On the Organisation of the Fossil Plants of the Coal-Measures. Part XVII

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IV. *On the Organisation of the Fossil Plants of the Coal-Measures.*—Part XVII.

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[Plates 12--15.]

Lyginodendron Oldhamium and *Rachiopteris aspera.*

In the fourth of this series of Memoirs ('Phil. Trans.,' 1873, p. 377, *et seq.*) I described a remarkable plant under the name of *Dictyoxylon Oldhamium*; I also gave reasons for substituting the late Mr. Gourlie's generic name of *Lyginodendron* for that of *Dictyoxylon.* In the same Memoir (p. 403) I referred to some petioles, to which I proposed to assign the name of *Edraxylon*; but later researches demonstrated the necessity for abandoning this as a generic term and substituting for it the more comprehensive one of *Rachiopteris.* In my Memoir, Part VI. ('Phil. Trans.,' 1874, Plate 2, p. 679, *et seq.*), I described this proposed *Edraxylon* under the name of *Rachiopteris aspera.* Certain similar features exhibited by the above two plants led me to remark in Memoir IV., p. 403, after showing that the *Rachiopteris aspera* was obviously the petiole of a Fern, " I think it far from impossible that these may prove to belong to *Dictyoxylon (Lyginodendron) Oldhamium*; but since I have not yet succeeded in correlating them with any certainty, I shall add no more respecting them at present."

Since 1873 I have accumulated a vast amount of material illustrative of the structure and relations of these two plants, and am now in a position to demonstrate that they respectively represent the stem and petiole of the same organism which proves to be a Fern. I was long under the conviction that the remarkable exogenous development of the stems of many of the Carboniferous Cryptogams, which I have so continuously demonstrated to exist, and which is now so universally recognised by Palæontologists, had no existence amongst Ferns. I have now to show that this development did exist amongst Ferns as well as amongst the arborescent Lycopods and Calamites, in which it is so conspicuous. Fig. 1 (Plate 12) is part of a transverse section of a stem or branch of *Lyginodendron Oldhamium,* in which a represents the medulla; b, the exogenous xylem zone; c, the place of the inner cortex, wanting in this specimen; d, one of the pairs of vascular bundles, so characteristic of the cortex

of this plant; e, the outermost cortex, composed, in transverse sections, of radiating bands of sclerenchyma, g, alternating with parenchymatous areas, f. At k, k we find two bundles of tracheids, like those at d, forming the centre of the cortical structures of a petiole of *Rachiopteris aspera, i, i,* which petiole is organically united to the cortex e of the *Lyginodendron.* The two bundles k, k are assuming the oblique relative positions seen in the similar bundles of the free petiole of *R. aspera,* represented in fig. 2. Other sections in my cabinet, similar to fig. 1, demonstrate the same facts, viz., that the pairs of bundles, fig. 1, d, which form so characteristic a feature of transverse sections of the middle cortex of *Lyginodendron Oldhamium,* pass outwards, through the outer cortex, to become the tracheæeal* bundles of the petioles of the plant, and which petioles I had previously designated *Rachiopteris aspera.* I may state that my friend GRAF SOLMS-LAUBACH, who has obtained numerous specimens of the *Lyginodendron* associated with others of *Rachiopteris aspera* from a locality on the continent, agrees with me in the conclusion at which I have arrived respecting their unity. The more perfect specimens of the *Lyginodendron* obtained during the last seventeen years have thrown yet further light upon those figured in 1873. In the latter, as at fig. 1, c, no traces of the middle bark were preserved; but examples from Halifax, for which I am indebted to my friends Mr. CASH and Mr. SPENCER, of Halifax, have supplied what was wanting. Fig. 3 is a transverse section in which this inner cortex, c, is shown to consist of a zone of extremely delicate, thin-walled parenchymatous cells, scattered throughout which are numerous gum-canals, l. Three of these canals are represented, enlarged 250 diameters, in figs. 4 and 5, embedded in the thin-walled cells, c, c, of the cortex.

These canals are obviously formed by a schizogenetic separation of the cortical cells, c, and display no signs of having possessed the linings of epithelial cells so frequently seen in the similar canals of living plants. Each canal is lined by a thin carbonaceous layer, a, within which is a free carbonaceous rod, b, with a round or oval section. I presume that both these black elements are the carbonised remains of gums or resins with which the canals were primarily filled.

Fig. 3, b′ b′, shows an unusual occurrence of laminæ of tracheids growing inwardly into the medulla, to be referred to later.

Another feature characterising equally the outer cortex of *Lyginodendron* and that of its petioles is well shown in fig. 6, which represents a superficial tangential section of the cortex of *Lyginodendron Oldhamium.* At its lower part this section represents the structure already described in Memoir IV. The fibrous bands g and the cellular areas f correspond to those indicated by the same letters in figs. 1 and 3, but

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* I have, throughout this Memoir, used the term *tracheæ* in the sense in which it is used by DE BARY as comprehending both the shorter, thickened, but elongated cells, *tracheids,* and the longer *tracheæ* or vessels. DE BARY does so "specially in those cases where it is not certainly decided whether a tube belongs to the one or to the other subdivision," which is almost always the case amongst these coal plants. (See DE BARY 'Comparative Anatomy of Phanerogams and Ferns,' p. 155.)

h, h', and h'' represent various sections of numerous peculiar peripheral appendages. Though so conspicuous when present, examples of this cortex are common in which no traces of these organs can be found. When perfect, each one is bottle-shaped, having a length of ·05 of an inch and a maximum diameter of ·02. The superficial layer of each of these appendages is prosenchymatous, the cells being especially elongated and narrow near and at the terminal neck of the bottle. Internally the appendage consists of a very regular parenchyma, as is shown by the longitudinal and transverse sections h'', h''. Owing to the slight obliquity of the entire section fig. 6, at h' h' only the isolated projecting tips of these organs are seen. Many of my transverse sections of the *Lyginodendron* exhibit similar appendages; thus, they are seen in fig. 1, h, and the basal portion of one is intersected at fig. 3, h. This latter, like many other similar ones, illustrates the nature of these structures. They are emergences, not hairs. Their internal parenchyma, h, is seen in fig. 3, to be an extension of the subjacent parenchyma, f', of the outer cortex, whilst the prosenchymatous superficial coat is derived from the two fibrous bands, g', g', by which f' is bounded laterally. This explanation is yet better demonstrated by fig. 9, in which the two portions, h, h', of the emergence are seen to be respectively developed from the fibrous laminæ, g, g, and from the intermediate parenchyma, f, of the outer cortex.

The very characteristic emergences, h, of figs. 1–3 and 6, reappear in the petioles hitherto described under the name of *Rachiopteris aspera*. In my Memoir VI., I pointed out* the existence, on the periphery of these petioles, of numerous " abortive hairs" or " tubercles," but I was not then aware of their full significance.

Fig. 7 represents a characteristic example of a transverse section of a young *Rachiopteris aspera*, from the periphery of which a number of these emergences, h, h, are given off. The origin of the superficial layer and of the internal parenchyma of each emergence is seen to be identical with that demonstrated in my description of fig. 9. Fig. 8 represents a longitudinal section of a similar petiole, in which these emergences are again seen at h, h, variously intersected.

The above facts combined make it clear that *Rachiopteris aspera* is merely a petiole of *Lyginodendron Oldhamium*; hence the former name must disappear from our lists. It also follows that *Lyginodendron Oldhamium* is a true Fern, most probably belonging to some Sphenopterid type. This determination carries along with it the further one that the stems of some, at least, of the Ferns of the Carboniferous age developed their xylem or vascular structures exogenously, through the instrumentality of a meristemic zone of the innermost cortex, which practically must be regarded as a cambium layer. But the history of this interesting plant is not yet ended.

