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XVI. On the Relations of Calamodendron to Calamites. By Professor W. C. WILLIAMSON, LL.D., F.R.S.

Read October 5th, 1886.

[PLATES XIV., XV., & XVI.]

THE relations in which the genus *Calamodendron* of Brongniart stands to that of *Calamites*, originally established by Suckow, and adopted by Brongniart and later authors, are involved in a considerable amount of confusion; this confusion is partly due to some indefiniteness in the statements of Brongniart himself on the subject, and partly to differences of opinion existing amongst palæobotanists as to what those relations really are.

In 1828 Brongniart published his 'Prodrome d'une Histoire des Végétaux Fossiles,' in which, for the first time, a serious attempt was made to classify the various types of fossil vegetation. In that volume Brongniart divided the family of the *Equisétacées* into the two genera *Equisetum* and *Calamites*, thus recording his opinion that the latter plants were true members of the Equisetaceous family.

But in 1849 Brongniart published, in the 'Dictionnaire universel d'Histoire naturelle,' his ''Tableau des Genres de Végétaux Fossiles.'' In the interval he had become acquainted with some fossils from Autun, belonging to deposits occupying the boundary-line between the uppermost beds of the Carboniferous series and the lowest Permian ones. These fossils had meanwhile been studied by M. Cotta, who gave to them the generic name of *Calamitea*.

It appears that, under this generic term, Cotta comprehended some Conifers; two plants, however, to which he

B. TABLE Volatile Organic Matter contained in 100 parts of the Solid Matters in Solution (see Tables A and C).

	-	1								-		
1885.	Per cent.	95.54	20.02	01.00	10.00	20.11	60.07	00.14	14-51	10 11		CONTRACTOR NOT AND A
18	Sample.	No 53	5.4	5 1	. 00 E0	. 54		eo "	-	* 604		
Per cent.	22:09	24.24	37-50	37-93	26.66	23-38	20.34	31-33				
Sample.	No. 45	. 46	47	. 48	. 49	" 50	" 51	., 52		11 11 1 1		
Per cent.	29.95	17-84	24-29	22.76	27-27	21.22	23-43	29-10	16-55	35.60	35-75	
Sample.	No. 34	" 35	., 36	., 37	. 38	" 39	., 40	" 41	. 42	., 43	, 44	
Per cent.	30-53	38-25	21.58	21-46	32-17	25-26	22.66	30.65	24-01	31-59	20-27	
Sample.	No. 23	24	" 25	., 26	., 27	., 28	., 29	., 30	., 31	., 32	. 33	
Per cent.	26.35	27-74	28-47	27-70	23-07	33-11	27-06	33.29	23-31	27.08	26.06	
Bample.	No. 12	,, 13	, 14	" 15	,, 16	. 17	" 18	., 19	., 20	., 21	., 22	
Per cent.	25-44	14-72	26.64	35-57	26-65	29-72	25-25	27-24	27-64	23-46	26-94	
Sample.	No. 1	., 2	. 3	. 4	. 5	. 6	T	80 "	6 "	,, 10	п "	

TABLE C.

Results of Analysis of Samples of Irwell Water, taken during the year 1885, on the same day in the week, and at the same spot, as in Table A.

