar.' p. 248, Mr. Brown describes this stigma as not papillose; but it is so represented in my drawings taken from the living plant.

cells, with minute points on their surfaces, but no formed crystals (fig. 27). The outer surface of the scale is provided with stomata; the inner (fig. 23) has none.

The rachis of the cone (Plate VIII. fig. 1; Plate XIII. figs. 1 & 2) is fusiform, broadest below the middle, and almost terete, of a soft spongy texture, and covered with a very delicate epidermis. The arrangement of the vascular cords is curious: of these there are, I believe, normally twelve principal ones, in four sets of three each, corresponding to the positions of the four rows of scales, and various smaller supplementary ones; they all run just within the periphery, in wavy lines from the base to the summit of the rachis, anastomosing here and there by lateral branches. On removing the outer layers of cellular tissue (Plate XIII. figs. 1 & 2, which are diagrammatic sketches), three nearly parallel wavy bundles are seen beneath the scale, of which the middle one is supplementary, not communicating directly either with scales or flowers, but anastomosing here and there with the lateral ones. Below the insertion of the scale, each of the lateral nerves gives off externally one ascending branch, which enters the scale, and ramifies in it (fig. 1), as described under that organ. The two nerves of the perianth, on the other hand (fig. 2), are derived from the lateral nerves themselves, and not from branches of these. It follows, from this arrangement, that the bases of the nerves that ramify in the scale are further apart than the bases of those that ramify in the perianth. I have seen a scale with an additional nerve on one side, placed nearer the margin than the normal one of the same side, and this was supplied by a branch from the adjacent bundle of the adjoining triplet, which anastomosed with its neighbours. Other deviations no doubt occur.

The smaller vascular cords which traverse the rachis anastomose together; they generally run between the main ones, but are for the most part free; more rarely they overlie the main cords, and sometimes they unite with them.

The parenchyma of the rachis (fig. 3) is by far the most delicate in the whole plant, and consists of loosely packed, very thin-walled utricles (figs. 4 & 5), with pitted walls; these pits are remarkably oblique (fig. 5), so as to present the appearance of an overlapping double boundary.

The female cone of *Welwitschia* resembles that of *Ephedra* in very many particulars, and especially in the remarkable bilateral venation of its scales, in the abundance of stomata, in the liber-cells ramifying through its wings, and in the presence of spicular cells; furthermore, in *E. alata* and other species the scales are as beautifully membranous, and the two vascular bundles enclose a similar hyaline transparent area. *Ephedra*, as elsewhere stated, differs in all the scales being connate at the base, and in their becoming larger upwards to the terminal pair, which alone are floriferous.

Female Flower, Perianth, and Pericarp (Plates VII., VIII., IX., & X.).

Perianth.—This, which ultimately attains a great size, as the pericarp of the seed, does not appear till after the formation of the nucleus of the ovule. I have traced its development in the immature flowers taken from the apical scales of the half-ripe cones. In all these the eight or ten uppermost scales (Plate IX. fig. 1) were extremely minute, and

the terminal ones invariably subtended a minute papilla, which is the naked nucleus of the ovule; lower down, in the same cones, I find this nucleus surrounded at the base by a compressed thickened ring, rising into shoulders on each side (Plate IX. figs. 2 & 3), which ring is the first appearance of the perianth.

In the next stage (fig. 4) the perianth is dilated upwards, and, by the time that the integument of the nucleus appears, the perianth is saucer-shaped (fig. 5); and becoming more concave, its upper margin rises to a level with the apex of the nucleus (fig. 6). When about $\frac{1}{300}$ inch long, the orifice dilates and becomes obscurely 2-lobed (fig. 7), the lobes being right and left, or parallel to the scale of the cone. At this period the nucleus is often surmounted by its integument, but as often it remains exposed till a considerably later period. The perianth next dilates above the base, and contracts at the orifice, becoming much compressed and urceolate (fig. 8); the orifice is manifestly lobed, but most deeply opposite the scale.

The next manifest change is when the perianth is about $\frac{1}{20}$ inch long, and the lobes of its mouth converge (fig. 9). The wings next appear as narrow membranous margins running up to the lobes of its mouth; and the ovular integument is produced far beyond the nucleus (Plate VIII. figs. 6, 7, 8). When $\frac{1}{4}$ to $\frac{1}{3}$ inch long (Plate VIII. figs. 9 & 10), the perianth is flattened, membranous, and translucent, with a flagon-shaped cavity, is much dilated below, and has a bifid dilated mouth (fig. 11), which opens towards the scale.

The nascent female flower is at first formed in close contiguity to the base of the scale, but on the rachis of the cone, and is sometimes torn away with the subtending scale, and sometimes not; but it is gradually carried up, as it were, beyond the scale, and becomes placed on a conical prominence of the rachis, which is confluent below with the narrowed base of the scale (Plate VIII. figs. 4, 9, 10). At about this stage, or soon after it, two pairs of vascular bundles appear in the perianth, one pair ascending on each side at the base; the inner bundle of each pair runs to the base of the ovule, the outer traverses the walls of the perianth.

The wings next rapidly dilate upwards and outwards, till the perianth becomes obovoid in circumscription (Plate VIII. fig. 12), its orifice almost closes, leaving a small notch at its apex, through which the styliform prolongation of the ovular integument often protrudes. Finally, as the wings dilate further, and the base contracts into a stipes, it assumes its nearly orbicular form, and acquires almost the dimensions of its subtending scale.

The above-described flowers have rarely presented evidence of being fertilized; and it is probable that the development of the flowers in the lower parts of the same cones, which were all formed at a much earlier period, and duly impregnated, has presented some deviations from the above described, as these vary to a very considerable degree amongst themselves,—the relative dimensions of the perianth and its wings, the ovular coat and nucleus, differing much in one and the same cone.

Pericarp.—The persistent pericarp, enclosing the ripe seed of *Welwitschia* (Plate VII. figs. 2 & 3), consists of a central cavity surrounded by a very large membranous hyaline wing of exquisitely beautiful structure and appearance. The central portion is obovoid or pyriform, suddenly contracted above into a narrow canal, traversed by the styliform process of the ovular integument, and below into a flat stipes; it is compressed, almost

flat towards the axis, and tumid opposite the scale. The walls of the cavity are thin, coriaceous or chartaceous, and slightly thickened at the edges; they consist of four layers of tissue: 1, a cellular epidermis; 2, a thick layer of felted filiform liber-cells (Plate VII. figs. 11 & 12), which are cylindrical, transparent, tortuous, and blunt at either end; 3, a very delicate layer of thin-walled, spirally-marked, fusiform cells, the markings very close and delicate (fig. 10); 4, an inner epidermis, often broken up at the edges. A few spicular cells (fig. 8) are scattered here and there in the substance of the walls of the cavity. The hyaline wings have an undulated appearance, owing chiefly to the arrangement of their tissues: these consist of two layers of epidermis, enclosing thread-like liber-cells: the latter, towards the cavity, form a loose cottony mass that is very conspicuous when the pericarp is torn open, but in the wings they are reduced to a very thin stratum, and run in so tortuous a manner towards the periphery as to give the wings the undulated appearance mentioned above; they terminate close to the margin, in blunt apices. The vascular bundles that traverse the wings, run in arches from the main bundles along the edge of the cavity, and are lost before reaching the periphery.

The perianth of the female flower corresponds to the outer (lateral) leaflets of that of the hermaphrodite; for not only is their position the same (right and left of the axis), but the winged keel of the hermaphrodite leaflets answers to the beautiful wing of the female; and the greater distance apart of the bases of the hermaphrodite leaflets on the side towards the scale, corresponds with the mouth of the female perianth opening in the same direction.

The female perianth corresponds to the outer coriaceous covering of the ovule in *Ephedra* and in *Gnetum*, differing only in form, and perhaps in being developed after the nucleus of the ovule makes its appearance. In anatomical structure it is almost identical with *Ephedra*, in which I find the same abundance of liber-cells (though running in straight lines) and a similar layer of delicate spirals. The perianth of *Ephedra* differs in being trigonous, unwinged, and having three vascular bundles: in *Gnetum*, again, it is, as in *Welwitschia*, often compressed and bifid when young, of a much denser texture, and traversed by many vascular bundles*; it possesses comparatively little liber, and no spiral vessels†, but a profusion of rigid acicular cells; and the mouth of the perianth surrounds and tightly embraces the styliform process of the ovular integument.

Ovule of the Female Flower previous to Fertilization.

I have described the earliest observed condition of the ovule in the flowers contained in the uppermost scales of the half-ripe cones, as presenting a minute naked blunt papilla, about $\frac{1}{200}$th of an inch long (Plate IX. fig. 1), around the base of which the

* In *G. scandens* there are seven or eight bundles in the short stipes of the immature fruit, which divide into two series of numerous parallel branches: one series traverses the pericarp, the other supplies the ovular coats.

† These, however, probably occur in *Gnetum*; for Griffith describes these rigid acicular cells in the outer or baccate coat of the fruit of that genus as sometimes being spirally marked (Linn. Trans. xxii. 303).

perianth is developed; and I have stated that its solitary integument appears, as a tumid ring, round the base of the nucleus within the perianth, immediately after its first appearance.

Up to the stage figured at Plate VIII. fig. 6, the perianth is seen by transmitted light to have grown much more rapidly than the ovule, the nucleus of which is now wholly immersed in its integument, and the embryo-sac has made its appearance. At fig. 7 the ovular coat has risen far above the nucleus, and forms a conical body with a tubular mouth, as is also shown in the section of another ovule (Plate IX. fig. 9), which is about $\frac{1}{25}$th of an inch long. At this period the embryo-sac (Plate VIII. fig. 18) may easily be removed entire from the nucleus, and is a circular or transversely oblong, compressed, hyaline sac, containing a pale yellow transparent mass of endosperm-cells. In the next stages (Plate VIII. figs. 8, 9, 10), the apex of the ovular integument is more produced into a tube (better seen at figs. 15 and 16), which is contracted above the middle, and browned at the lacerated apex: the browning indicates that the parts so coloured have ceased to grow, having become almost horny in consistence. The nucleus, which varies a good deal in form, is now either conical or subhemispherical, with a terminal mamilla, depressed at its apex.

The ovule of the female flower has now attained about the same stage of development and dimensions as that of the hermaphrodite flowers figured at Plate VI. figs. 11 & 14; but there are the following essential differences between them:—in the female flower the styliform apex of the integument of the ovule is straight, rigid, browned, and lacerated at its apex; whilst that of the hermaphrodite flower is shorter, stouter, with more fleshy walls, is never sphacelated, is bent in a sinuous manner, and terminates in a broad, papillar, expanded disc, with a funnel-shaped orifice.

The tissues of the ovule present nothing different from those of other plants; the nucleus consists of a dense, soft, cellular tissue. The integument is a very delicate cellular membrane (Plate VI. fig. 15), becoming rigid towards the tubular portion, which consists of three to six layers of delicate cells, of which those of the inner layer have their inner walls much thickened and rendered horny by secondary deposits (Plate VII. fig. 17). There is no vascular tissue in the ovule itself; but, as in the hermaphrodite flower, two vascular bundles ascend the axis below, and terminate abruptly exactly at the insertion of the integument round the base of the nucleus (Plate IX. figs. 11, 12).

The general resemblance of the ovule here described to that of other Gymnosperms is very obvious, whether as regards the structure and position of the integument and its tubular prolongation, or the large embryo-sac, so easily removed, in which cell-formation has commenced previous to impregnation. In all these plants, too, the ovular integument (or the innermost, when there are two of these) is more or less carried up by the growing ovule, and often forms a small calyptriform pileus at the apex of the seed,—a fact which will call for attention when considering the relations of the seed, after the description of that body and its contents.

The ovule of *Welwitschia* entirely accords with that of *Ephedra*, except in the discoid apex of the integument of the latter, which is oblong and obliquely truncate. The ovule

of *Gnetum*, again, differs from that both of *Ephedra* and *Welwitschia*, in having two integuments, of which the interior corresponds to the single one of the other genera, and, as in these, terminates in the styliform process. In *G. scandens*, however, this styliform process is shorter, far more rigid, swollen below the middle, and again much contracted at the base; as the seed developes, it dilates, becomes almost woody, and its cavity is closed up by the pressure of the thickening lips of the outer integument of the ovule, which closely embraces its lower portion, as the orifice of the perianth does its upper portion. The outer integument of the ovule of *Gnetum* is developed after the inner or styliform; but, as nothing analogous to it exists in *Welwitschia*, I need not further allude to it here *.

Viewed in reference to its position on the rachis of the cone, and its terminating the axis of the flower, the ovule of *Welwitschia* presents many puzzling points for consideration. Though subtended by a scale, the female flower does not bear organically the same relation to the vascular cords in that scale that usually obtains between flowers and the cords of their subtending bracts; for not only is each organ (scale, perianth, and ovule) bilateral, and each furnished with a double vascular system, but the insertion of the scale is, as shown in Plate XIII. figs. 1 & 2, at a considerable interval below that of the perianth; and the scale is not supplied by vessels directly from the principal bundles on its own side of the rachis of the cone (as the perianth and ovule are), but from lateral branches, which leave the principal bundles almost at a right angle.