In various preceding memoirs, but notably in Part XVI., I have provoked a strong opposition amongst some botanists whose studies have been chiefly limited to living forms of vegetation, by revealing the existence, amongst the Lycopodiaceous plants of the Coal Measures, of a mode of development of a medulla which differs so widely from

* Plate 52, figs. 8, 9, and 13, k, k'', pp. 681–2.

what occurs amongst living plants that the sceptics are unable to accept my account of it. My late friend Professor DE BARY, when his students occasionally declared that certain suggested explanations were "impossible," usually replied, "in scientific research nothing is 'impossible.'" I utilise this philosophic reply, and commend it to some of my new opponents.*

I now advance further and proceed to show that the process of medullary development which, as demonstrated in my Memoir XVI., occurs so commonly amongst the Lepidodendroid stems and branches, takes place, if possible, in even a more striking manner in the young growths of *Lyginodendron Oldhamium.*

In Plate 25 of my Memoir IV., fig. 16, I represented a young lateral branch, bursting outwards through the cortex of an older stem. The development of these branches was demonstrated in several other figures in the same memoir. I have through many past years accumulated numerous additional examples of these young branches, which now enable me to speak decisively respecting their structure and development.

Plate 13, fig. 10, exhibits a transverse section of one of these young branches as it emerges through the cortex of the parent stem, and before it has become invested by an independent cortex of its own. Its centre, *a*, appears to consist of a solid cluster of barred tracheæ, of variable diameters, grouped in no special order. Springing directly from the periphery of this central mass, a considerable number of tracheæal laminæ, *b*, radiate outwards, in regular order, constituting the xylem zone; these laminæ are separated by numerous conspicuous medullary rays—both being obviously the result of a process of exogenous growth. Fig. 11 represents a second specimen, similar in most respects to fig. 10, but differs, first, in being of larger dimensions (both being drawn to the same scale), but, secondly, in a change which is taking place in its vascular centre, the tracheæ composing which axis are now becoming dissociated, producing an irregular cavity, *a*, which is forming in their midst; by this change the tracheæ are separated into four or five irregular groups, *a' a'*, each of which adheres closely to the inner border of the exogenous xylem cylinder, *b*. Such examples show no trace of the proper bark of the branch; but in another specimen in my cabinet (Cabinet number 1885 D), the growth of which has advanced slightly beyond that of fig. 11, and in which the cavity, *a*, has increased yet more in size, the characteristic cortex of *Lyginodendron* is fully developed, showing that this branch had completely emerged from the outer cortex of the parent stem.

In fig. 12 we have a third similar, but yet larger, section, in which the central cavity, *a*, has not only undergone a further increase of area, but is now occupied by a

* Some of our older botanists scarcely realise the progress made during the last few years in the study of what may be designated "anomalous" features in the tissues of living plants. Such "anomalies" are less rare, even now, than many botanists are aware of. In the primæval plant-world they abounded. (See D. H. SCOTT, "On some Recent Progress in our Knowledge of the Anatomy of Plants." 'Annals of Botany,' vol. 4, No. 13, p. 147, November, 1889.)

perfectly developed parenchymatous medulla; whilst the four fragments, $a'\,a'$, of the primary central tracheæal axis of fig. 10 are still further separated from one another.

Fig. 13 is an outline sketch of the central part of a *Lyginodendron Oldhamium*, very advanced in growth, but only enlarged less than eight diameters instead of thirty, as is the case with figs. 10, 11, and 12.

The line b represents the inner border of the exogenous cylinder. The five points, a', a', are the five dissociated segments of the originally solid tracheæal bundle, corresponding to those $a'\,a'$ of figs. 11 and 12. On making accurate measurements, I find that whilst the outer surfaces of these five bundles continue to be in the closest contact with seventy-one parts of the circumferential line b, the intervening spaces, $a''\,a''$, non-existent in the young state of the branch, occupy 164 parts: so that whilst, in the first instance, the circumference of the circle b and that of the aggregate of the united bundles, $a'\,a'$, were absolutely coincident, the circle has enlarged, at the least, to more than three times its original circumference. Such an enlargement was necessarily accompanied by a corresponding increase in either the number, or size, or both, of the tracheæal laminæ and their intervening medullary rays, constituting the exogenous xylem zone.

Some of my botanical friends have endeavoured to explain the corresponding phenomena amongst the Lepidodendra, by supposing that, where such differences exist in the size of the medullæ, they did not represent different stages of growth of similar branches, but were characteristics of different kinds of branches; but no such improbable hypothesis is for a moment admissible in the case of this *Lyginodendron*. The effects of growth, and of growth alone, as described above, are seen in every one of the innumerable specimens of *Lyginodendron* that have yet been discovered. In this case, that these are the effects of growth, is seen, first, in the breaking up, by dissociation, of the solid axial bundle of tracheæ; secondly, in the formation of an area in the centre of this bundle, which became occupied by a steadily expanding parenchymatous medulla, and, lastly, in the secondary effects of these central expansions on the tracheæal xylem and the cortical zones which enclose the medulla. To dispute this is, in my opinion, alike unscientific and futile.

When we note that the medulla of the largest stem of *Lyginodendron* which I have yet obtained has advanced from little more than a point to above an inch in mean diameter, it is clear that such an enlargement must have been accompanied by considerable changes in the relations of the more external tissues, however apparently permanent they might be.

In order to obtain some fairly accurate data in reference to this strain put upon these more external structures, I have counted as accurately as the subject admitted of, the number of the radiating laminæ of the tracheæ comprising the xylem zone which started from the inner margin of that zone, and also the number of those which reach its outer or cortical zone. The results of these observations made on sixteen

sections of stems and branches of various ages and sizes, are given in the following table :—

Cabinet numbers of the slides containing the specimens examined.	Number of the vascular laminæ in the		
	Inner margin.	Outer margin.	
Slide A. 1885 C.	44	54	Central axial bundle dissociating
,, B. 1885 A.	46	66	Central axis solid, fig. 10
,, C. 1883 A.	58	93	Central axis solid
,, D. 1885 A.	61	96	Central axis solid
,, E. 1883	62	95	Central axis solid. Branch not yet emerged from the parent stem
,, F. 1885 D.	65	89	Specimen a corticated independent branch
,, G. 1141	71	85	Specimen with a central medulla, fig. 12
,, H. 1885 H.	74	97	Central axis dissociating, fig. 11
,, I. 1885	78	99	Central axis solid
,, K. 1884	84	139	Independent corticated branch, medulla much enlarged
,, L. 1885 F.	95	150	Independent corticated branch, with a medulla
,, M. 1138	116	200	Independent branch, medulla large
,, N. 1885	135	233	Independent branch on stem
,, O. 1885	272	499	
,, P. 1128	364	642	The specimen represented in the outline, fig. 13
,, Q. 131	1120	5460	

The above table shows that as each stem or branch increased in size, an increase also took place in the number of the radiating laminæ that originated close to the medullary border of the exogenous zone, as well as of those which reached its cortical margin. We find that the eight very young sections, A, B, C, D, E, G, H, I, had a mean number of 69 such protoxyloid laminæ, whilst the seven larger branches, F, K, L, M, N, O, P, all of which had become independent or corticated branches, completely emerged from the parent cortex, had a mean of 161 such laminæ, the example P having 364.   The very large stem Q shows even a much further increase, having 1120 of these primary laminæ.   That the second column should show a large number of secondary laminæ intercalated between the periphery of the medulla and the innermost cortex was to be expected where an exogenous mode of growth had obviously existed.

It is clear that many of the laminæ thus indisputably added even to the *inner* border of the vascular zone, must have been intercalated chiefly in the intervals corresponding to a'', a'', of fig. 13 ; and it is perfectly clear that wherever they were developed along this expanding medullary margin they must have pushed apart the older lamellæ between which they were so intercalated.   Since every one of the larger and older branches in the lower half of my table must once have been small and young, like those of the upper half, it seems indisputable that we have here a phenomenon of growth and expansion which has no parallel, that I am aware of, amongst living

plants. That 44 laminæ of my example A can be represented by 1120 similarly arranged ones in the section Q shows a remarkable expansion of the medullary border that was produced not by the mere enlargement of the existing tissues, but by the intercalation of new ones. That such must have been the case is, as I have already observed, demonstrated by the dissociation of the primarily contiguous tracheæ of the central axis a of fig. 10, already described. We realise the extent of this separation when we compare the intervals separating the bundles a' of fig. 13 with the corresponding ones a' of fig. 12. In estimating the sizes of those intervals we must remember that fig. 12 is enlarged more than fig. 13 by at least four times.