No. of	When taken	during	Suspended	Volatile Matter in	Total Matter in	Volatile Matter in	Chlorine=Sodium	Amn	Ammonia.	Oxygen	Oxygen absorbed by Organio Matter in	Organio
		week, in inches.	Matter.		Solution.	Solution.	Chloride.	Free.	Albuminoid.	3 minutes.	1 hour.	3 hours.
1	Jan. 23rd	100.0	2-040	3-500	51.520	13-160	7-770=12-821	0.1904	0-1792	1.0434	1-3208	2-3954
	Feb. 27th	0-437	5.768	3.388	35-280	12-880	3.944 = 6.508	0.0672	0-1232	0.6860	1-3306	1.6240
	March 6th	0-837	5.120	3.260	30-440	10-920	4.061= 6.702	0.0672	0.0840	0-4532	0-9304	1-1330
	April 3rd	0-875	2-912	1-512	29-969	21-280	3.178= 6.242	0.0672	0.0840	0.4032	2602.0	0.8548
-	May 1st	0-437	4.480	2-770	52-990	14-070	8.123=13.383	0.1624	0.1288	0.1648	1-9782	2.6424
	May 22nd	0-737	4.760	1-400	42.000	11.480	4.238 = 6.981	0.1792	0.1344	0-5259	1.4112	1.5322
	May 29th	0.425	6-300	4-200	51.300	21-900	4.238= 6.981	0.0448	0.0616	0-7560	1.4602	1.8284
	June 5th	0-025	7-840	5-740	52-080	7-560	9-830=16-198	0.2016	0.2800	1.3181	2.0832	2-4760
-	June 5th		2.632	1-232	26-320	6-020	2.472= 3.479	0.0560	0200-0	0.2206	0-5297	0-9944

TABLE D.

Comparative Analysis of the Irwell and its Tributaries, during the year 1886.

				-		2					
Organic	3 hours.	1-2032	1.0242	1-3413	0.6855	1.1995	2.7821	1.0715	0.9778	0.2940	3.4122
Oxygen absorbed by Organic Matter in	1 hour.	1.0528	0-8764	1-0392	0.5740	0.7862	2-3587	0-8266	0.7358	0.2940	2.7286
Oxygen	3 minutes.	0.4652	0-1351	0-3878	0-2772	0-4133	1-4616	0-4636	0-3528	0.0840	1-8802
onia.	Ammonia.		0.1470	0.1750	0.0504	1-9040	0-4704	0.2128	0.1064	0.0224	0.0260
Amm	Free.	0-0210	0.0070	0-0350	0.2240	0.3248	0.4424	0.1628	0-2072	0.0140	0200-0
Chlorine=Sodium Chloride.		2.822= 4.657	2.822= 4.657	2.822= 4.657	3.551= 5.852	4.939= 7.894	6.914=11.393	4-939= 7-894	4.939= 7.894	1.273= 2.098	3.461= 5.710
Volatile Matter in Solution	.HOMMON	096-8	8-960	7-840	12.600	15-400	18-200	14.000	6.300	5.600	10.080
Total Matter in Solution		27-440	26-320	26-880	30.800	45.500	63-700	39-900	35-700	14.700	26.600
Volatile Matter in	Matter.	1-845	1.400	1.400	001-0	5-600	000.1	2.100	2.100	1.050	5-940
Suspended Matter.		3.808	3.640	3-920	1.400	8-400	10.300	4.200	4-900	1.400	3-360
SAMPLES.		Irwell at Bury before the Roach Bioms it, Sept. 17th	Irwell, Sept. 17th	it, Sept. 17th	River Irk, at the Lancashire and	Yorkshire Railway Station, Oct. 30th	the Irwell at Throstle Nest October	Trinell at Bouton choice the T	Oct. 30th at Our the Mocks,	Turton, Jan. 21st, 1885	entering the Irwell, June 5th



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gave the names of *Calamitea striata* and *C. bistriata*, seemed to have true Equisetiform affinities. Specimens of the former of these species in which the internal organization was preserved, were obtained by Unger, and were described by that palæontologist in Petzholdt's work *.