The structure of the scale, and its relation to the rachis, would thus have favoured the *à priori* supposition that it was a compound body, and that still stronger traces of composition would be found in the floral organs. Such, however, is only partially the case. The female perianth appears, indeed, at its earliest stage as a lobed or double organ (which the scale does not), and its form and obvious correspondence with the male perianth

* The development of the coats of the ovule of *Gnetum* is the subject of a communication from Dr. Griffith to Dr. Lindley (Veg. King. p. 233); and his detailed memoir on the same subject were afterwards published by the late Prof. Henfrey in our Transactions, vol. xxii. p. 299.

My observations on Griffith's specimens of *Gnetum scandens*, *G. Gnemon*, *G. Brunonianum*, and others, differ much, however, from those of that skilful investigator, whose account of the development of the ovular coats is certainly erroneous. In none of these species do I find the appearance of the inner coat to be either sudden or subsequent to the formation of the outer; on the contrary, the inner coat is first gradually developed around the nucleus as a cup with a fimbriated mouth, and it often overtops the nucleus before the outer coat makes its appearance. The latter first appears as a ring round the base of the inner coat, with a lobed or irregularly crenate, often oblique mouth; both integuments grow together, but the inner at all periods exceeds the outer. The tissues of both are similar, viz. elongated cells; neither contains vascular tissue when young, nor does the inner at any time; but the outer becomes full of parallel vascular cords. I have found female flowers of *G. scandens* in which there has been no trace of the outer coat, though the inner had already grown far beyond the nucleus. There is a common monstrous state of the flower of *G. Brunonianum*, in which the perianth is globose and fleshy, and the nucleus of the ovule is elongated, naked, and seated on a fleshy disc.

It should be borne in mind that, at the time Dr. Griffith's paper was written (Aug. 4, 1835), he was unacquainted with the true nature of the gymnospermous ovule, and also with Brown's remarks on *Gnetum*. I cannot, however, but consider that his observations relating to the ovule, and to the discrimination of the species (of which all the original materials and drawings are preserved at Kew), were probably not intended for publication *in extenso*. Both his figures and descriptions are inferior in accuracy to the beautiful analyses of Decaisne, in Blume's 'Rumphia,' iv. t. 176, where the development of the ovular coats is represented (figs. 18 & 19) as I have found it to be.

tend to show that it is compound. The ovule, on the other hand, up to this period of growth, shows no further traces of composition than the double vascular system which terminates at the base of its nucleus; it is organically absolutely terminal, being erect, central, and continuous with the axis of the perianth, without constriction, both in the male and female flowers: lower down, these two vascular cords are confluent with the two main vascular bundles of the perianth; and the cellular tissue which is contained between these cords is similarly continuous with that of the nucleus of the ovule.

I believe that, in respect of this anomalous disposition of vascular cords at the base of the ovary, *Welwitschia* presents but a slight deviation from the arrangement which obtains in other *Gnetaceæ*, of which *Ephedra* has three corresponding bundles, and *Gnetum* many; but it presents a remarkable contrast to what occurs in *Coniferæ*, and, in connexion with the other peculiarities of the ovule, and with the relations of the flower to the scale, it renders it impossible to reduce the inflorescence of the three genera (*Ephedra*, *Gnetum*, and *Welwitschia*) to the same type with that of Conifers as generally understood.

Assuming Brown's view of the ovule of Conifers, and mine of that of *Gnetaceæ*, to be correct, that each presents a nucleus with one or more integuments which are not of carpellary origin, we have, then, in biovulate *Coniferæ* two ovules lying on an open scale, regarded by most as carpellary, but by some as ramal, and this again subtended by another scale, which is regarded as bracteal. The obvious mode of harmonizing the relations of these organs is, to regard the ovuliferous scale of *Coniferæ* as not carpellary, but perigonial, or the perianth of *Gnetaceæ* as carpellary. It would be out of place to discuss here the first proposition, because (though by no means proven) the balance of evidence is decidedly in favour of the carpellary nature of the ovuliferous scale, at least in the *Abietineæ*; and the second proposition is entirely negatived by the structure of the hermaphrodite flower in *Welwitschia*. Then, again, the ovuliferous scale in *Abietineæ* supports two ovules; and the fact that Braun and Caspary * have found it replaced by two leaves would indicate that, if carpellary, either the ovarium is here compound, or each bract supports two flowers, each flower being represented by a uniovular carpel, and that, for comparison with *Welwitschia*, we must resort to the uniovulate *Coniferæ*, such as *Araucaria*, *Dacrydium*, *Podocarpus*, &c., the correspondence of whose scales with those of *Abietineæ*, &c., is not in all cases ascertained.

There is nothing in the development of this ovule that favours the opposite theory, that the integument of the nucleus in gymnospermous plants is of carpellary origin, except the singular form and relative position of that organ in the hermaphrodite flower. In position, texture, structure, and development, it entirely resembles the coat immediately investing the nucleus in all other Gymnosperms; like these, and unlike carpellary organs, it is entirely devoid of vascular tissue in its substance, and of conducting

* Caspary "On the Morphology of the female Flower of the Abietineæ;" translated in Nat. Hist. Review, 1862, p. 19. Parlatore (Ann. Sc. Nat. sér. 4. xvi. p. 215) considers the scale to be a shortened branch, having its leaves or bracteoles more or less confluent together and with the bract and the pistil (ovule).

tissue in its styliform prolongation; unlike a carpel, it rises symmetrically round the nucleus, and in the hermaphrodite flower presents a symmetrical terminal disc, and it ceases to grow long before the maturation of the seed; and still more unlike a carpel, it is carried up with the growing seed, till its base is on the apex of the latter. In all these respects, except in the long styliform process, it accords with the inner ovular integument of phænogamic plants, which, indeed, have not unfrequently tubular orifices prolonged beyond the nucleus, though not so far as that of *Gnetaceæ*.

To these considerations must be added that of the exterior integument of *Gnetum*, which is as clearly an appendage of the ovule as the interior, but which must be considered to be either staminal or a production of the disc, if the inner coat is considered as carpellary.

Lastly, ovular integuments are singularly uniform in their structural anatomy, which seldom deviates from one common type; and in the normal condition of the ovule, it is devoid of appendages, or of other external or internal characters whereby those of allied species, or even genera and orders, can be distinguished from one another. I am not aware that a single natural family or genus of Angiosperms presents any structural peculiarity of the outer or inner coats of its ovule: on the other hand, the carpel is, of all the floral whorls, one of the most various; and, as often happens with other organs, the more reduced it is, and the more it deviates from the foliar type, the more liable it is to vary: whence it is all but inconceivable that the ovular integument of Gymnosperms should be carpellary, and yet constant in structure.

If, then, we were to assume the ovular integument of Gymnosperms to be carpellary, we must admit, first, that it has neither the form, structure, nor functions of an angiospermous carpel; secondly, that it has those of an angiospermous ovular coat; and thirdly, that while the carpel is a singularly varying organ in the genera and even species of Angiosperms, it is a singularly uniform one in those of Gymnosperms.

Fertilization and Embryogeny. Seed.

Fertilization.—I know nothing definitely of the epoch at which fertilization normally takes place in *Welwitschia*, nor indeed of its flowering and fruiting seasons. Dr. Welwitsch gathered young male flowers, together with nearly mature fruit, in September; and the fine specimens last sent by Mr. Monteiro, on which are old male cones, must have been gathered at about the same period of the year. Mr. Baines's sketch, again, which represents ripe cones, bears date May 10th.

It is reasonable to suppose that impregnation is effected by insect agency, and that when the pollen is ready for transport the female cones are still very small, and the nucleus of their ovules is neither covered by the ovular integument nor by the perianth. At such a period the staminate and female cones are probably of about the same size, and their scales more patent than they afterwards are in the female. Such an arrangement, indeed, appears necessary; for it is obvious that, after the ovular integument has assumed its styliform shape (which is long antecedent to any change taking place in the nucleus), it would be extremely difficult to introduce a single grain of pollen by any conceivable means to the apex of the nucleus, and impossible to convey there the

forty and more grains that I have found with their tubes all produced. Furthermore, as is stated above, I have found pollen-grains on the nucleus before the elongation of its integument, and this in ovules contained in the extremely immature uppermost scales of an otherwise half-mature cone—ovules which, as I have reason to suppose, are developed long after the usual period of fertilization.

In connexion with this subject, I may mention that the nearly mature cones are often bored through and through after the manner of flower-buds attacked by the larvæ of *Curculionidæ*, and that a pollen-feeding group of Coleoptera, the *Cetoniæ*, abound in the regions inhabited by *Welwitschia*.

The pollen remains on the apex of the nucleus for some time before any change takes place in the embryo-sac; and its large solitary tubes are apparently slowly emitted, and slowly make their way down the dense tissue of the nucleus. I have never seen more than one tube emitted; but this, after emission, sometimes elongates in both directions, or even forms a crutch or fork, between the arms of which the empty wall of the pollen-grain persists (Plate IX. fig. 38). The tubes reach about one-third down the conical apex of the nucleus, apparently always keeping near its periphery; they are terete and even, they never branch, and swell at the base, only when they touch the secondary embryo-sac.

Changes after Fertilization.—These commence within the nucleus of the ovule after it has assumed the form, &c., represented in Plate VIII. fig. 7, Plate IX. figs. 8, 9, and are conspicuous after it arrives at the stage seen in Plate IX. figs. 11, 12, which represent ovules taken from a perianth such as is figured at fig. 10. From this time onwards the nucleus developes rapidly in all directions, but the parts above the embryo-sac grow less than those below it; and as the greatest increment of all takes place at the very base, below the level of the insertion of the integument, the latter is carried up, and, assuming a higher and higher relative position as the seed ripens, is found at last towards the apex of the seed. This mode of ovular development is common, in a greater or less degree, to all *Gnetaceæ*, *Cycadeæ*, and to many *Coniferæ*.

At the period last mentioned, the embryo-sac (Plate VIII. fig. 18, & Plate X. fig. 2) is a delicate membrane, more or less loosely investing an ovoid, orbicular, or transversely oblong compressed mass of endosperm-cells, in which, however, there is no visible differentiation of parts, nor any defined sharp boundary to the individual cells. At the next stage (Plate X. fig. 1) the nucleus is elongated both upwards and downwards, is dilated opposite the sac, and its integument is carried up considerably above its base; the contained sac is also elongated, and rather broader above than below, becoming obovoid. Still later (fig. 4), the integument is carried up above the middle of the nucleus, and the yet more elongated sac has descended, as it were, below the level of the insertion of the integument. The nucleus is now divisible into two distinct portions—an upper one above the embryo-sac, which I shall call the *cone*, and a lower one, containing the embryo-sac, which I shall call the *body* of the nucleus: the insertion of the integument marks externally the positions of these parts. Sometime between the last two stages, the membrane of the embryo-sac is found to have disappeared over the summit of the endosperm, and blunt tubular processes (Plate X. fig. 3) appear rising above the endosperm-

mass and becoming entangled with the cellular substance of the cone above it. I have made many dissections of the embryo-sac at about this stage, and before it, but have failed to detect any cells of the endosperm set apart, as it were, for this purpose. I find the whole endosperm-mass at the now open mouth of the sac to consist of loose or slightly coherent transparent ovoid utricles, with dark contents, of which many elongate upwards, and many do not. Of those which elongate, some, towards the centre of the mass, are quite free; others, towards its margin, remain firmly coherent to the denser tissue of the margins of the endosperm-mass. The central ones become the secondary embryo-sacs, and correspond to the corpuscula of *Coniferæ* and *Cycadeæ*.

At Plate X. fig. 3, a few of these secondary sacs are seen protruding from the embryo-sac; at figs. 5 & 7 they are still further developed; and above fig. 5 is represented a small portion of the endosperm-mass, from immediately above the main body contained in the sac. At fig. 6 some of the young secondary sacs are shown, all the surrounding endosperm-mass being cleared away.

Though at first entirely resembling the other cells of the endosperm, the secondary sacs rapidly assume a different character, become tortuous, often inflated in parts, and, when preserved in alcohol, contain very diffused amorphous contents, together with minute globular vesicles, which turn bright yellow with iodine. Some of the transition stages are represented at Plate X. fig. 8.

There next appear, in the substance of the cone of the nucleus, interrupted dark lines, radiating upwards and outwards from the summit of the embryo-sac. The lower portion of the embryo-sac is still quite evident, and may be readily withdrawn from around the endosperm, which forms an oblong body, pendulous from the base of the cone. The endosperm-mass is oblong (Plate X. fig. 9), its cells are well defined, and the outermost of the upper series cohere with the tissue of the cone above. A dark area now occupies the base of the axis of the cone, consisting of a tissue intermediate between that of the cone and of the endosperm-cells; and within this tissue the secondary embryo-sacs lie (Plate X. fig. 11), being, as it were, lifted out of the mouth of the sac by the interstitial growth of cells therein.