I repeat, therefore, that however brought about, we have two separate and independent proofs of the origination and development of the medullary area. First in the separation of the clusters of tracheæ which primarily formed one united cluster, and secondly in the enormous increase in the number of the vascular laminæ, the inner extremities of which, though commencing their growth at different periods of the plant's life, alike start from the medullary border of the vascular zone, and extend to its periphery.*

The origin of the cellular medulla in the young branches of *Lyginodendron* presents no real difficulties. Plate 26, fig. 24, of my Memoir, Part IV., shows that these branches were derived from the exogenous xylems of the parent stems. The medullary rays of those woody zones are large and multicellular (Plate 13, fig. 3, b''), hence we can easily understand how a few small examples of these cells could be enclosed amongst the tracheæ of a central axis like fig. 10, a, and yet escape detection. Personally, I have no doubt that such was their origin. There is no reason for supposing that the area a of examples like fig. 11 was not normally occupied by the young medulla. The cells in such examples have merely failed to be preserved. In one of my slides (Cabinet number 1883) is an obliquely transverse section of a very young branch, in which the tracheæ are readily distinguishable by the conspicuous reticulations of their walls; running through the central axis of this branch is a very thin line, consisting of a small number of minute, but distinct cells. These germs would amply suffice for commencing a meristemic action, which would produce such a medulla as I have described above. But another question is less easily answered. What has occasioned the expansion of the medullary area and its surrounding tissues? Has it been due to the centrifugal pressure of the growing medulla alone, or have other forces taken part in the process?

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* It is scarcely necessary to remind any botanist that though, as recent exogenous stems grow, an enormous increase takes place in the number of the radial laminæ of the wedges composing their woody zone, little or no increase is seen in the number of those laminæ, of which the inner extremities reach the central medulla, or the point which that medulla originally occupied. All the additions are intercalated more or less peripherally.

Heterangium Grievii.

In the Memoir, Part IV., already referred to, I also described under the above name a plant from the Cliff of Petticur, near Burntisland, in Fifeshire. Some months ago my young friend, Mr. LOMAX, of Ratcliffe, found, for the first time, specimens of the same plant from Dulesgate, in Lancashire. But along with these he brought from the same locality a series of sections of what at first seemed to be a different species of *Heterangium*. But long and careful comparison of all the examples of that genus in my cabinet convinced me that the supposed new forms were merely the *H. Grievii* in a younger state of growth. The specimens previously described were characterised by the existence of a central mass composed of irregular clusters of tracheæ, imbedded amongst numerous parenchymatous cells (*loc. cit.*, Plate 28, fig. 30, *a*), surrounded by an exogenously developed zone of tracheæ (*ibid.*, *b*). This plant was also invested by a well-defined zone of sclerous prosenchyma, which, in the transverse sections, was seen to be more or less subdivided radially into cubical masses (*loc. cit.*, fig. 30, *k*, and Plate 29, fig. 35, *k*).

The central part of the transverse section (Plate 14, fig. 14, *a*) resembles the Petticur plant in consisting of numerous clusters of tracheæ aggregated into a large axial mass, into the composition of which many parenchymatous cells enter. That these cells may have become carbonised is probable from the fact that, when examined under a higher power, the appearances shown in fig. 15 are observed. Two of the clusters of tracheæ, enlarged 75 diameters, are here represented. In the centre of each cluster we have a number of larger tracheæ, *a*, *a*, surrounded by still more numerous smaller ones, intermingled with some cells, *d*, *d*. The investing zones, *c*, *c*, seem to me to be the carbonised remains of the inter-tracheæal cells which occupy similar positions in the Petticur plant. At fig. 14, *a'*, a tracheæal bundle is passing outwards from the central mass to some external appendage.

A thick cortex, fig. 14, *b*, *b*, invests these central tissues ; it is fundamentally parenchymatous, but the forms and arrangement of its component cells vary much in different portions of it, as will be shown when describing longitudinal sections of this tissue. The outer cortical zone is a layer of sclerous fibres, *e*, *e*. The aspect presented by these fibres, as seen in transverse sections, is shown in fig. 16. The lignified wall and central lumen of each cell are very distinctly seen. These fibres reappear at *e* in fig. 17, which represents a longitudinal section through the centre of a stem like fig. 14. At *a* we have the central vasculo-medullary axis, consisting of intermingled barred tracheæ and vertical rows of cells, the latter having chiefly rectangular transverse septa. Immediately external to this vascular axis we find an innermost layer, *b*, *b*, of the cortex, the cells of which are arranged in rather regular perpendicular lines, but more externally these cells become larger and more irregular in size, form, and arrangement, though still retaining a tendency to dispose themselves in vertical rows. This zone of the cortex is bounded externally by an irregularly undulating, ill-defined line, *b'*, *b'*. Outside this

line the cortex, *c, d,* assumes a very different aspect. Its cells still arrange themselves in vertical but undulating lines of a peculiar character. At the points *c', c',* we find transversely disposed bands of very strongly defined cells, alternating with intermediate areas, *d, d,* through which the same lines of cells continue their vertical course but with altered flexures. The cells themselves, also within these areas, have very much thinner walls. The cell-clusters, *c', c',* as seen in these vertical sections, are parts of numerous masses of more or less definite lenticular form, which abound in this part of the cortex ; on making broad tangential sections through the same we note that, whilst many of these masses are arranged in horizontal transverse lines, many of them incline at very various oblique angles. Fig. 18 represents a small portion of a very superficial tangential section, in which *c* is the part of the cortex under consideration, and *e, e,* the fibrous investing layer. The section of one of the lenticular clusters of cells *c'* illustrates the peculiar symmetrical arrangement so frequently observable within these clusters. The longitudinal section, fig. 17, shows that at their inner margins these lenticular cell-masses compress the inner cortex *b,* those margins projecting into the concave flexures of the line *b'.* Similar clusters to those seen at fig. 18, *c',* in the transverse sections of these stems. The sclerous cells of the zone *e* of fig. 14 are seen in figs. 17 and 18 to be narrow fibres of very great length in proportion to their diameters. This zone cannot fail to remind the histologist familiar with the structures of the rhizomes of recent Ferns of the very similar hypodermal layer seen in some species of *Nephrolepis.*

The true affinities of this plant are as yet undetermined, but I have strong conviction that it will be eventually proved to be a true Fern.

Bowmanites.

In volume 5 of the third series of the Transactions of the Literary and Philosophical Society of Manchester, I published, in 1871, a description of a fruit to which I gave the name of *Volkmannia Dawsoni,* and further illustrations of the same fruit were given in my Memoir, Part V., of this series.* At that date the verticillate-leaved plants of the Coal Measures were ill understood, and much confusion has resulted from that imperfect knowledge ; a confusion which a few words of explanation may help to remove.

Palæobotanists have for more than a century been familiar with the existence, in the Carboniferous strata, of a number of plants, the leaves of which were arranged in verticils. In his 'Prodrome,' published in 1828, BRONGNIART threw a considerable number of these plants into two groups to which he gave the generic names of *Sphenophyllum* and *Asterophyllites.* The former genus he defined, among other characters, as " feuilles verticillées, au nombre de six à douze, distinctes jusqu'à leur

* ' Phil. Trans.,' 1874, p. 54, Plate 5, figs. 28–30.

base, cunéiformes, entières, ou émarginées, ou même bifides, à lobes plus ou moins profondément laciniés."

His genus, *Asterophyllites*, he defined as having " feuilles planes, plus ou moins linéaires, aiguës, traversées par une nervure moyenne simple, libres jusqu'à la base."[*] In his ' Tableau des Genres de Végétaux Fossiles,' published in 1849, he again defines the two above genera in almost identical words, adding, however, that *Sphenophyllum* differs from *Asterophyllites*, " par le nombre beaucoup moindre ce ces organes à chaque verticille, 6 à 8 ou 10, et par leur forme qui est triangulaire, tronquée au sommet, ou dentée et lobée, quelquefois très profondément " (*loc. cit.*, p. 52).

In 1864 Messrs. COEMANS and KIKX published their " Monographie des Sphenophyllum d'Europe."   In it they define the leaves as " cuneatis, sessilibus, verticillatis, nervo medio destitutis ; nervulis autem æqualibus, dichotomis " (*loc. cit.*, p. 414).