Brongniart concluded, from Unger's observations, that the two plants referred to above were distinct from the true Calamites; and he also objected to Cotta's generic term Calamitea as approximating too closely to Suckow's Calamites; he therefore substituted for it the term Calamodendron. Describing the C. striata of Cotta, he says :--"Cette tige, comme toutes les autres de ce genre, présente une moëlle très volumineuse, souvent réduite par la compression à une forme elliptique ou même linéaire, entourée par une zone ligneuse de quelques centimètres d'épaisseur, sans zones d'accroissement distinctes, mais formée de bandes rayonnantes alternatives fort différentes de couleur et d'aspect, presque égales en largeur dans le Cal. striatum, alternativement larges et étroites dans le Cal. bistriatum. On croirait au premier abord que ce sont de très larges rayons médullaires alternant avec des faisceaux ligneux à peu près de même dimension. Mais l'anatomie microscopique a montré dans le Cal. striatum, que la moitié des lames rayonnantes sont formées par des vaisseaux rayés, ou plutôt par de larges fibres rayées comme celles des Psaronius et des Stigmaria, séparées par des rayons médullaires très étroits, d'un seul rang de cellules, et peu étendus en hauteur ; les lames qui alternent avec celles-ci sont formées de fibres ligneuses, plus fines, très nombreuses, disposées aussi en séries rayonnantes, et chaque lame est partagée dans son milieu par un rayon médullaire plus large, continué et composé de deux ou trois rangées de cellules dirigées, comme dans les

* Ueber Kalamiten und Steinkohlen.-Bildung. 8vo. Dresden, 1841.

rayons médullaires, du centre à la circonférence "*. The above description agrees with sections in my cabinet, for which I am indebted to Professor Edouard, Graf von Solms, of Göttingen, with the exception of the *continuity* of the central medullary ray last referred to. I find that this ray is not regularly continuous, but decidedly irregular and interrupted in its continuity: indeed tangential sections of these fibrous zones exhibit rather numerous narrow, vertically elongated, lenticular, medullary rays, composed of one, two, or three vertical rows of cells; those rays nearest the centre are undoubtedly the largest and most conspicuous, but they are not continuous, merely *primi inter pares*.

Had the above description stood alone, no confusion would have resulted; but on p. 48 of his Tableau, M. Brongniart makes the following observations :--

"Je serais donc porté à penser, qu'on a confondu sous le nom des Calamites deux groupes des végétaux très différents. L'un, comprenant les Calamites à écorce mince, régulière, recouvrant le noyau central d'une couche charbonneuse qui en suit tous les contours, qui montre à sa surface externe des stries et des articulations très nettes des insertions de rameaux appliqués sur des articulations dépourvues de gaînes ou en offrant quelquefois une étalée. Leur structure est celle que je viens de décrire.

L'autre, comprenant les Calamites à écorce charbonneuse, épaisse, qui, extérieurement, offre à peine des traces de stries longitudinales et d'articulations, dont le noyau interne correspondant à la tige est, au contraire, profondément sillonné et présente des articulations très marqués. Ces tiges, lorsque leur partie centrale a conservé sa structure, paraissent offrir celle décrite par MM. Cotta, Petzholdt et Unger dans les *Calamitea*, c'est-à-dire une moëlle

* Loc. cit. p. 50.

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centrale, un cylindre ligneux, partagé par de nombreux rayons médullaires très réguliers, en faisceaux rayonnants, composés eux-mêmes de lames rayonnantes, de tissu vasculaire strié, analogue à celui des Fougères, des Lepidodendron, des Sigillaria et des Stigmaria, et de tissu plus fin, sans stries ou ponctuations."

As I shall show directly, this latter description includes within M. Brongniart's genus *Calamodendron* the group of objects which for many years past I have demonstrated to be true Equisetiform Calamites, but which M. Brongniart thus unites with objects which he believed to be dicotyledonous Gymnosperms. I may observe here that M. Brongniart had no conception of the existence of an enormous number of Carboniferous Cryptogams which possess largely developed, exogenous, vascular or xylem zones within their cortical layers; he believed such a combination to be impossible; therefore the fact that a plant possessed such a zone was to him, as it has long been to some of his disciples, a clear proof that it could not possibly be a Cryptogam.

In 1869 I published, in the 'Transactions of the Literary and Philosophical Society of Manchester'*, a memoir "On the Structure of the Woody Zone of an undescribed form of Calamite," in which I demonstrated the existence of an exogenous woody zone, and also I arrived at the conclusion, "that the Calamites constitute essentially one large group of plants, with some considerable range of variation in the details of their internal organization" (loc. cit. p. 179). This conclusion, as might be expected, was rejected by many who had been trained in the school of Brongniart. A few remain who still reject it.