The secondary sacs are now elongated, club-shaped, membranous, with rounded apices and bulbous bases (fig. 12), in which are very opaque amorphous contents; transparent globules abound in the upper part: they vary in number from 20 to 40 or 60, are nearly erect, and radiate outwards, their bases being in close contiguity.

As the nucleus elongates with the growing sac, it contracts at the base into a broad stipes; and vascular cords, either simple or branched, traverse it on each side. In some nuclei it happens that there is an apparent arrest of development of the endosperm; this I found to be the case in many of Mr. Baines's specimens, where (Plate IX. figs. 18, 19) the endosperm forms a flat tongue-shaped body in which the cells were irregularly developed (fig. 25), very loosely invested by the embryo-sac*. There are, however, in the various

* In the cavity of these embryo-sacs, which were not filled by the endosperm, I fancied I detected a filamentous net-work, resembling a very delicate cellular tissue. At the time, I was at a loss to explain it; but in looking over Hoffmeister's valuable work on the Higher Cryptogamia, I find a structure described in *Pinus*, which, if my observation was correct, may throw some light on it. In this genus, at one period, when the endosperm-mass is much

specimens examined, great differences to be found in the relative size of the nucleary cavity, embryo-sac, endosperm-mass, secondary embryo-sacs, and cone of the nucleus.

As the endosperm-mass increases, it becomes hollowed out at the top, below the base of the cone, into a cavity containing loose endosperm-cells; and the body of the nucleus becomes reduced to a thick fleshy coat, on the sides of which the vascular bundles ramify but little. This endosperm, now densely cellular, is the whole albumen of the seed, and consists of a *body* of granular substance and a constricted collar or *neck*, of a very different, looser, more fleshy, but very elastic tissue, which surrounds the cavity, and coheres with the base of the cone of the nucleus above.

The cone of the nucleus is next found to present an outer very cellular periphery, and an inner substance of much firmer, tougher tissue, traversed, along the dark radiating lines mentioned above, by many canals of various lengths and dimensions, which ascend outwards towards the periphery, to about two-thirds of the total length of the cone. Plate X. figs. 20–24 represent horizontal sections of a cone, taken at different heights, and show its loosely cellular epidermal layers of cells and dense interior substance, which is cancellated by these canals. The secondary embryo-sacs have grown upwards into these canals in great numbers, their bases being still gathered together, as it were, at the base of the axis of the cone, where they hang over the mouth of the cavity in the apex of the endosperm (Plate X. fig. 10). If the cone be now torn away from the top of the endosperm, and the tissues surrounding its base removed, the lower ends of these secondary sacs may be very easily exposed.

Fully formed secondary sacs taken out of these canals are shown at Plate IX. figs. 30, 31, and at Plate X. figs. 13, 14. These vary much in length and breadth, but always taper downwards, and are bulbous and very rarely branched (fig. 14) at the base. They are sometimes solitary in the canals, sometimes in twos or threes. When drawn out, they are often found to be longer than the cone itself, either from having been folded or from the canals being sinuous; but, owing to the transparency of these secondary sacs, and the tough, elastic, opaque nature of the tissue of the cone, I have never been able so to lay a cone open as to see the undisturbed sacs *in situ*. The sacs are, however, so large, so well defined, and so easily removed, that there is no difficulty in ascertaining their numbers, form, position, &c. with sufficient precision.

Another change that occurs about this time is the separation of the tissues of the nucleus forming the walls of the seed, into two layers (Plate IX. fig. 19) around the upper part of the endosperm. Of these layers, which are both continuous with the cone above, the outer one is the denser; and the inner one, like that of the neck of the endosperm-mass, is so tough, elastic, and troublesome to sever, as to render it difficult to expose the base of the cone and the apex of the endosperm-mass without tearing away the latter. This splitting of the nucleary walls into two layers is shown at the base of the cone, in Plate IX. figs. 26, 27, 29.

Development of Embryo.—At the period last described, and very often earlier, one or

smaller than the sac, the inner wall of the sac is covered by a very delicate cellular endosperm-tissue, filling up the space between it and the previously formed endosperm. The representation of this tissue would answer not inaptly to the appearances I saw. (See Currey's excellent translation, p. 408, t. lx. fig. 4.)

more of the secondary embryo-sacs is found to have elongated downwards into the cavity in the neck of the endosperm, and to have commenced to develope a suspensor at its base (Plates IX. fig. 28; X. figs. 20, 21). In almost every such case, when I have removed the secondary sac entire from the cone (which I have done many times), I find a pollen-tube adherent to its apex (Plate X. figs. 15–19). In every such case, also, I have found pollen-grains on the apex of the nucleus, and their tubes penetrating the tissue of the cone just within its margin, and passing downwards near the periphery. I have never succeeded in removing a pollen-tube entire from the apex of the secondary sac to the pollen-grain, but I have on several occasions so nearly done so, as to have seen its continuity before rupturing it; and in two instances (sketched before the dissection was completed, Plate X. figs. 15, 16) I failed at one point only, leaving no possible room for doubt. The fertilized secondary sacs, in every case examined, had advanced from one-half to two-thirds up the cone; and their apices occupied the termination of the canal, which was always close to the periphery of the cone, in the direction of the descending pollen-tubes.

The number of secondary embryo-sacs which are thus impregnated varies. Usually, I think, only one is so; but there are often two or three (Plate IX. figs. 26–29 & 32), and I have several times found four, six, and even eight (Plate X. fig. 20). I have, however, never found more than one embryo in the seed, nor seen a secondary sac branching downwards, as might be expected to occur in the one figured at Plate X. fig. 14.

After the contact of the pollen-tube, great changes commence in the bulbous base of the secondary embryo-sac, which elongates, and its contents collect into an obovoid mass —the germinal vesicle.

After elongating, the bulbous base of the secondary embryo-sac first presents a constriction at the neck, and its basal contents, now bounded by a cellulose wall, are obscurely lobed, first on the summit and sides, and later at the apex (Plate X. fig. 22). Soon the constriction becomes more marked, separating the bulb, which is now a rounded cone with the broad end uppermost, from the tubular portion above it, whilst the lobing has so far advanced that the upper part of the contents of the terminal cell consists of eight or ten separate masses (fig. 23); these shortly acquire proper cell-walls, and become the first series of cells of the suspensor (fig. 24). The terminal cell now again divides as before, longitudinally and transversely, and adds a second series of cells to the suspensor (fig. 19).

The cells of the suspensor elongate with rapidity, and are developed in great numbers; and as they go on forming and elongating faster than the secondary sac elongates, the base of the latter is removed further and further from the terminal cell. At the same time that the base of the sac elongates, it becomes excessively attenuated, and finally forms a slender tube sheathed by the upper tubular cells of the suspensor (fig. 27).

I have never had any difficulty in dissecting out the end of the secondary sac from the top of the suspensor (fig. 27); indeed, I have frequently pulled it out perfectly entire to the tip: but I have found much difficulty in tracing the early development of the suspensor from the terminal cell at the base of the secondary sac, and especially in proving the early retirement of the tubular prolongation of the sac after its bulbous base has been cut off by that terminal cell (as shown in Plate X. fig. 24).

Though well convinced that the contents of the bulbous base of the fertilized secondary embryo-sac thus gives rise to the suspensor by the division of its mass and the formation therefrom of long tubular cells that sheath the retiring portion above the bulbous base, I am by no means clear as to the exact process. It would, probably, be necessary to examine fresh specimens to prove whether the germinal vesicle may not burst through the base of the sac, and whether it may not divide longitudinally into four, as in the *Coniferæ*, and thus give rise to four rudimentary suspensors, of which, in *Welwitschia*, only one is developed. All I can affirm is, that I saw no evidence of either of these phenomena, and that the figures (22 to 24) are faithful (camera-lucida) representations of the structures, whose deficiencies in matters of detail are owing to the specimens having been preserved in alcohol.

The number of cells thus developed upwards, as it were, from the terminal cell of the suspensor, varies at different parts of the suspensor and in different individuals; the first series often consists of six, eight, or ten, and the subsequent series always of more, till, towards the end of the fully formed suspensor, they are thrown off (so to speak) in great numbers, and coalesce into a fleshy mass continuous with the apex of the embryo. The first formed (Plate X. figs. 18 & 24) are of nearly equal length, and elongate most of all, attaining sometimes nearly $\frac{1}{4}$th of an inch; the next series (fig. 19) are more irregularly developed. Finally, towards the lower end of the suspensor, as the power of production declines, they lengthen upwards less and less, and form an imbricating bundle, of which the outermost are free and patent, and sometimes recurved wholly or in their upper parts (fig. 25). After this last stage of funicular development, the terminal cell commences rapidly to enlarge and form an embryo.

The suspensor appears to be very rapidly formed: it is developed wholly within the cavity at the apex of the endosperm, and in a loose tissue of endosperm-cells; it is extremely tortuous, and sometimes attains the great length of three inches. The terminal cell appears to burrow amongst the endosperm-cells at the sides of the cavity; sometimes it gets entangled amongst the coalescing cells of the rapidly-forming albumen, but I think, in all such cases, it never produces a mature embryo.

In most cases it is easy, after carefully dissecting away the tissues of the neck of the endosperm, to free the cone of the nucleus, and in removing it to draw out the whole suspensor from the cavity of the endosperm (Plate IX. figs. 26, 28; Plate X. fig. 20). As the endosperm hardens and the embryo becomes developed, this can rarely be done; for then the suspensor usually is retained within the endosperm, whilst the tubular prolongation of the secondary sac is stretched (Plate IX. fig. 27) and may often (as observed above) be withdrawn, quite entire, from out of the apex of the suspensor.

During these changes the endosperm has been rapidly acquiring bulk and consistency, becoming an obovoid, compressed, granular mass, with an obconic central cavity (Plate IX. fig. 32), whilst its fleshy annular neck detaches itself from the cone of the nucleus above. The membranous remains of the embryo-sac may often be found on the surface of the nearly mature endosperm: arrested secondary sacs may up to a very late period be found adhering to the margins of its fleshy annular neck; and numerous unimpregnated secondary sacs are always present within the canals of the cone of the nucleus.

Ripe Seed.—This (Plate VII. fig. 13) occupies the centre of the pericarp (figs. 3, 4), is obovoid, compressed, terminated by the calyptriform membranous integument of the ovule, with its rigid styliform apex. Removing the calyptriform integument (fig. 14), the cone comes into view, the outer tissues of which are continuous with the walls of the nucleus, now the only integument of the albumen. The granular albumen, with its fleshy neck, is quite free; and the suspensor forms a coil within or over the mouth of the neck, on the summit of the contained embryo; the connexion between the suspensor and cone (by means of the tubular prolongation of the secondary embryo-sac) is usually ruptured, but sometimes persists (fig. 15).

The embryo (figs. 15, 16) is linear, terete, or slightly flattened, about $\frac{3}{4}$ths the length of the albumen, and occupies the cavity in the axis of the latter. The lower end is contracted into two small flat cotyledons, which are closely applied to one another, and include no plumule. The radicular end swells out into an uneven fleshy mass, which is the cellular base of the suspensor, and is lodged in the equally fleshy annular neck of the albumen.

I have throughout described the thick vascular investing coat of the seed, which is developed as the endosperm enlarges and descends, as appertaining to the nucleus, because it is continuous downwards uninterruptedly from the body of the nucleus as that nucleus existed previous to impregnation, at the time when the insertion of the ovular integument coincided with the base of the ovule; but Prof. Oliver has forcibly directed my attention to the claims which this seminal integument may have to be regarded as an urceolate prolongation of the axis of the flower, and not a development of the nucleus, which the parts above the insertion of the calyptriform integument indisputably are. In favour of regarding it as belonging to the axis are, 1, the two or more vascular bundles which are carried up in its walls, and whose terminations coincide at all periods with the base of the calyptriform integument, thus marking in the seed, as they did in the ovule, the boundary of what is certainly ovular, and what axial; 2, some important considerations suggested by the embryogeny of *Loranthaceæ*, upon which Prof. Oliver is at present engaged.

Against this axial view may be urged, 1, the absence of any ring or thickened margin on the integument of the seed, at the point of union of the axial and ovular portions, and the unbroken continuity of the tissues of the integument, externally with the calyptriform integument, and internally with the substance of the cone; 2, the circumstance that, of the two integuments investing the albumen of *Gnetum*, the inner one corresponds with that of *Welwitschia*, and must thus also be considered axial; which requires us to believe, either that the axis of the flower of *Gnetum* is produced upwards within the base of the outer integument of the ovule (whose insertion, unlike that of the inner coat, is found at the base of the seed), or that this outer coat of *Gnetum* is not ovular at all; 3, that in respect of the carrying up of the integument immediately investing the ovule of *Welwitschia*, that ovule differs only in degree from those of many angiospermous plants, and that under this view the two vascular cords do not inaptly represent a double raphe of very anomalous development and character.