In my Memoir, Part V.,[†] I described a plant in which each foliar verticil consisted of 18 *linear uninerved leaves*, which characters identified it unquestionably with *Asterophyllites*.   That these leaves have the characteristics of *Asterophyllites* and not of *Sphenophyllum*, is demonstrated by the numerous long and transverse sections of them in figs. 5, 14, 15, 16, and 17 of the above memoir, in which also the remarkable structure and development of the stem of the plant is described.

In May, 1870, M. RENAULT had presented to the French Academy a memoir, " Recherches sur l'Organisation des *Sphenophyllum* et des *Annularia*," but owing to the siege of Paris, during which the drawings were lost, the plates were only published in the 'Annales des Sciences Naturelles, Botanique,' 5e série, tome 18, 1873.[‡]

In this memoir, M. RENAULT described the internal structure of *Sphenophyllum Stephanense*, which structure proved to be identical, in most respects, with that of my Asterophyllitean stem.   On the strength of this resemblance, M. RENAULT and H. GRAF ZU SOLMS-LAUBACH, have contended that I ought to have designated my plant a *Sphenophyllum*, and not an *Asterophyllites*.   I, on the other hand, still insist that, in accordance with the definition of every author who has written on the subject, my uninerved leaves prove my plant not to be a *Sphenophyllum*, but rather demonstrate the very intimate relationship, not to say identity, of the two genera, at least, so far as some forms of *Asterophyllites* are concerned.   Some others are unquestionably the leaves of Calamites.

The position of the *Volkmannia Dawsoni* referred to above, is affected by this controversy.   In M. RENAULT's memoir, p. 9, there appears a note by M. BRONGNIART, *apropos* of my memoir of 1871 in the Manchester Transactions.   M. BRONGNIART says, " Ce travail s'accorde dans plusieurs points importants avec les résultats obtenus un

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* 'Prodrome,' pp. 68 and 159.

† 'Phil. Trans.,' 1874, p. 41, *et seq.*, but delivered to the Royal Society on May 17, 1873.

‡ By a coincidence M. RENAULT's memoir, as now constituted, was only delivered to the Academy on May 13, 1873, four days before mine was delivered to the Royal Society.

an auparavant par M. RENAULT, sans que M. WILLIAMSON eût de son côté connaissance de l'article des *Comptes Rendus* du 30 Mai, 1870.

"La plante fossile étudiée par M. WILLIAMSON, et nommée par lui *Volkmannia Dawsoni*, diffère cependant sans aucun doute, au moins spécifiquement, de celle décrite par M. RENAULT, par la forme du faisceau vasculaire central et par l'absence des zones de cellules quadrangulaires qui l'entourent dans les échantillons de France, cellules qui, par suite de l'epaisseur de leurs parois, ne doivent pas se détruire facilement."

My plant to which M. BRONGNIART refers, is a strobilus, not an ordinary stem. Herr CH. E. WEISS, of Berlin, believes it to belong to the genus *Bowmanites* established by the late Mr. BINNEY.* No remains of the specimens described by Mr. BINNEY appear to be now discoverable, but since the important little sketch, Plate 12, fig. 3, of BINNEY's memoir, was made by Mr. BOWMAN, who was an accomplished botanist—made too when all the fragments of the original specimen were in his own possession—I presume that it may be accepted as representing a true form. If so, it certainly approaches nearer to what we find in my plant than any other hitherto described. If so, however, the objects which Mr. BINNEY designated macrospores, must be regarded as sporangia, which the rows of similar interbracteal spheres in my *Volkmannia Dawsoni* certainly are.

Notwithstanding the above facts, this subject would have been left in a very unsatisfactory position had not Professor CH. E. WEISS fortunately obtained in Germany a specimen, which he has named *Bowmanites Germanicus.†* These figures correspond so closely with those of Mr. BOWMAN reproduced in Mr. BINNEY's memoir, that the genus *Bowmanites* can now be accepted as representing an extremely distinct type of Calamarian fructification. But until my memoir on *B. Dawsoni* was published, nothing was known of the internal organisation of this fruit ;‡ and until now, nothing was known of the structure of its vegetative organs.

But my friend, Mr. GEORGE WILD, of Bardsley, near Ashton-under-Lyne, whose name has so often been recorded in these Memoirs, brought me the section represented in Plate 15, fig. 19, and which is beyond all doubt a transverse section of a stem of *Bowmanites Dawsoni*. In its general features the structure of this section is identical with similar ones of my *Asterophyllites*, and of M. RENAULT's *Sphenophyllum Stephanense*, which latter differs materially from the Autun *Sphenophyllum* described by the same author. All these plants agree in having a central vascular

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* "Observations on the Structure of Fossil Plants found in the Carboniferous Strata," by E. W. BINNEY, F.R.S., F.G.S.—Part 2 ; "Lepidostrobus and some Allied Cones." (Palæontographical Society, 1870, p. 59.)

† 'Atlas von neunundzwanzig Lichtdrucktafeln zu der Abhandlung : Beiträge zur Fossilen-Flora, III. Steinkohlen-Calamarien, II.' CH. E. WEISS. Berlin, 1884. Tafel XXI., figs. 12, 12 A, 12 B.

‡ [I have recently obtained important specimens throwing additional light on the organisation of this interesting fruit, which will be described in my next Memoir.—September 9th, 1890.]

axis, the transverse section of which is a triangle with each of the three angles more or less prolonged in equal measures. But in my fructification of *Bowmanites* the transverse section of this axis is very broadly robust, instead of being drawn out into three very long and slender radii. Not only so, but the extremity of each short arm is very broadly truncated ; a form that hitherto has only been seen in my *Bowmanites Dawsoni*. In fig. 19 the central triangle *a* is composed of a cluster of tracheæ grouped in no special order, except that the central ones are larger than those occupying the periphery of the triangle. In my fructification this central truncated triangle constitutes the sole vascular axis, a fact easy of explanation. Referring to my Memoir V., Plate 1, I have shown that in the very young twig of my *Asterophyllites*, fig. 1, this triangle constituted the only tracheæal bundle, but as the vegetative twig grew in age and size, it developed exogenously zones of tracheæ which were successively added, investing the triangular centre, as in figs. 2, 3, and 4, resulting in the conditions seen in Plate 2, figs. 9, 10, and 11 of the same memoir. The present figure 19 is as nearly as possible in the condition of the figure 9 just referred to. Its exogenously added tracheæ are arranged in equally regular radial and concentric lines; the sizes of the individual tracheæ enlarging as they were successively superimposed upon those previously developed. Portions of a layer of a cork-like cortex, *c*, are still preserved. A similar layer is seen, not in the *young* twigs of my *Asterophyllites* 1 and 2, but in the older ones 9, 10, and 11. It also appears in the middle of the cortex, enclosed, between an inner and an outer parenchymatous zone in M. RENAULT's Autun *Sphenophyllum* (*loc. cit.*, Plate 1, figs. 4 and 5, *g*), as well as in my fig. 16. The French savant designates it a " partie subéreuse."*

That this stem of *Bowmanites Dawsoni* is constructed on the same plan as that of my *Asterophyllites*, and of M. RENAULT's *Sphenophyllum Stephanense* is obvious enough, but to place all these three plants in the genus *Sphenophyllum*, because of this vegetative resemblance, as my friends M. RENAULT and GRAF SOLMS-LAUBACH wish to do, would be wrong. I have already shown that the leaves of my *Asterophyllites* are *not* those characteristic of *Sphenophyllum* ; and the fructification of my *Bowmanites Dawsoni* is altogether distinct from the strobili of *Sphenophyllum*. It must further be remembered that evidence is now being obtained from various quarters that there are Carboniferous plants, the branches of which bear both *Asterophyllitean* and *Sphenophylloid* leaves.