Like myself, M. Göppert obtained specimens of Calamites with distinct, exogenously developed, vascular zones,

* Vol. iv., 3rd ser.

such as had been found in Brongniart's Calamodendron, but he saw that the radiating masses of cellular tissue (the primary medullary rays of my memoir) which alternated with the vascular wedges, differed from those of Cotta's plant; therefore he left the latter in Brongniart's genus Calamodendron, whilst for the reception of the others he instituted the new genus Arthropitus *. Brongniart's genus Calamodendron, as defined on p. 256, undoubtedly comprehended Göppert's new genus; the French author had been misled by his ignorance of the fact that both these genera possessed an exogenous vascular zone, which zone he obviously regarded as the chief feature distinguishing his Calamodendron from Calamites. Μ. Grand'Eury has followed Göppert in accepting his genus Arthropitus; but consistently with the Brongniartian views which he adopted when he published his 'Flore Carbonifère du Département de la Loire,' he there placed the genus along with Calamodendron in his "Famille des Calamodendrées," regarding both as Gymnospermous genera.

From 1869, the time of the publication of my Calamitean memoir already referred to, I have continued to demonstrate that all the Carboniferous Calamites began to develop exogenously a vascular zone even in their youngest state, and that the supposed non-exogenous Equisetiform type existed only in the minds of a few men, unbelievers in exogenous Cryptogams. Unger's *Arthropitus* is, I have long been convinced, merely an ordinary Calamite, in which the development of the exogenous zone has made some conspicuous progress. M. Grand'Eury himself has advanced so far as to recognize this fact. In his 'Détermination Spécifique des Empreints végétales du terrain houiller" †, he says :—" J'ai assez bien

^{* &#}x27;Die fossile Flora der Permischen Formation,' p. 179.

^{† &#}x27; Comptes Rendus,' Séance du 22 février, 1886.

reconnu que les Calamites cannæformis et varians vont avec les Asterophyllites du type Equisetiformes, Schl., et les Volkmannia gracilis, Pr., que le moule des tiges de ces végétaux est l'empreint de la structure du bois d'Arthropitus ;" and in a private letter to myself, that eminent geologist says, "Comme vous, j'ai reconnu que le bois d'Arthropitus appartient aux Calamites du type C. cannæformis." Since the contrary idea prevailing in the French school of palæontologists has chiefly rested, of late years, upon the discoveries of M. Grand'Eury himself, I presume we shall now hear no more of that mistaken hypothesis.

The identity of *Calamites* and *Arthropitus* being thus established, the latter genus disappears; but there yet remains for consideration the relationship subsisting between *Calamites* and *Calamodendron*, regarding the latter genus as identical with the *Calamitea* of Cotta.

On this point, I think, some light is thrown by a study of the plant which I described in 1869*, under the provisional name of *Calamopitus*. The figures in the accompanying Plates will facilitate an apprehension of what I propose saying on this subject.

Fig. I represents an ordinary form of a fossil Calamite, with its transverse nodal constrictions, a, and its longitudinal internodal ridges and furrows, b. When covered with a very thin film of coal moulded upon the contours of figure I, this form represents the ordinary Equisetiform Calamite of the Brongniartian school. But all parties now see in such a specimen something more. I long ago pointed out that these fossils were merely the inorganic casts of the fistular medulla of a Calamite, in which a nodal medullary septum extended more or less completely across the medullary cavity at each node, and to the presence of which the transverse constrictions

* Trans. Lit. and Phil. Soc. Manchester, 3rd ser. vol. iv. Session 1868-9.

of the cast, fig. 1, a, are due. In like manner, the origin of the longitudinal grooves and ridges, b, running vertically along each internode is illustrated by fig. 2, which represents a fragment, including a node and parts of two internodes, of a decorticated Calamite. Here a is the fistular medullary cavity; b a thin film of medullary parenchyma which surrounds the fistular cavity; c c is a ring of vascular wedges; the sharp apex of each wedge projects inwards, encroaching upon the medullary zone, at which latter point a narrow vertical canal *, d, is present. All the wedges of each internode extend vertically in parallel lines, e', as do the homologous vascular bands of living Equisetums, through the entire length of the internode; but those of each internode alternate at each node, f, with the corresponding wedges of the next internode above and below. Each of these vascular wedges originated in a few vessels in contact with the longitudinal canal, d; but as each wedge grew exogenously, its peripheral, tangential diameter increased.