I am unable further to discuss this curious point, which, for further elucidation, must await Prof. Oliver's researches on the embryogeny of *Loranthaceæ* and *Gnetaceæ*, both

of which Orders present many correspondences in the structure and functions of their organs of fertilization with *Welwitschia*. It must, however, be borne in mind, that as yet no "Ovular Theory" has been advanced that meets general acceptance, and that, until one shall be forthcoming, all such questions can only be answered by guess: at present, the whole subject is in a state of confusion, to which the ovule described in the present monograph adds not a little. Under many points of view, every ovule must be considered a terminal organ, and hence axial in relation to the vascular system of the plant, whether developed in the apex of a floral axis, as in *Welwitschia*, or on the surface of a carpellary leaf, as in *Nymphæa*, &c., or on the edges of the same, as in most plants. Its integuments may correspond to floral discs, or may represent hairs or other epidermal appendages, or may be foliar in origin. However this may be, the desideratum is, some general view of the relations of the ovule to the other floral organs, under which all the apparent deviations from any hitherto received theory of its origin shall be harmonized.

I am unable to indicate an exact counterpart to the process of impregnation and embryo-formation above described, amongst either angiospermous or gymnospermous plants. There is a general agreement in many most essential particulars with *Cycadeæ* and *Coniferæ*, especially in the structure of the ovule, its simple integument, the application of the pollen-grain to the nucleus, the free embryo-sac being filled with endosperm-cells previous to fertilization, the numerous secondary embryo-sacs, the position of the germinal vesicle at the base of these sacs, and in the high development of the long tortuous suspensor. The prominent differences are,—the absorption of the membrane of the upper part of the embryo-sac; the growth upwards of secondary embryo-sacs from out of the embryo-sac into the cone of the nucleus, apparently without the intervention of "rosette cells;" the impregnation of those secondary sacs in the cone of the nucleus when far removed from the embryo-sac (impregnation thus being, in one sense, extra-uterine); and the germinal vesicle at the base of the secondary sacs not giving origin to a plurality of suspensors and embryos. In this character of the secondary embryo-sacs, which answer in function to the embryo-sac itself in angiospermous plants, being for the most part developed and always fertilized in the nucleus outside the primary sac, *Welwitschia* presents an embryogenic process intermediate between that of Gymnosperms and Angiosperms.

There seems to be much variety in the early development of the secondary embryo-sacs in *Coniferæ*. In *Juniperus* especially many irregularities are described, the sacs sometimes originating in a remarkable increase of size in the deep-seated cells of the endosperm; and sometimes a secondary sac opens in the middle of one of the lateral surfaces of the endosperm (Hoffmeister, 'On the Higher Cryptogams,' &c., Currey's transl. p. 410). This is a step towards what occurs in *Welwitschia* when they actually leave the endosperm.

In *Coniferæ* it would appear that there are always two separate periods of the elongation of the pollen-tube; that is to say, that after the pollen has been placed on the apex of the nucleus, its tube descends and rests within the nucleus at a certain distance from its apex and from the embryo-sac, and that, after a considerable interval, the tube elon-

gates further, and reaches the sac (Hoffmeister, *l. c.* p. 415). Perhaps the whole course of the pollen-tube in *Welwitschia* corresponds with its first growth in *Coniferæ*, and the necessity for a second elongation is obviated by the ascent of the secondary embryo-sac. In *Coniferæ* the lower part of the pollen-tube always dilates more or less as it approaches the embryo-sac; in *Welwitschia* it behaves as in angiospermous plants, only dilating, if at all, on reaching the secondary sac.

My very imperfect knowledge of the embryogeny of *Gnetum* does not enable me to compare it with that of *Welwitschia*; but in *G. scandens*, *G. Brunonianum*, and *G. Gnemon* I find many remarkable points of coincidence with it. In *Gnetum*, the cone of the nucleus is comparatively very small indeed; the embryo-sac is early filled with endosperm, of which the upper cells are in *G. scandens* so very large, lax, and oblong, that I at first supposed them to be young secondary sacs, but abandoned the idea in favour of numerous filiform tubular delicate cells that traverse the endosperm longitudinally, within the embryo-sac. These thread-like secondary sacs (?) closely resemble those of *Welwitschia* in many respects, and they appear to be developed from cells which originally are not distinguishable from the surrounding endosperm-cells; but they want the bulbous base, are found at all heights in the axis of the endosperm, and even towards its base, they sometimes branch downwards, and very few of them ascend and project beyond the mouth of the sac. Of those that did so ascend, one or two appeared to me either to enter the cone or to adhere to its base—I could not make out which; and I thought I found a pollen-tube adherent to the apex of one. As in *Welwitschia*, the apex of the sac in *Gnetum* seems to disappear early, and the large endosperm-cells to protrude from its cavity. I have failed to detect any canals or structure of any sort in the cone; and I have never found an embryo or funiculus in the very young state of the seed.

From angiospermous plants *Welwitschia* differs in the naked ovule, free embryo-sac full of endosperm previous to fertilization, in the presence of secondary sacs, in the position of the germinal vesicle at their base, and in the compound highly developed suspensor; it, however, agrees with them in the germinal vesicle giving rise to one embryo only.

There is a remarkable analogy in one respect between the processes of fecundation in *Welwitschia* and *Santalum**, and still more in *Loranthus*†, as described by Griffith, in both which genera the embryo-sac is produced beyond the nucleus of the ovule, ascends in the cavity of the ovarium, sometimes penetrating up the style, where it meets the pollen-tube descending an open cavity leading downwards from the stigma. The canaliform style of *Loranthus* thus representing the canal in the cone of the nucleus of *Welwitschia*, it follows that in this respect the latter plant presents an intermediate stage between most Angiosperms, in which the pollen-tube perforates style and nucleus to reach the embryo-sac, and most Gymnosperms, in which it perforates the nucleus and embryo-sac too, and *Loranthaceæ*, in which it perforates the style only. If, as I suspect may be

* See Griffith in Linn. Trans. xviii. 59 & 71; xix. 171 & 487; also Henfrey, *ibid.* xxii. 69.

† Linn. Trans. xix. 178. The late Prof. Henfrey possibly alludes to this, when he observes (Linn. Trans. xxiii. 299) that his investigations on *Gnetum* lead him to regard favourably the opinion expressed by Prof. J. G. Agardh, that the *Gnetaceæ* are related even more closely to *Loranthaceæ* than to *Coniferæ*.

the case, the secondary sac of *Gnetum* is impregnated below the cone of the nucleus, and externally to the embryo-sac, it will complete the network of cross affinities thus afforded by the behaviour of the pollen-tube and embryo-sac respectively in plants which, in many other respects, differ very widely.

Summary.

From the anatomy of the trunk of young and middle-aged specimens of *Welwitschia*, it appears to be the only perennial flowering-plant which at no period has other vegetative organs than those proper to the embryo itself,—the main axis being represented by the radicle, which becomes a gigantic caulicle, and developes a root from its base and inflorescences from its plumulary end, and the leaves being the two cotyledons in a very highly developed and specialized condition. The consequence of the persistence of the cotyledons, and of their performing all the functions of leaves, is the arrangement of the principal vascular system in one horizontal stratum, which increases at its periphery, and which transmits vascular bundles upwards and outwards to the inflorescence, and downwards to the stock and root.

Owing to the centrifugal direction of growth in the stock and crown, above, below, and beyond the leaf-insertions, these enclose between them a deep slit or groove in which the bases of the leaves are lodged and protected from external injury throughout the life of the plant.

There is no proper separable bark to the plant, which is invested by a hard periderm, formed by the indurated outer cellular system of the stock, crown, and root, and is absent only over the growing tissues at the circumference of the trunk, and within the groove between the crown and stock. A general cambium-layer underlies the periderm everywhere, and there are special cambium-layers within the vascular bundles throughout the plant.

The parenchyma is crowded with rigid spicular cells of great size, covered with crystals, and which, by their arrangement, form, and surface, give solidity to the delicate cellular tissue of which the main part of the plant is composed,—acting in a manner analogous to the siliceous spicula of sponges. The vascular system is referable to the exogenous plan; but its arrangement into concentric wood-wedges is very rude, and confined to the axis of the stock and root. In the root the wood-wedges are frequently disposed round two cellular axes, a plane passing between which is continuous with that passing between the leaf-bases.

The gum which flows freely from various parts of the plant is due to a collenchymatous swelling of the cell-walls of the parenchyma, and sometimes also of those of the spicular cells.

Occasionally flower-buds are developed in the periphery of the stock, below the insertion of the leaves. This is an analogous case to the recorded ones of the formation of buds on the caulicle of species of *Euphorbia* and *Linaria*.

The venation of the leaf is strictly parallel and free, like that of Monocotyledons in general appearance; but there is a total absence of lateral vascular communications between the bundles, in which respect it more closely resembles the venation of many

Cycadeæ, *Dammara*, some *Podocarpi*, and other *Coniferæ*. This venation favours the early splitting up of the leaf into innumerable laciniæ—an arrangement that subserves some purpose in the economy of the plant.

The binary arrangement of its parts and bilateral venation of the floral organs of *Welwitschia* are remarkable characters, and seem to be interrupted in the staminal whorl only (which is senary): thus, there are two leaves, two floriferous lobes, often two medullary axes in the root, a dichotomous panicle, decussating bracts to the cone, vascular cords in pairs in its rachis, two vascular bundles in each bract, two in the perianth of the female flower, two at the base of each ovule, two leaflets in each whorl of the hermaphrodite perianth, and two cotyledons to the embryo.

The general plan of the plant is that of a Dicotyledon, as the structure of its embryo indicates; the principal deviations being the straight venation of the leaves, the six stamens, and the isolated vascular bundles which are superadded to the generally exogenous vascular system of the stock and root.

The male flowers are structurally hermaphrodite, and contain a naked ovule in the axis of the flower, which, though containing no embryo-sac, is provided with a very highly developed stigma-like disc at the apex of the ovular integument. *Welwitschia* thus presents the hitherto unique case of a structurally hermaphrodite-flowered gymnospermous plant.

The cones of *Welwitschia* are functionally unisexual, and the plant is probably truly dicœcious; fertilization being effected by insects, before the nucleus of the ovule of the female flower is enclosed by its integument or by the perianth.

The membrane of the embryo-sac, which is full of endosperm before fertilization, ruptures or disappears at its summit; and the secondary embryo-sacs, which are developed at its apex, ascend into canals in the substance of the nucleus, where they meet the descending pollen-tubes, and are thereby impregnated outside the embryo-sac, and removed from it.

After impregnation, the bulbous base of the secondary embryo-sac elongates, and descends into the cavity of the endosperm, when the germinal vesicle at its base gives rise by cell-division to a single suspensor, at the apex of which the embryo is developed.

Welwitschia is a Dicotyledon and an exogenous exorhizal perennial plant, belonging to the gymnospermous group of that class, and having a very close affinity with both *Ephedra* and *Gnetum*, but differing from all previously known Gymnosperms in wanting the disc-bearing wood-cells. Notwithstanding this peculiarity, I place it in the same Natural Order with the above genera, and after *Ephedra*, of which genus it is the South-African representative.

In its hermaphrodite flowers, its want of disc-bearing wood-cells, and in the impregnation of its secondary embryo-sacs taking place in the nucleus of the ovule exterior to the primary sac, *Welwitschia* is intermediate in character between angiospermous and gymnospermous plants.

In common with *Gnetum* and *Ephedra*, *Welwitschia* presents some very curious points of resemblance with *Loranthaceæ* and *Santalaceæ*, a further investigation of which will, I doubt not, lead to important discoveries, and to some further modifications of our accepted theories regarding the classification and morphology of flowering plants.

DESCRIPTION OF THE PLATES.

Plate I.

Fig. 1. Copy of a drawing of the entire plant, made by Don Ferdinand da Costa Leal for Dr. Welwitsch, said to be about 15 to 20 years old, and apparently from the specimen figured, Plate II. fig. 1.

Fig. 2. Copy of the coloured sketch made by Mr. Thomas Baines in Damara Land.

Plate II.

Fig. 1. Two views of the youngest specimen sent by Dr. Welwitsch, of the natural size, showing the leaves in an entire condition.

Figs. 2 & 3. Side and end views of a more advanced specimen, also from Dr. Welwitsch, showing the laceration of the apex of the leaf; of the natural size.

Fig. 4. Transverse section of the root of the same, showing an unusually regular arrangement of the root-bundles.

Plate III.

Side view of Dr. Welwitsch's largest specimen, reduced to about half the natural size. A portion of a leaf is cut away to show the areolated surface of the stock.

Plate IV.

The same, viewed from one end. To the left-hand side of the right-hand leaf, at its base, are seen the pits left by peduncles developed on the upper ridge of the stock, and below the leaf-insertion. Some pebbles are imbedded in the root, near its summit.

Plate V.

Figs. 1–4. Much-reduced sketches of the largest specimens sent by Mr. Monteiro.