I therefore conclude once more that we must unite *Sphenophyllum* and some forms of *Asterophyllites* in one and the same genus ; it is equally clear that *Bowmanites*, though its peculiar fructification demonstrates that it constitutes a perfectly

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* The facts here referred to illustrate conditions so frequently seen amongst these Carboniferous plants, in which the exogenous development of a xylem zone as well as the differentiation of separate zones of the cortex mark advance of age. The fructifications, being young and temporary organs, seem invariably to have a central axis, the internal structure of which is identical with that of the youngest vegetative twigs of the parent plant. The *Bowmanites* described above is a good illustration of this truth.

distinct genus, has strongly marked features of affinity in the structure of its stem to the Sphenophylloid type. Hence all these plants may be recognised as constituting one of the several groups which collectively form the great family of the *Calamariæ*, and of which family the modern genus *Equisetum*, instead of being the central *type*, is but a poor, feeble, and degraded member.

Calamites.

My attention has long been drawn to the fact that, whilst sandstone casts of considerable dimensions, moulded in the interiors of the fistular medullæ of Calamitean *stems* are notoriously common, similar casts of the interiors of the smaller branches are extremely rare. Fig. 20, which represents (natural size) the interior cast of a single internode of such a branch is the smallest one preserving the common features of cylindrical form, longitudinal ridges and furrows, and, at the two ends, the two nodal transverse constrictions, that I have met with during fifty years of research. I have thought it desirable to demonstrate the cause of this state of things. The example here figured is ·5 of an inch in diameter. Comparing a medulla of this size with those of other decorticated specimens in my cabinets, in which the exogenous woody zone is preserved, I have no doubt that fig. 20 belonged to a branch or stem that was at least an inch in diameter, independently of its thick cortical zone. Seeing that I possess sections of decorticated Calamitean twigs not more than ·03 in diameter, myriads of similar ones must exist, but which are never represented by these sandstone casts. I possess a very fine leaf-bearing branch in sandstone, for which I am indebted to my old friend Sir WILLIAM DAWSON, of which the diameter, when uncompressed, has been about ·16 of an inch, including its cortex. It displays longitudinal internodal ridges, but these are but the irregular products of the shrivelling of a semi-herbaceous tissue, and have no affinity with the regular ridges and furrows of fig. 20.

I have brought together in my cabinet a graduated series of specimens which illustrate and explain the conditions referred to. Two of these specimens are represented in figs. 21 and 22. Fig. 21 is the centre of a decorticated branch, the entire diameter of which is ·25 of an inch, whilst that of its fistular medullary cavity, a, is about ·05. This cavity is filled with inorganic matter, whilst at a' a zone of medullary parenchyma is still preserved, which is about ·005 in. in thickness. This medulla intervenes between the circumferential border of the inorganic cast, a, and the inner angles of the vascular wedges, b, b. This zone of undisturbed medullary tissue protects the periphery of the once plastic cast, a, from the pressure of the elongated inner angles of the woody wedges, b. It is to be remembered that in the *very* young Calamitean twigs this medulla is *entire*—not fistular; but that at a very early stage of growth the centre of this entire medulla becomes ruptured. The incipient cavity thus formed increases in diameter as the branch grows, partly in consequence of the absorption of the medullary cells, and

partly through the transverse enlargement of the entire stem. The result is that so long as these changes do not extend beyond the state represented by fig. 21, the exterior of the cast, a, neither can, nor does, become longitudinally ridged and furrowed. But in the specimen represented in fig. 22, all these conditions are altered. The entire diameter of this specimen is about ·55 of an inch, whilst the maximum of its medullary cavity reaches ·4. It will be observed that not only all the medullary cells have disappeared from this specimen, but even the larger and less dense cells composing the medullary extremities of the primary medullary rays, c, c, have also been absorbed; the inner angles of the various trachææal woody wedges, b, b, have alike resisted pressure and absorption, and have thus given to the longitudinal ridges and furrows so characteristic of the exteriors of these inorganic casts their rounded undulating contours. This specimen thus answers a question that has been put to me by some of my correspondents, viz., " If the ridges of an ordinary Calamite were formed in accordance with your hypothesis of internal casts, how is it that the ridges have a rounded outline instead of projecting as radiating, vertical plates, corresponding to the entire forms of the primary medullary rays to which you say those ridges owed their existence?" The reply is, the process of absorption only reached the innermost extremities of those primary rays. As the latter organs passed outwards through the xylem zone, their component cells became smaller and more capable alike of resisting pressure and decay. I have not seen a single instance in which these more external cells had been absorbed during the lifetime of the plant. The fistular cavity thus formed has ordinarily been filled with sand or mud, but in the present example, as is so frequently the case with the plants preserved in our Lancashire and Yorkshire nodules from the Gannister Coals, this cavity is occupied by calcareous matter, which has been in a state of solution, and which has filtered through the tissues of the plant. The first deposits from this solution have formed, in fig. 22, stalagmitic layers, a', a', lining the walls of the fistular cavity; but in the central part, a, the intruded material has assumed a crystalline condition. These secondary details, however, in no way affect the general conclusion, viz., that the ridges and furrows marking the exteriors of transverse sections of these internal casts exhibit rounded contours, and not stellate ones. The above specimen was obtained from above the Upper Foot Coal at Sholver Lane. My cabinet contains various other specimens which lead to the same conclusions.

The section, part of which is represented in fig. 21, is one of a series of nine, made from the same stem or branch. Eight of these are transverse sections, which show a gradual increase of from 14 to 24–25 in the number of the trachææal wedges of the xylem as we ascend from below. I am indebted to my old auxiliary, Mr. GEORGE WILD, not only for this series, but also for the section fig. 22. The *specimen* from which the latter section was cut was collected by another of my valued coadjutors, Mr. JAMES NIELD, of Oldham.

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Fig. 4.
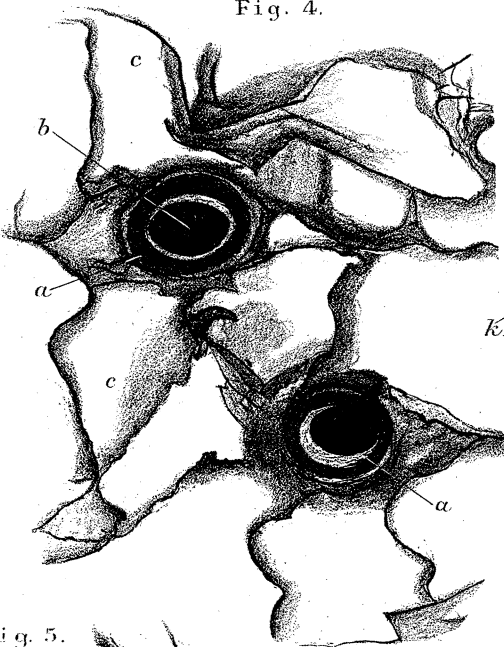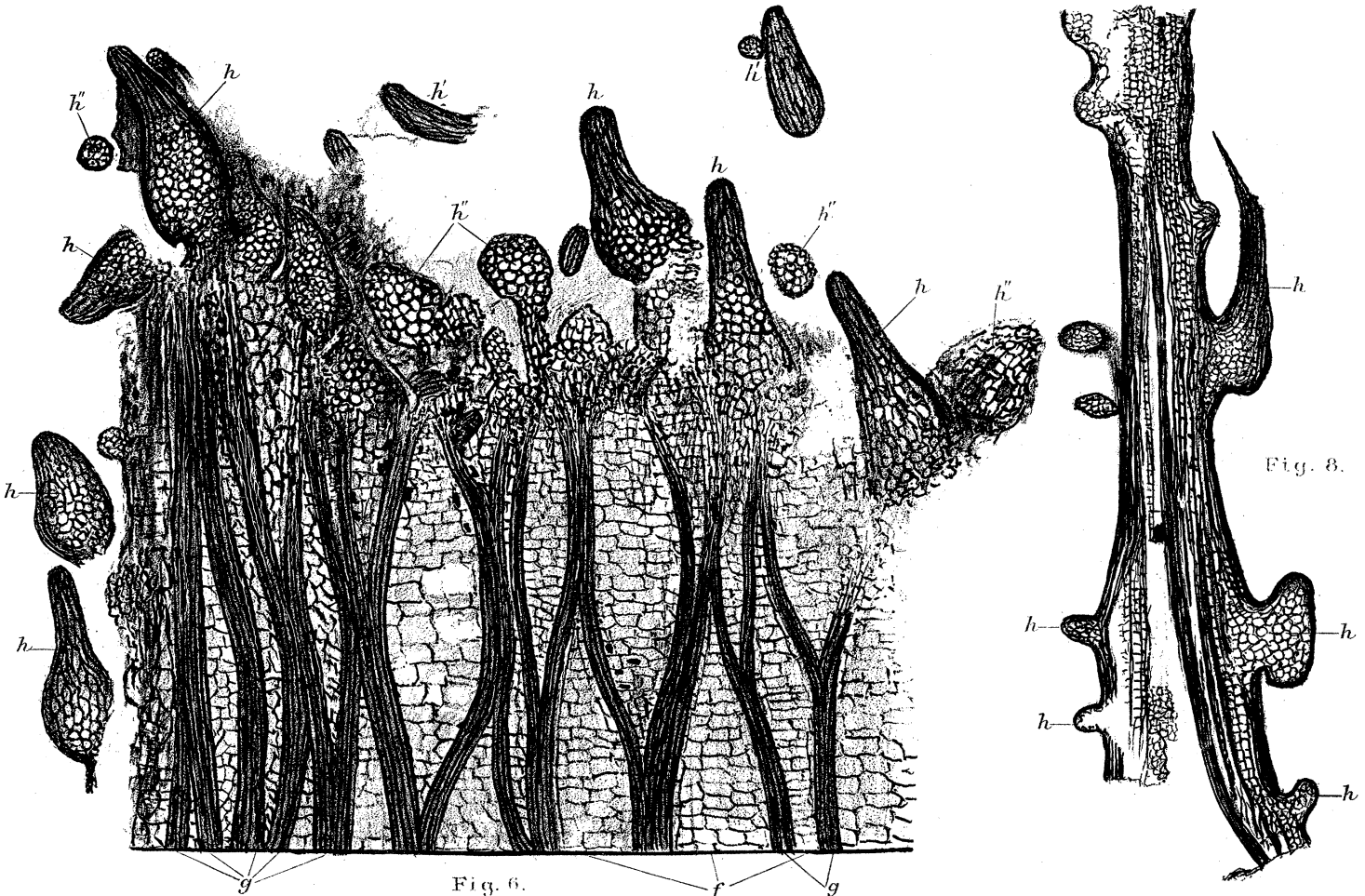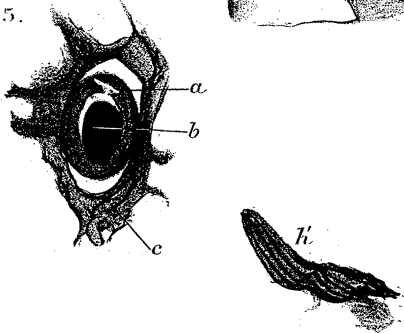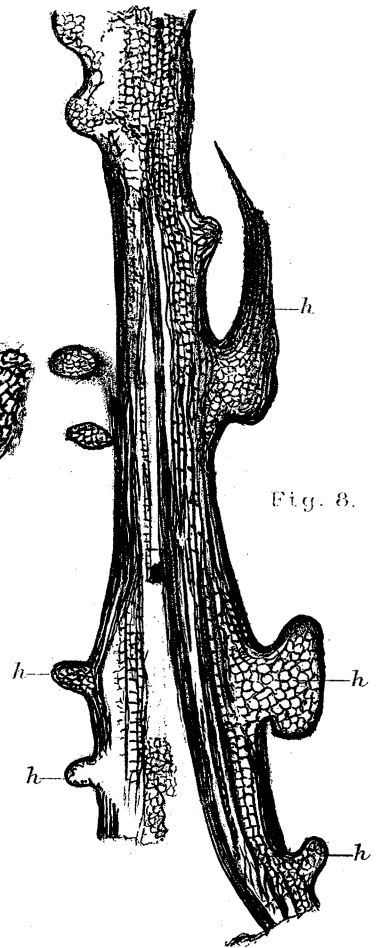
Fig. 1.

Fig. 5.

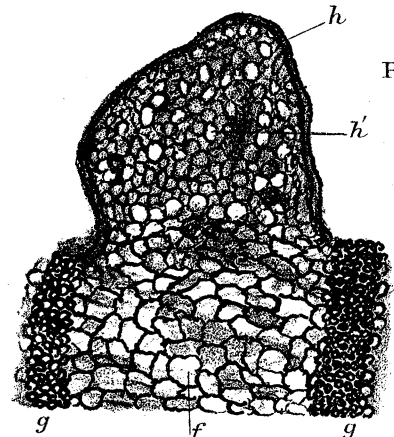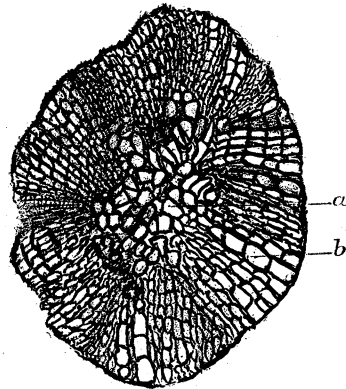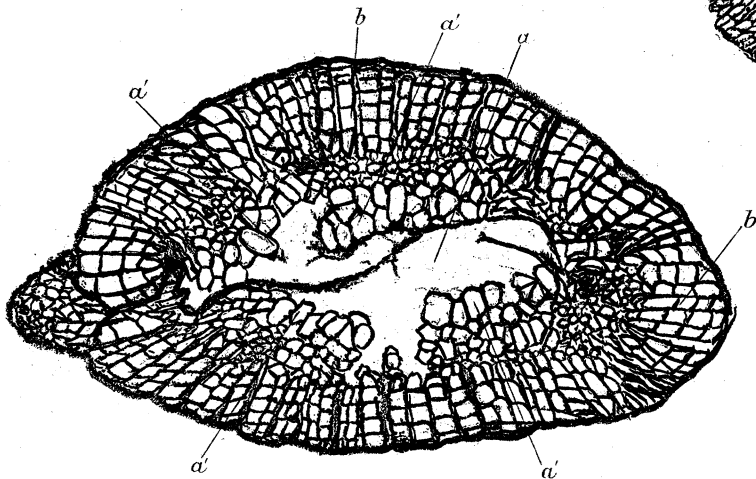Fig. 6.

Fig. 8.