Fig. 5. The large specimen sent by Mr. Andersson, also very much reduced.

Plate VI. Hermaphrodite flowers (p. 21).

Fig. 1. Peduncle and cones of hermaphrodite flowers, immediately previous to the expansion of the flowers; of the natural size.

Fig. 2. The same, magnified about 2 diameters.

Fig. 3. Bract of the peduncle, with imperfectly developed cone in its axis.

Fig. 4. Imperfect cone, from the same.

Fig. 5. Scale of the cone, with bud of hermaphrodite flower in its axis.

Fig. 6. Flower-bud just before expansion, seen from the opposite side of fig. 5.

Fig. 7. Flower with the inner perianth-lobe drawn back, showing the staminal tube and discoid apex of the ovule.

Fig. 8. One of the inner perianth-lobes, showing the disposition of the spicular sclerogen-cells in its tissue.

Fig. 9. Epidermal cells and spicular cells, from the same.

Fig. 10. Stamens and enclosed ovule.
Fig. 11. The same laid open, showing the position of the ovule.
Fig. 12. Summit of filament and anther.
Fig. 13. Pollen-grains, magnified about 240 diameters.
Fig. 14. Ovule, with the lower part of the integument removed in front, exposing the nucleus.
Fig. 15. Tissue of the integument of the ovule.
Fig. 16. Transverse section of the nucleus of the ovule, showing a dark line occupying the position of the embryo-sac in the ovule of the female flower.
Fig. 17. Diagram of the scale of the cone and floral whorls.

(All the above magnified, except fig. 1.)

Plate VII. Female cones (p. 24) and fruits (p. 37).

Fig. 1. Branch of the panicle, sent by Mr. Baines, of the natural size.
Fig. 2. Scale and pericarp, containing a nearly ripe seed, of the natural size.
Fig. 3. Pericarp, with the styliform apex of the integument of the seed protruding at the top.
Fig. 4. Transverse section of pericarp and seed.
Fig. 5. Portion of wing of apex of pericarp, and of styliform process of integument of the seed.
Fig. 6. Portion of wall of the cavity of the pericarp, showing the cottony liber-cells.
Fig. 7. Very highly magnified view of wing, showing the tortuous course of the liber-cells.
Fig. 8. Spicular cells from wall of cavity of pericarp.
Figs. 9 & 10. Spirally marked cells from cavity of pericarp.
Figs. 11 & 12. Liber-cells from cavity of pericarp.
Fig. 13. Ripe seed, and base of pericarp to which it is attached, showing the ramifications of vascular bundles in its walls.
Fig. 14. Longitudinal section of seed, showing the calyptriform integument at its apex, the only other integument being the nucleus terminating upwards in its fleshy cone. The obovoid mass in the interior is the albumen, crowned by the coiled-up suspensor.
Fig. 15. Longitudinal section of the albumen, showing the embryo with its suspensor still attached to the cone of the nucleus above.
Fig. 16. Two views of the embryo.
Fig. 17. Transverse section of the styliform process of the outer coat of the seed, showing the thickened inner walls of the innermost layer of cells.

(All the above, except figs. 1 & 2, are more or less magnified.)

Plate VIII. Development of female flower (p. 25) and scales of cone (p. 24).

Fig. 1. Rachis of cone of female flower, with the uppermost scales remaining, of the natural size.
Figs. 2 & 3. Two of the upper scales, also of the natural size, with an advanced female flower in each.
Fig. 4. View of a young scale (as viewed from the rachis), with the female flower seated on a conical prominence of the rachis, which is confluent with the base of the scale, and removed with it.
Fig. 5. Back view of the same scale.
Fig. 6. Very young female flower, the wings developing on the perianth, and the integument of the ovule overtopping the nucleus, as seen by transmitted light.
Fig. 7. More advanced flower, with the embryo-sac distinctly seen.
Fig. 8. More advanced flower on its conical receptacle.
Figs. 9 & 10. Female flowers at the period when changes commence in the embryo-sac.
Fig. 11. Apex of perianth, showing the anticous position of its mouth (towards the scale).

Fig. 12. Perianth more advanced, with immature ovule.
Fig. 13. Perianth at the stage where it assumes its intermediate or oblong form.
Fig. 14. Perianth still further advanced, and becoming orbicular.
Figs. 15 & 16. Ovules of different forms from figs. 13 & 14.
Fig. 17. Longitudinal section of body of ovule, showing a very large embryo-sac.
Fig. 18. An embryo-sac of unusual broadly transverse-oblong form.
Fig. 19. Front and (fig. 20) back views of two scales from different parts of a female cone.
Fig. 21. Membranous margins of the scale, showing the course of the liber-cells.
Fig. 22. Small portion of ditto, showing the individual liber-cells running towards the margin, and terminating within it, in blunt apices.
Fig. 23. Epidermis from inner surface of coriaceous green part of a scale.
Fig. 24. Epidermis from membranous outer part of a scale, showing the liber-cells.
Fig. 25. Portion of a liber-cell, showing its transverse striation.
Fig. 26. Epidermis of central area of scale, with liber-cells and spicular cells.
Fig. 27. Spicular cells, with minute points on their surface, from the coriaceous part of the scale.
Fig. 28. Lowermost free, but empty, scales of cone.
Fig. 29. Lowermost connate (empty) scales of cone.

(All these figures, but 1, 2, & 3, more or less magnified.)

Plate IX. Development of female flower (p. 25) and embryogeny (p. 31).

Chiefly from Mr. Baines's specimens.

Fig. 1. Uppermost imperfectly developed scale of cone, with naked nucleus of ovule at its base.
Fig. 2. Another, more advanced, the nucleus surrounded with a thickened ring.
Fig. 3. Very young ovule from the same.
Fig. 4. Ovule with the thickened ring, which becomes the perianth.
Fig. 5. More advanced flower, the perianth supporting the still exposed nucleus, girt by another ring (its integument).
Fig. 6. Flower still further advanced, the perianth having risen to a level with the ovule.
Fig. 7. Flower further advanced, the perianth becoming 2-lipped.
Fig. 8. The perianth much more advanced, in its urceolar compressed stage; the ovular integument produced far above the nucleus.
Fig. 9. Longitudinal section of the same.
Fig. 10. Perianth in its oblong condition (of the natural size).
Figs. 11 & 12. Ovule and longitudinal section of the same, showing the embryo-sac and the two vascular bundles beneath the nucleus.
Fig. 13. Perianth at a much later period, from which the ovule, fig. 15, was taken (of the natural size).
Figs. 14 & 15. Ovules from the perianths, figs. 10 & 13.
Fig. 16. Ovule with the outer integument carried up halfway, and the embryo-sac descending.
Fig. 17. Ovule advanced still further, when the vascular bundles are developed on its walls.
Fig. 18. Ovule at a still later stage of development, but much shrivelled, the growth of the endosperm not appearing to have advanced with that of the nucleus and its cone.
Fig. 19. Longitudinal section of ditto, showing the loose embryo-sac loosely investing the tongue-shaped endosperm-mass. The dark lines have appeared in the cone above it.
Figs. 20–24. Transverse sections of the cone of a nucleus, after the canals are fully formed in its substance.
Fig. 25. An endosperm-mass apparently in an arrested condition, lying on a portion of the embryo-sac.
Fig. 26. Cone of a nucleus removed, showing the rudimentary embryos continuous by their suspensors with the tubular terminations of the secondary embryo-sacs.

Fig. 27. Apex of endosperm-mass and embryo-sac, surmounted by and dissected away from the cone of the nucleus, showing the stretched tubular ends of the secondary embryo-sacs between them.
Fig. 28. Another cone of a nucleus, with three rudimentary suspensors, which sheath as many tubular ends of secondary embryo-sacs.
Fig. 29. Longitudinal section of cone of nucleus, traversed with canals, and one suspensor descending into the cavity of the endosperm; the membrane of the sac still remaining.
Fig. 30. Secondary embryo-sacs of the usual clavate form, but without bulbous bases.
Fig. 31. Another secondary embryo-sac attenuated at both ends.
Fig. 32. Longitudinal section of a half-ripened endosperm-mass, showing its constriction above into an annular fleshy neck, its cavity containing the rudimentary embryo, and its suspensor attached by the tubular base of the secondary sac to the cone above.
Fig. 33. Very young embryo; its cotyledons formed at the base, the radicle very short, and above it the large cellular fleshy end of the suspensor; the whole covered with endosperm-cells.
Fig. 34. Apex of a nucleus, covered with pollen-grains.
Fig. 35. Portion of another, more magnified.
Figs. 36 & 37. Pollen-tubes of the ordinary form.
Fig. 38. Branching pollen-tube.

(All the above, except figs. 10, 13, 14, 15, more or less highly magnified.)

Plate X. Embryogeny, *continued* (p. 31).

Fig. 1. Longitudinal section of an ovule on the first disappearance of the summit of the embryo-sac over the endosperm.
Fig. 2. An embryo-sac very loosely investing the endosperm.
Fig. 3. Endosperm with the secondary embryo-sacs appearing above its apex.
Fig. 4. Longitudinal section of an ovule, when the endosperm has elongated, and dark lines appeared in the cone of the nucleus.
Fig. 5. Embryo-sac from the same, with the secondary embryo-sac protruding. The figure above represents the tissues torn away from the summit of the endosperm.
Fig. 6. Another embryo-sac, with the secondary sacs still further advanced.
Fig. 7. Apex of another embryo-sac and endosperm-mass, with secondary sacs protruding.
Fig. 8. Endosperm-cells and secondary embryo-sacs in a very early condition.
Fig. 9. Longitudinal section of an ovule, after the embryo-sacs have taken a position above the endosperm, in the base of the cone of the nucleus.
Fig. 10. Part of another, more highly magnified, showing the bases of the secondary sacs.
Fig. 11. Secondary embryo-sacs, in rather a younger state, *in situ*.
Fig. 12. A young secondary embryo-sac, showing the transparent globules and rudimentary germinal vesicle in its base.
Fig. 13. An older secondary embryo-sac (unimpregnated), with a hooked projection at the side.
Fig. 14. A mature secondary embryo-sac (unimpregnated), with a branching base, and appearance of two germinal vesicles.
Fig. 15. A pollen-tube, having penetrated the nucleary tissue of the ovule, is in contact with the apex of a secondary embryo-sac.
Fig. 16. Another secondary embryo-sac, with the pollen-tube at its apex, and its base sheathed by the suspensor.
Fig. 17. Apex of another, with base of pollen-tube applied to its side.
Fig. 18. End of pollen-tube, attached to a secondary embryo-sac, of which the terminal cell is free, and the lower end above it sheathed by the first series of cells of the suspensor.

Fig. 19. Another embryo-sac, with pollen-tube attached, and suspensor forming; the second series of cells here being developed.

Fig. 20. Cone of the nucleus removed, showing pollen-grains on its apex; eight impregnated secondary embryo-sacs, with their bases sheathed in the apices of their suspensors; between these the bulbous bases of the unimpregnated secondary embryo-sacs are seen.

Fig. 21. Base of cone from another ovule, with bases of many unimpregnated secondary embryo-sacs and four impregnated ones, of which two are cut off, one apparently aborted, and the fourth sheathed by the upper cells of the suspensor.

Fig. 22. Base of impregnated secondary embryo-sac after elongation, showing the lobed germinal vesicle and contracted base of the sac.

Fig. 23. The same further advanced, the lobes of the upper part of the germinal vesicle having given rise to six incipient cells above it.

Fig. 24. The same, with the cells above the terminal one developed and elongating, showing also the attenuated tubular base of the secondary embryo-sac retiring, as it were, from the terminal cell.

Fig. 25. Apex of a suspensor when nearly fully developed, but before the embryo commences to grow; showing the great accumulation of cells, of which the outer are gradually smaller, free wholly or in part, and often recurved.

Fig. 26. First series of cells of a young suspensor, torn away from the terminal cell.

Fig. 27. Attenuated base of an impregnated secondary embryo-sac, exposed by the removal of all but two of the upper sheathing-cells of the suspensor.

(All the above are very highly magnified figures.)

Plate XI. Vascular system of trunk (p. 13).

Fig. 1. A longitudinal section through the middle of both leaves of a full-grown but small specimen, reduced to about one-half; showing, to the right, the insertion of a peduncle and a bud; the deep groove in which the leaf-bases are inserted; the principal vascular stratum running across the trunk, parallel to the surface of the crown; the ascending vascular bundles in the crown, the descending ones in the stock, and the indefinite bundles in the axis and root.

Fig. 2. Transverse section of one of the lobes of fig. 1, taken at right angles to the plane of the cut surface, of the natural size. This section cuts through each vascular bundle of the principal vascular stratum in its course from the leaf-base to the axis of the plant.

Fig. 3. A longitudinal section of a portion of the stock, taken through the centre of the depression of fig. 1 (that is, between the bases of the leaves), of the natural size. This section shows how confused the vascular bundles are in the stock, towards the contiguous bases of the leaves, and that those in the crown pass inwards, parallel to the surface.