Fig. 3.
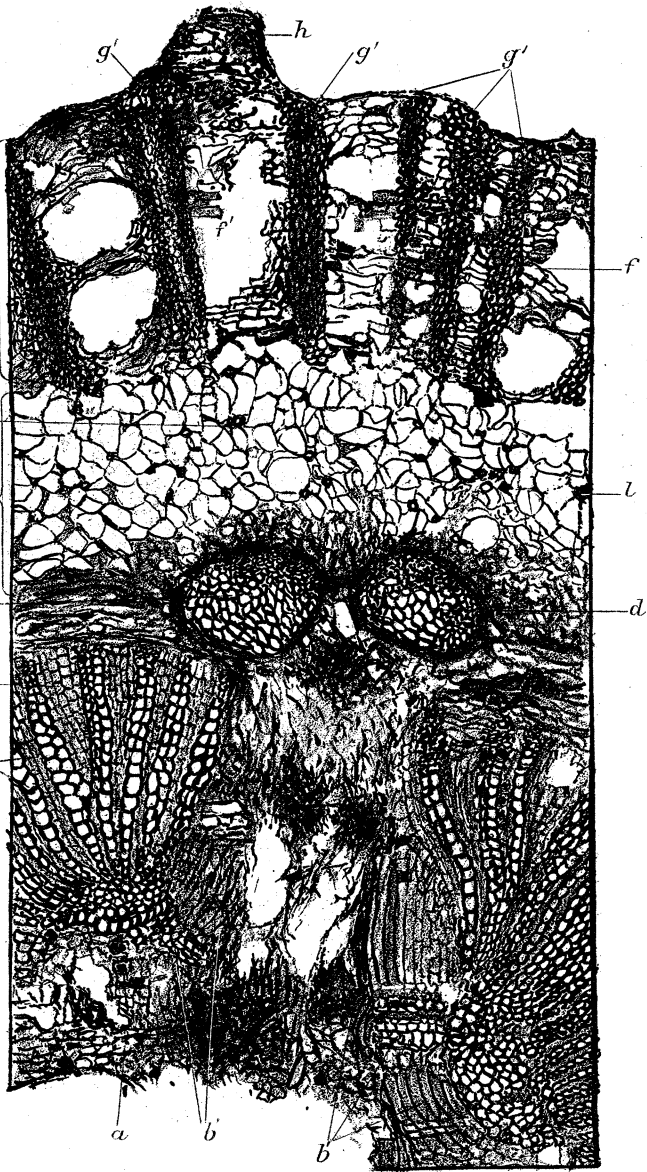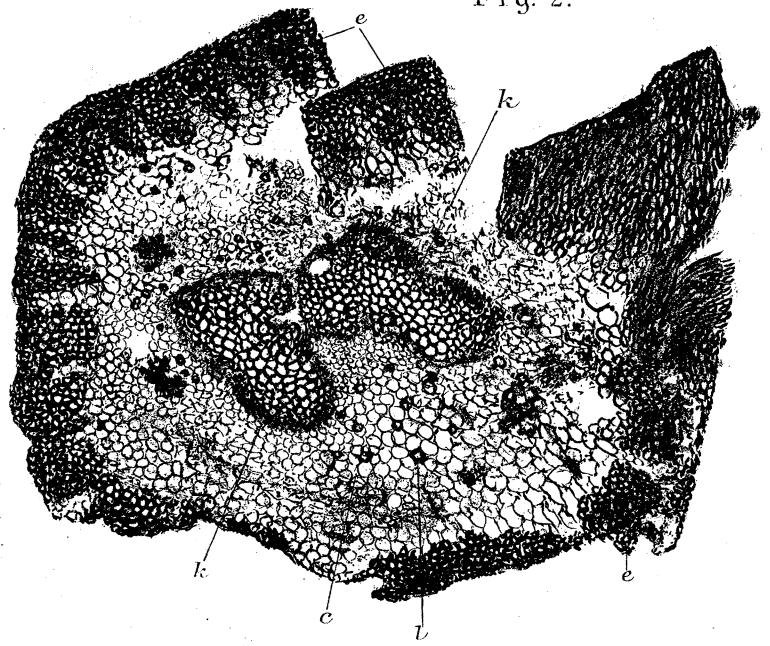
Fig. 2.

Fig. 2 A.
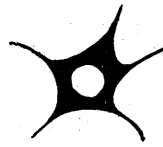
Fig. 10.
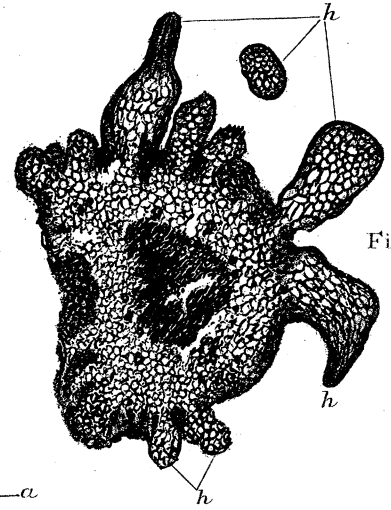
Fig. 7.

Fig. 11.
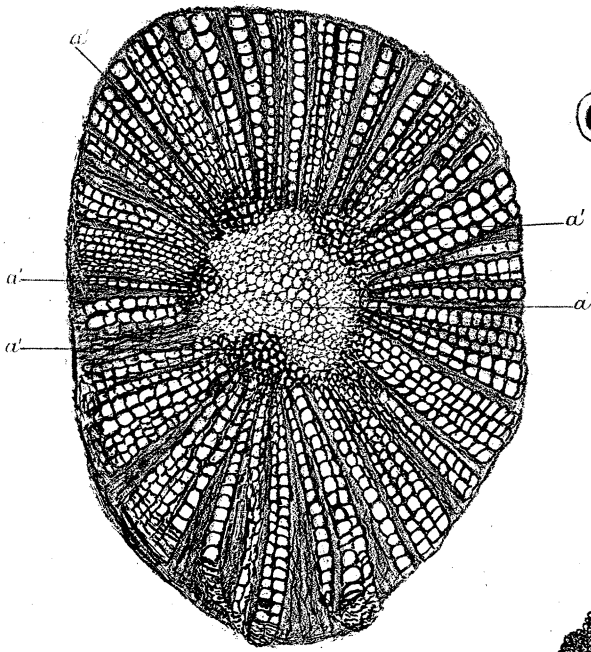
Fig. 9.

Fig. 12.

Fig. 16.
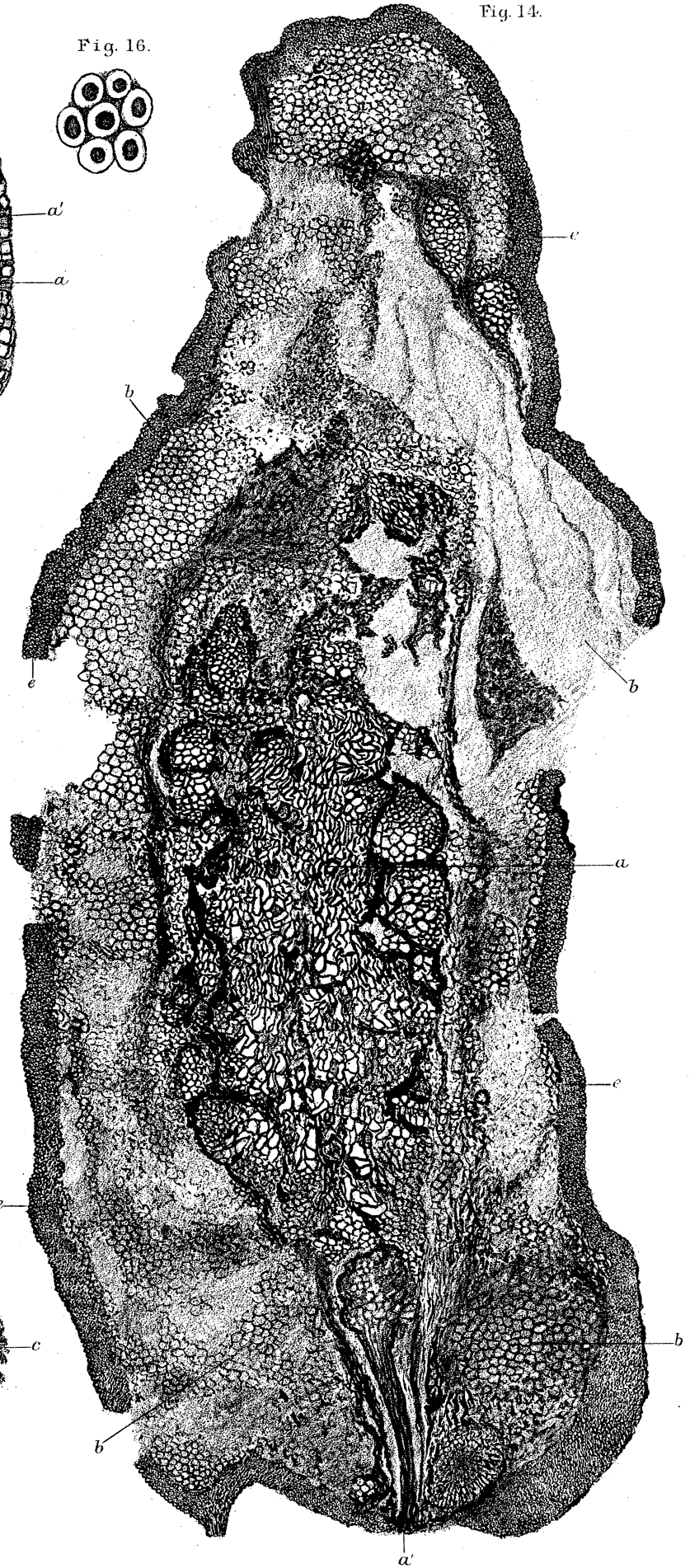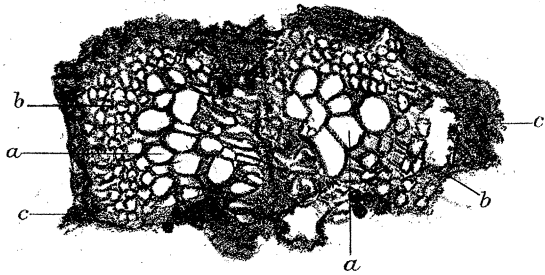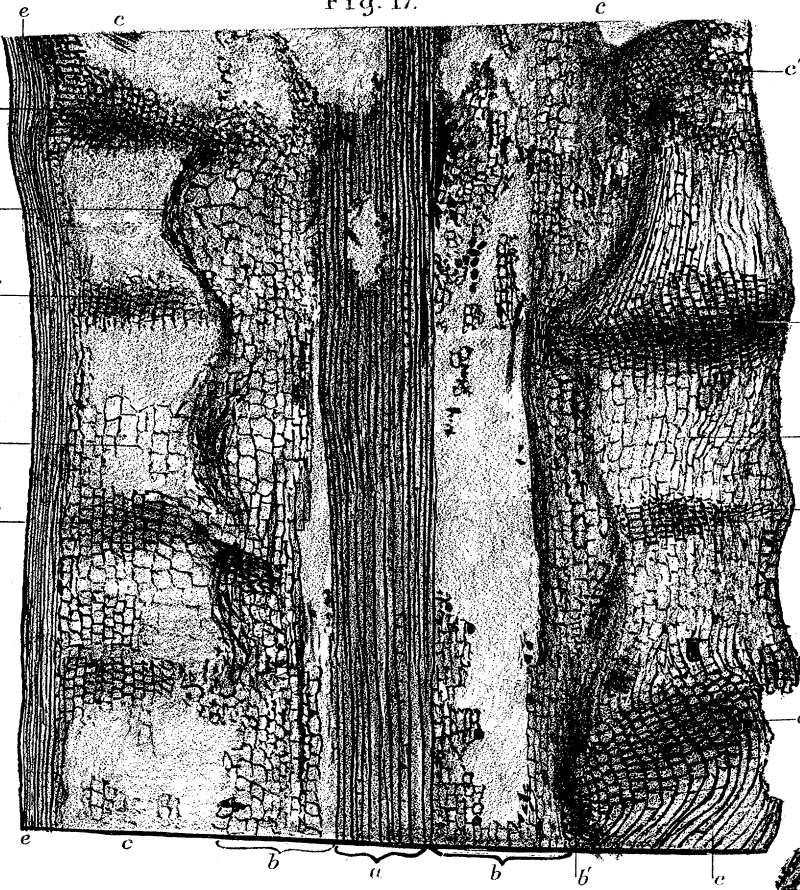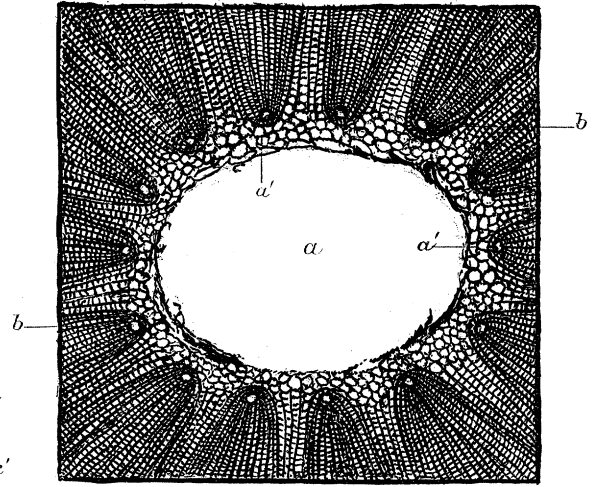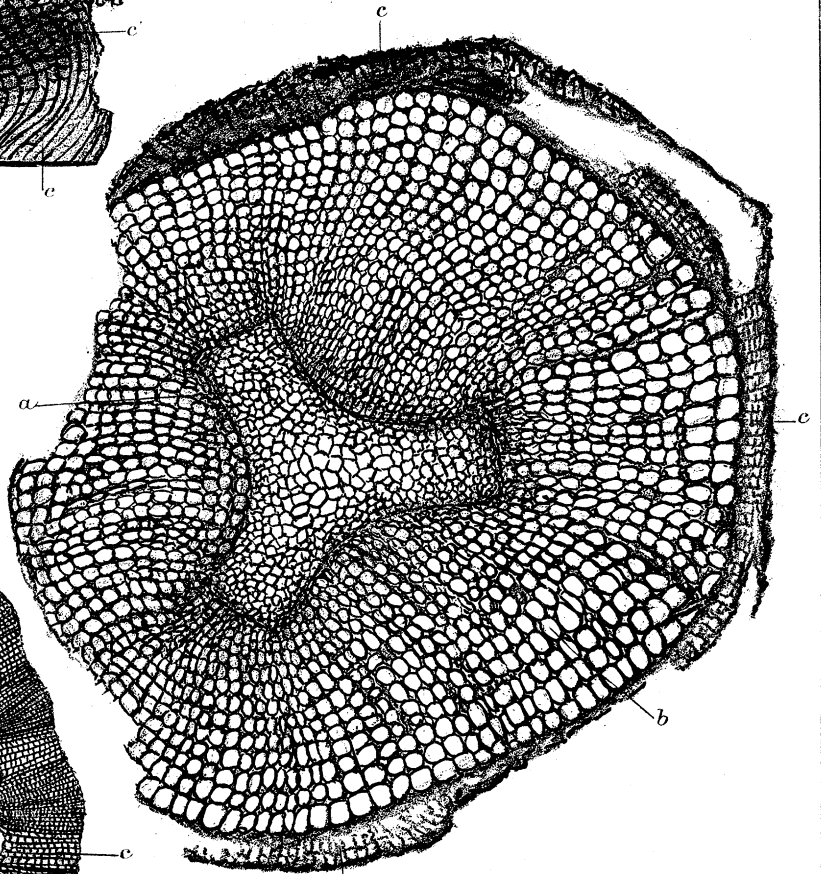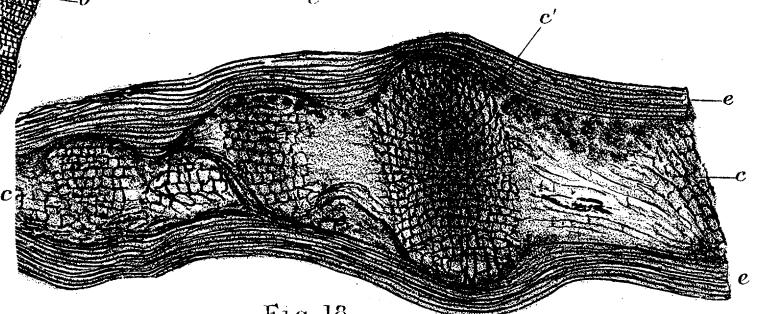
Fig. 14.

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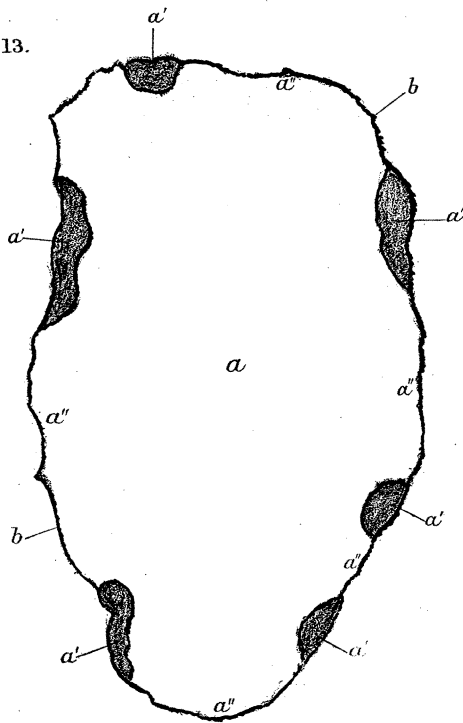
Fig. 15.

Fig. 17.

Fig. 21.

Fig. 19.

Fig. 20.

Fig. 22.

Fig. 18.