Fig. 4. Transverse sections of the crown and stock of one specimen, diminished less than one-half, showing, in the upper half, a section of the stock below the leaf-insertion; in the lower left-hand quadrant a section of the crown, and in the other quadrant the surface of the crown.

Fig. 5. Longitudinal section of part of a small specimen, between the bases of the leaves, of the natural size, showing the vascular bundles rudely collecting into plates (or wedges) on each side of the stock, thus giving rise to the two axes seen in fig. 8.

Fig. 6. Another section, from the same specimen, of the natural size, taken parallel to that in fig. 5, but through the base of a leaf (the same as fig. 2), showing the arched form of the vascular stratum, corresponding with the arched vertex of the crown.

Fig. 7. Longitudinal section through both leaves of another small specimen, of the natural size, in which the vascular stratum is very obscurely developed, though the ascending and descending bundles are very manifest.

Fig. 8. Transverse section of the root of fig. 5, of the natural size, showing great confusion of the wood-wedges.

Fig. 9. Transverse section of root of fig. 7, of the natural size, and showing two medullary axes.

Plate XII. Tissues of the stock, &c. (p. 10).

Fig. 1. Parenchyma of the stock, including vessels, liber-cells, and sclerogen-cells covered with crystals. Magnified 60 diams.

Fig. 2. Periderm of stock in longitudinal section, consisting of transversely elongated parenchyma and spicular cells.

Fig. 3. Epidermis and subjacent cellular tissue of periderm near the leaf-base. Magnified 400 diams.

Fig. 4. Vessel from the peduncle, showing that the narrow spiral bands are spaces between the secondary deposits. Magnified 400 diams.

Fig. 5. Portion of a spicular sclerogen-cell, covered with crystals. Magnified 240 diams.

Fig. 6. Smaller portion of ditto, magnified 430 diams., showing crystals of two forms.

Fig. 7. Transverse section of a very large spicular cell, enclosed in parenchyma. Magnified 240 diams.

Fig. 8. A thin-walled spicular cell, with the crystals very small. Magnified 60 diams.

Figs. 9 & 10. Small, branched spicular cells, with secondary deposits. Magnified 60 diams.

Fig. 11. Section of a small portion of another, after boiling in caustic potash. Magnified 60 diams.

Fig. 12. Branched liber-cell of very irregular diameter and unusual form. Magnified 240 diams.

Fig. 13. Portion of a liber-cell of the ordinary form, with transverse striæ. Magnified 240 diams.

Fig. 14. Parenchyma of stock, becoming colloid. Magnified 240 diams.

Fig. 15. The same, involving a spicular cell with crystals.

Fig. 16. Transverse section of the parenchyma and vascular bundles of the roots, showing, to the left, liber-bundles, to the right, barred vessels, to the extreme right, spicular sclerogen-cells with crystals. Magnified 60 diams.

Plate XIII.

Fig. 1. Portion of rachis of cone, with scale *in situ*, showing the disposition of its vascular bundles. Magnified 2 diams. (see p. 25).

Fig. 2. The same, with the scale removed, showing the relation of the vascular bundles to the perianth.

Fig. 3. Transverse section of rachis of cone. Magnified 2 diams.

Fig. 4. Pitted cellular tissue from the same. Magnified 60 diams.

Fig. 5. The same, showing the obliquity of the pits. Magnified 240 diams.

Fig. 6. Longitudinal section through the base of a cone and peduncle, taken through the centre; of the natural size.

Fig. 7. The same section, taken close to the periphery, showing the anastomoses of the bundles.

Fig. 8. Transverse section of the peduncle, showing the irregular arrangement of the vascular bundles. Magnified 2 diams.

Fig. 9. Transverse section of pitted parenchyma of central part of peduncles, with a few liber-cells. Magnified 240 diams.

Fig. 10. Longitudinal section of the same, with portion of a vascular bundle. Magnified 240 diams.

Fig. 11. Transverse section taken through the peduncle, showing the isolated vascular bundles and scattered liber-cells.

Fig. 12. Transverse section of a quadrant of a root, magnified $2\frac{1}{2}$ diams., showing the form and disposition of the wedges and isolated bundles.

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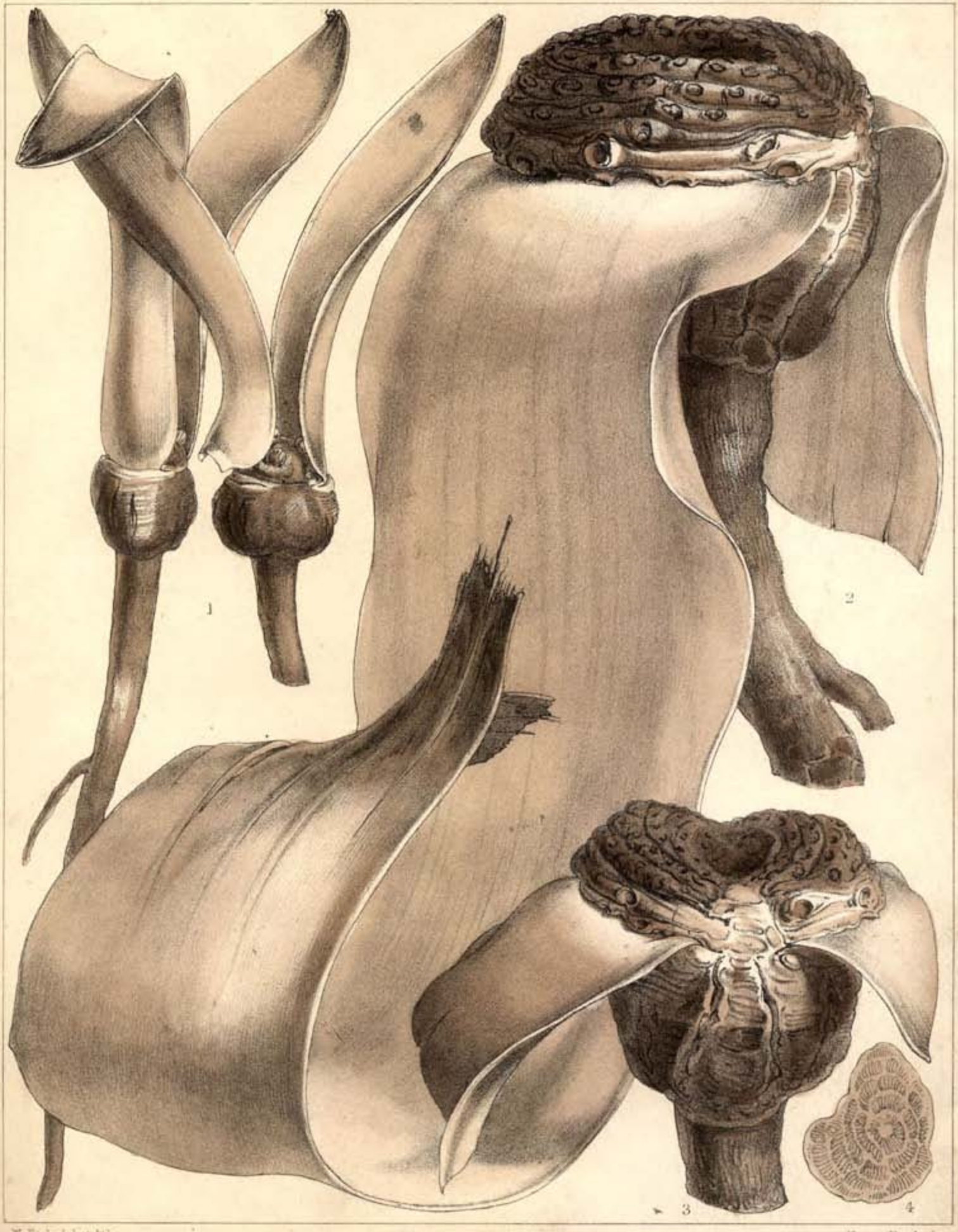

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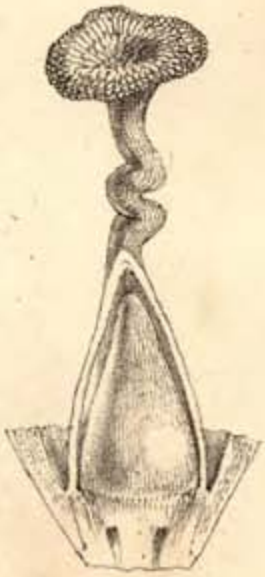
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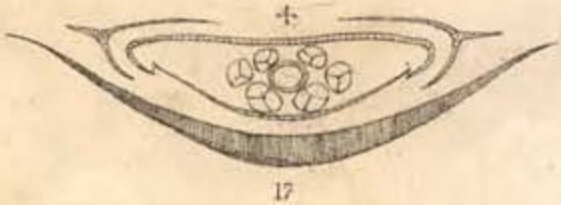
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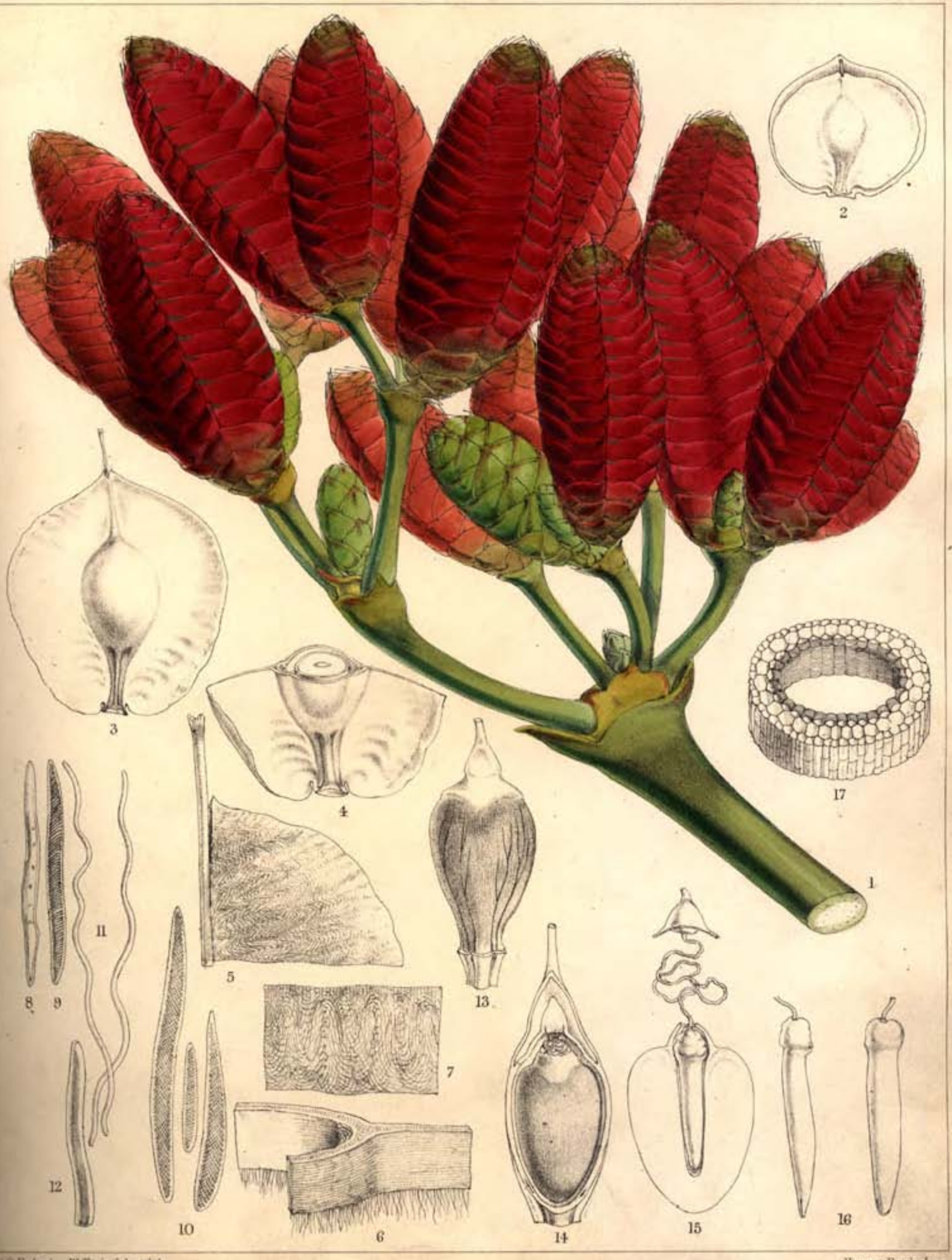
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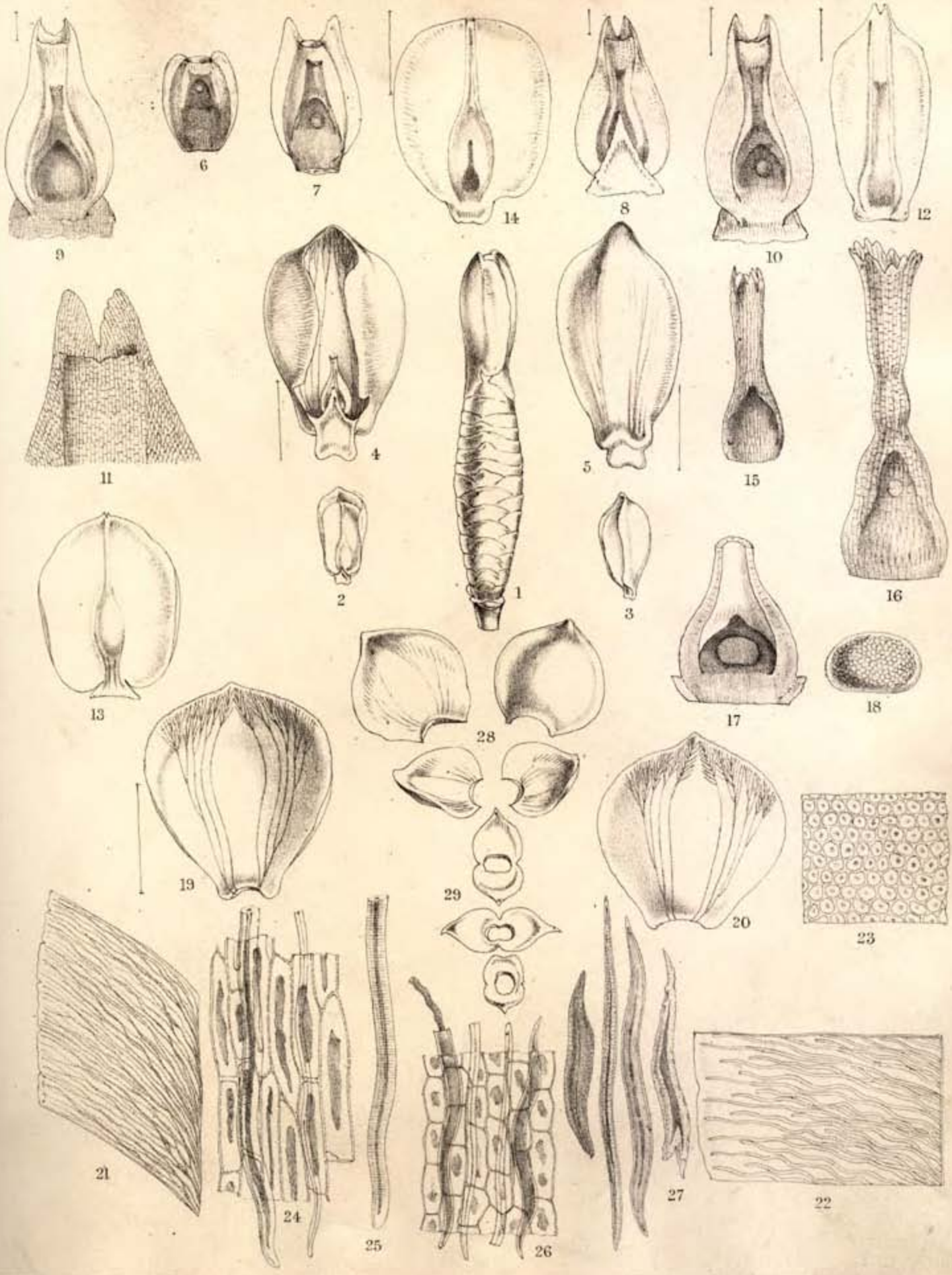
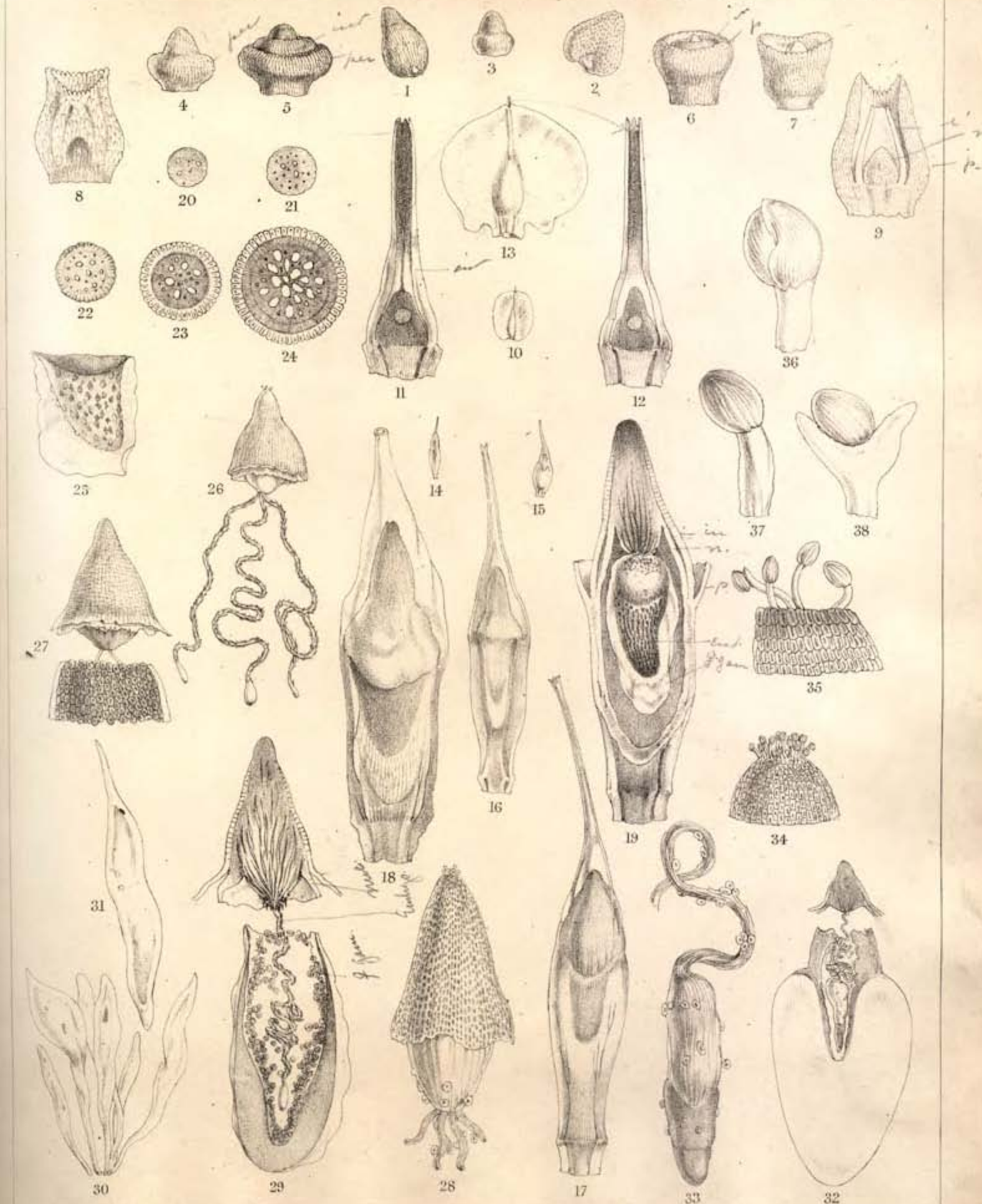


J. D. H. Anst. ___ W. Fitch, del et lith.

Vincent Brooks, Imp.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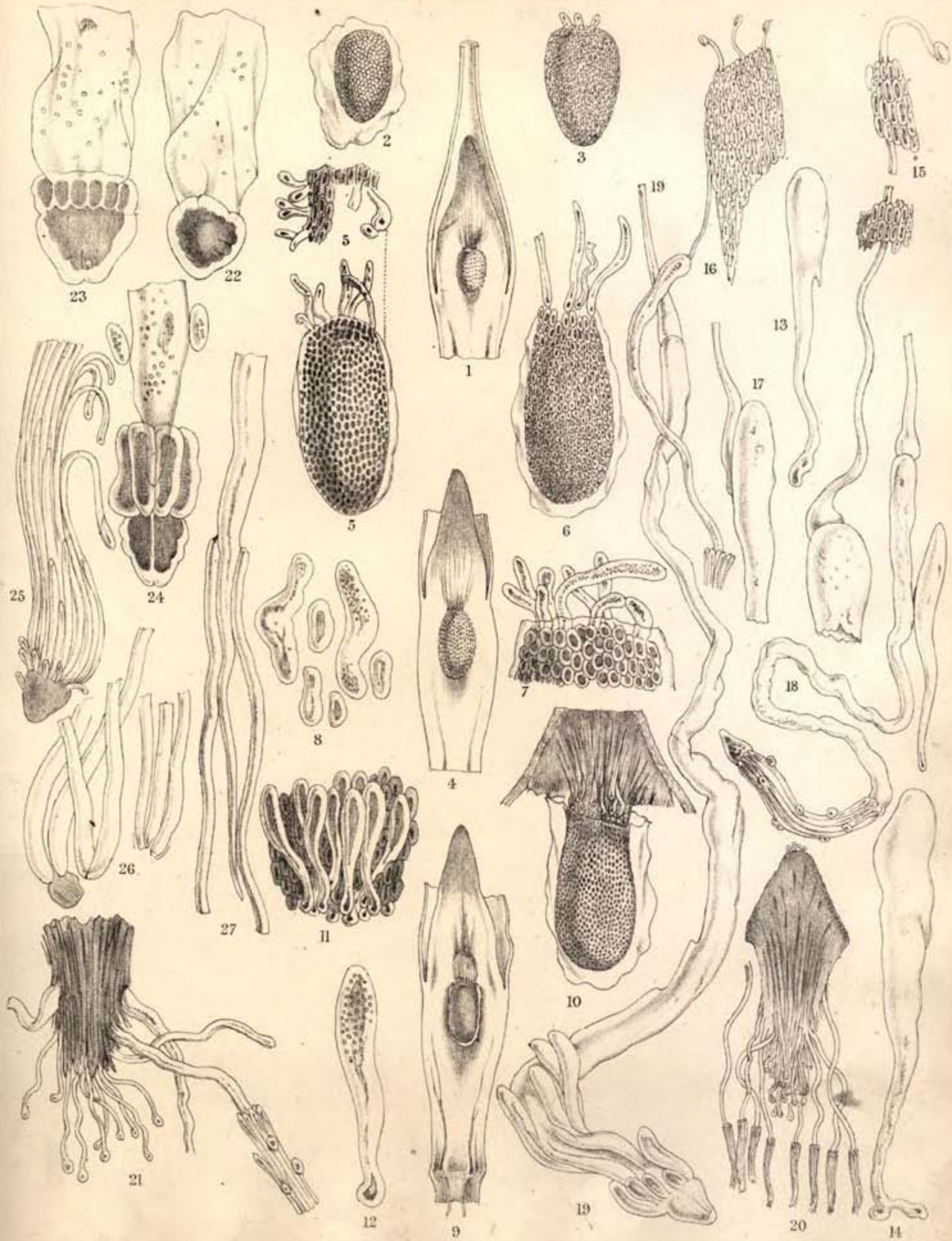
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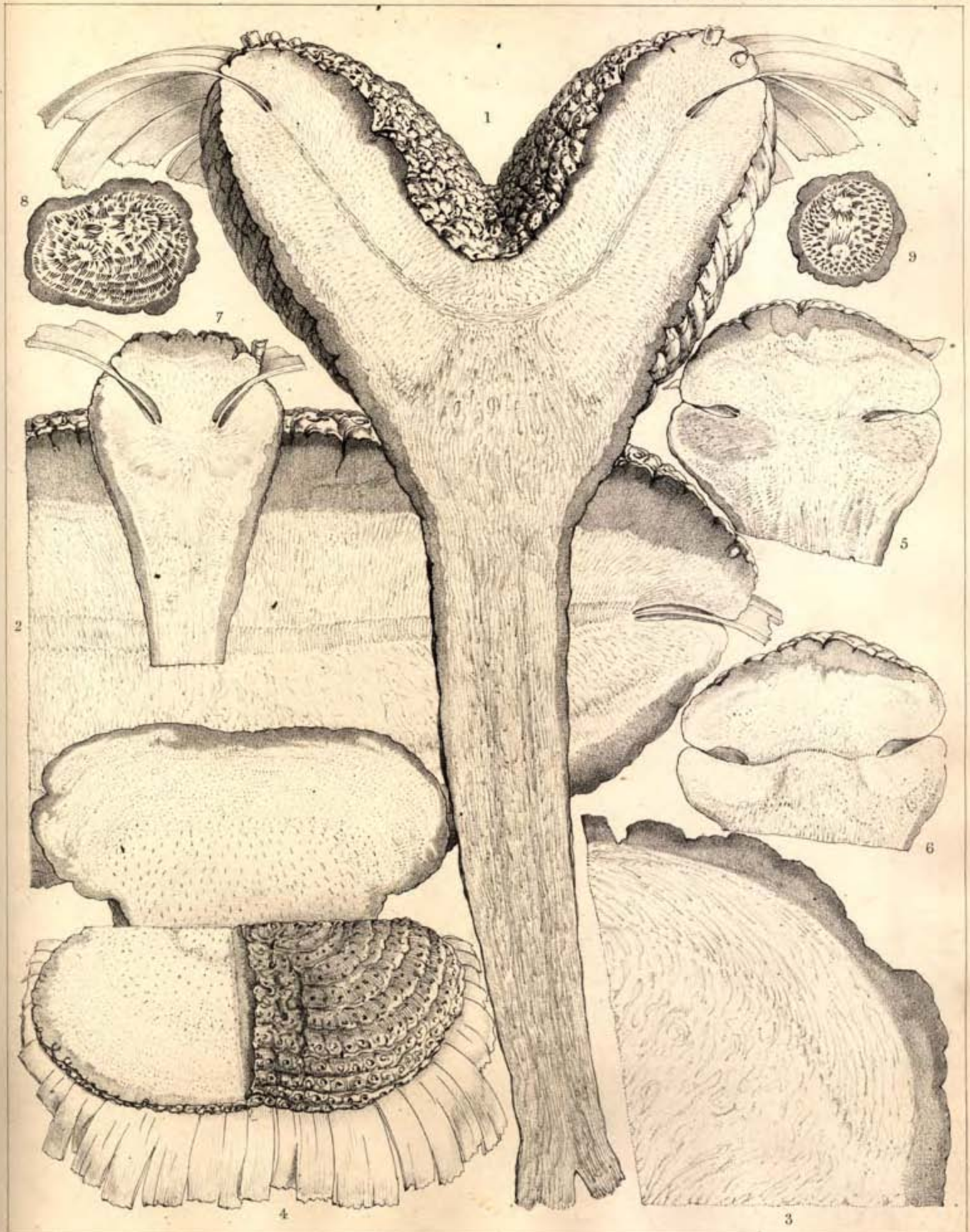
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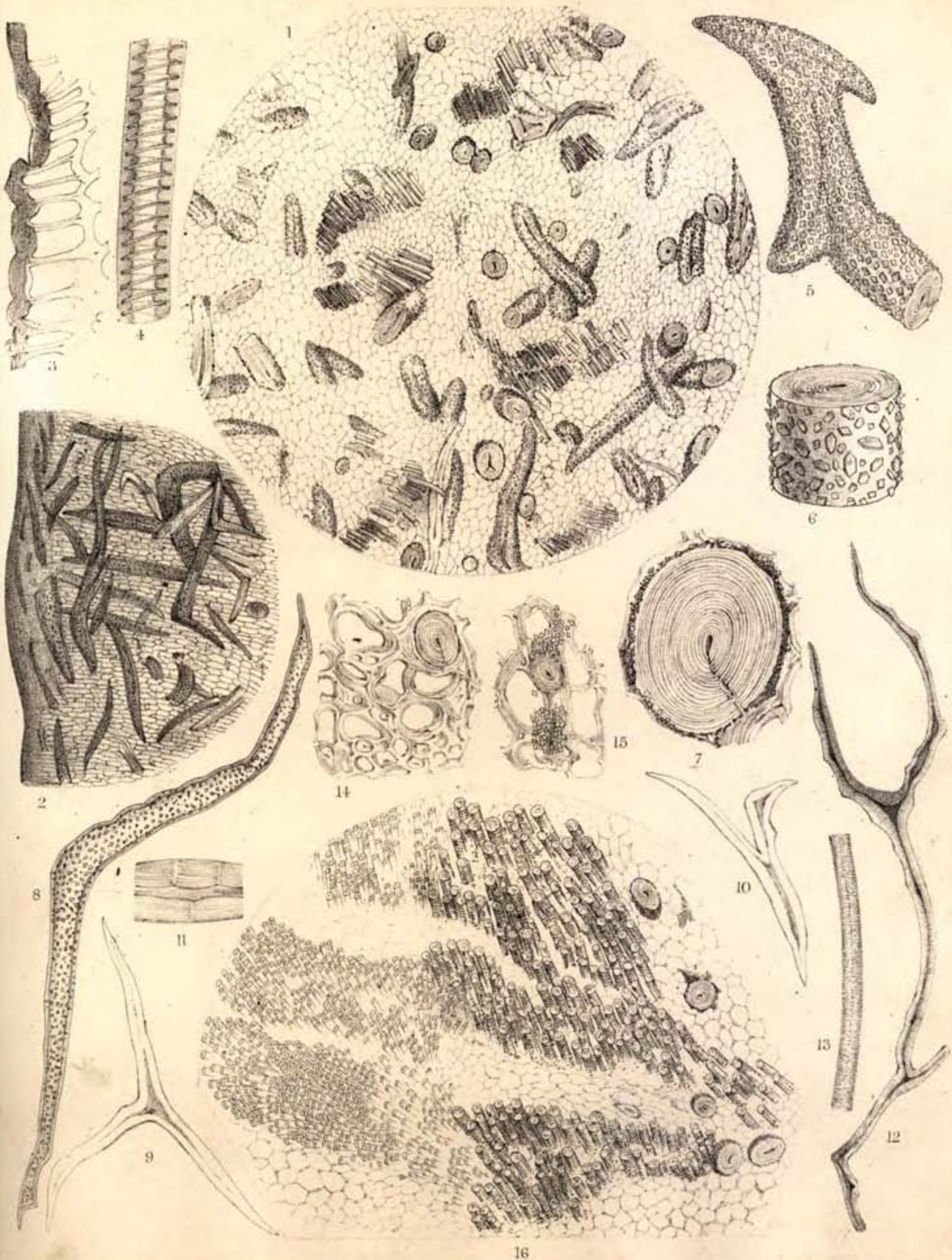
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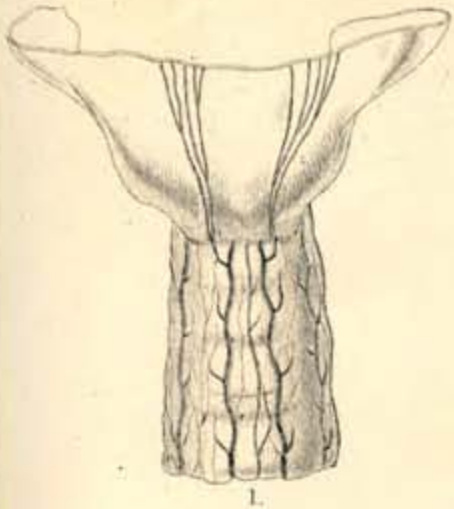
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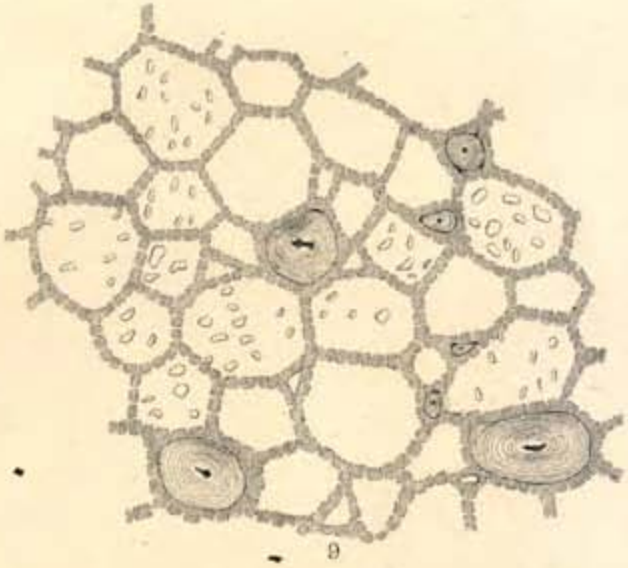
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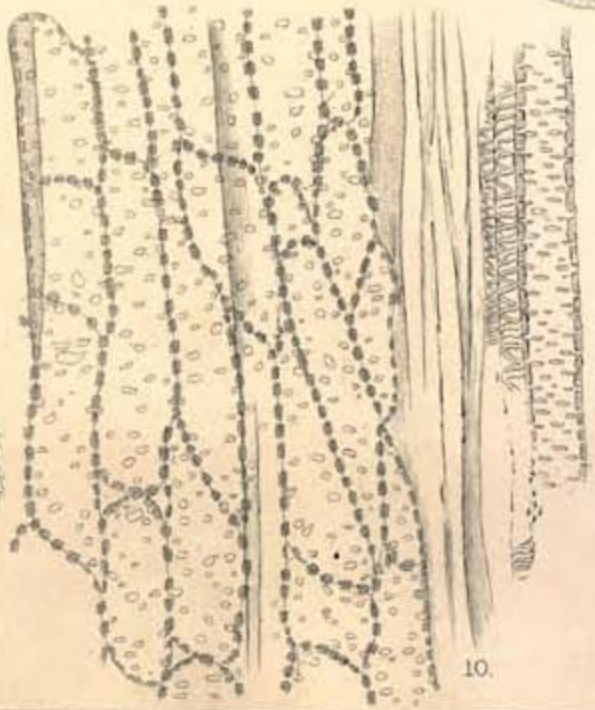
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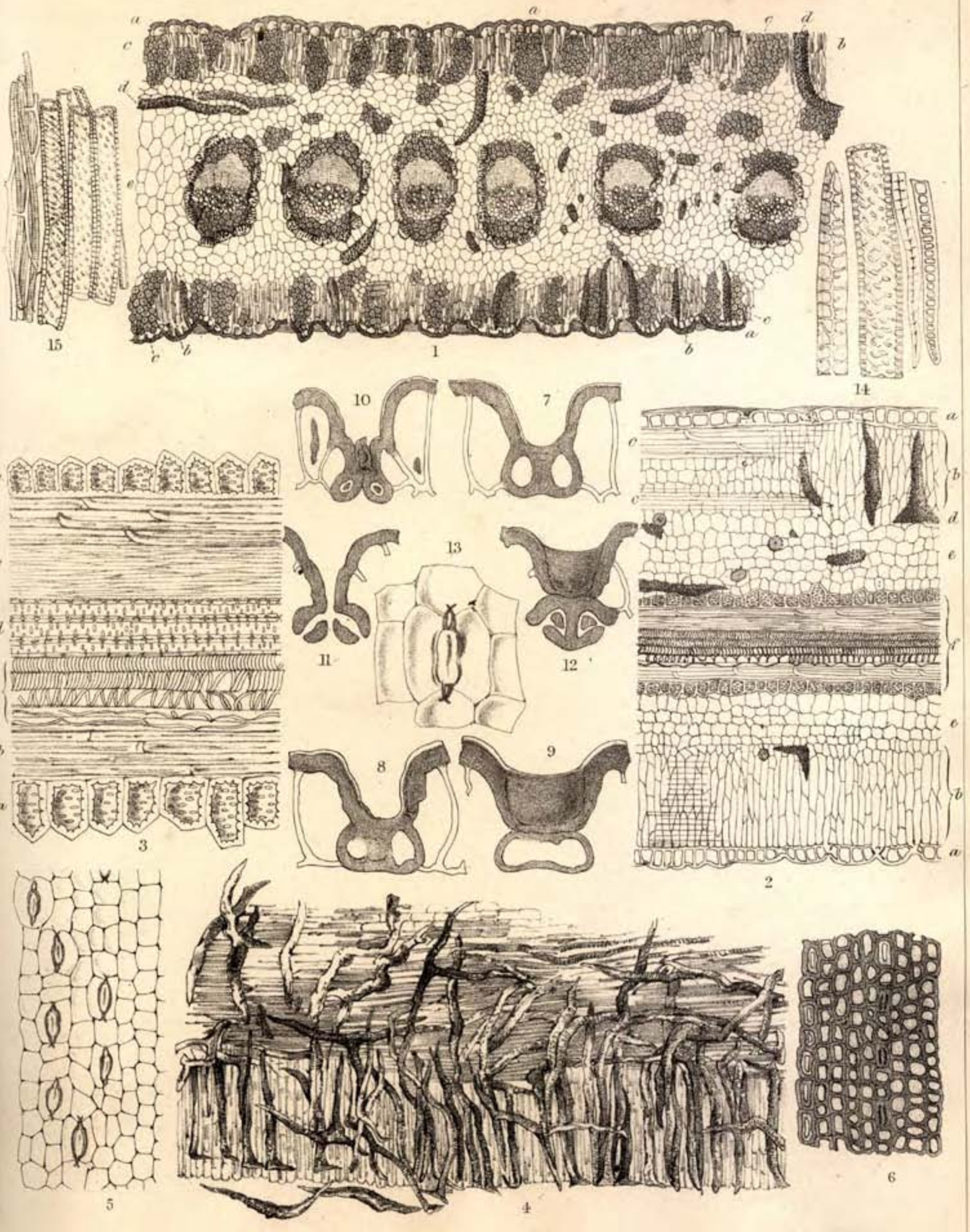
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