Viewed in transverse section, as in the upper part of fig. 2, we see that these wedges were separated widely from one another in their youngest state by a broad radiating band, g, of the fundamental parenchyma, connecting the medulla with the cortex, exactly as the protoxylems of any young, vascular, exogenous growths are separated from one another. In 1870 I applied to these cellular bands in the young Calamite, the name of *primary* medullary rays \dagger , to distinguish them from those which instead of commencing in the bark commence in the wedges, and to which latter I applied the term *secondary*

^{*} In my various writings I have designated this the *internodal* canal, regarding it as the homologue of the canals that accompany the vascular bundles in the recent Equisetums.

^{+ &}quot;On the Organization of the Fossil Plants of the Coal-Measures.--Part I.," Phil. Trans. (1871), p. 479.

medullary rays. As the vascular wedges grew radially, they also enlarged tangentially, and as they did so they encroached laterally upon the peripheral prolongations of the primary medullary rays (g, g), which, as we have seen, ran parallel to, and on either side of, each wedge, throughout the length of the internode. In this way the primitive medullo-cortical origin of each such ray was lost sight of, its peripheral extension becoming, both in its cambial development and in its aspect, like an ordinary secondary ray. It results that, when we examine the exterior of a young decorticated Calamite, such as is represented in the lower part of fig. 2, we find the longitudinally extended vascular wedges, e', separated throughout their entire length by tangential sections, g', of the parallel primary medullary rays. In stems with a more developed vascular growth, these alternations of tissue disappear, as shown in fig. 3g.

The alternations of these vertical lines of cellular and vascular tissue in contiguous internodes are brought about in exactly the same way in living Equisetums and in fossil Calamites. As each end of a vascular wedge approaches the node above and below the internode to which it belongs, it splits into two short diverging branches (fig. 2, e). Each one of these meets a similar branch, derived from the contiguous vascular wedge of the same internode, and the two halves thus derived from two distinct wedges form a third one, which continues its upward or downward course through the next internode, but in a line midway between those from which it sprang, as in the living Equisetums; the internodal canals, d, branch and recombine at the nodes of some of the fossil Calamites in exactly the same way as the vascular wedges do.

Fig. 3 represents a restoration of a Calamite like fig. 2,

only corticated and in a more advanced stage of growth. Here, again, we have the central cavity, a, the thin medulla, b, and the vascular wedges c, represented by the same alternations of black and white as in fig. 2; but by detaching the vascular zone, we have also represented, at b, b', the causes of the alternating ridges and grooves of specimens like fig. I; at c the exteriors of the vascular wedges project externally as their inner angles project inwardly into the medullary cavity *. At c' a vascular lamina of one of these wedges is seen in radial vertical section, showing the characteristic arched arrangement of its vessels where they cross the node f. At h'' is one of the infranodal canals passing out from the pith to the bark, through the upper end of each primary medullary ray, as at h, h', and at fig. 2, h, whilst at i, i', as at i, i of fig. 2, we have lines of cellular tissue passing outwards through both wood and bark, being apparently lines of communication, doubtless containing some vessels, between the interior of the plant and each of its verticillately arranged leaves. At k we have the bark with its absolutely smooth, ungrooved, and unconstricted exterior at k', its nodes being prominent, rather than constricted, as they are at fig. 1, a.

Independently of the bark which encloses them, we have here a complex series of structures :—a, the fistular cavity; b, medulla; c, vascular wedges; d, internodal canals; f, node; g, primary cellular medullary rays,— besides which each vascular wedge, c, is composed of a number of thin, parallel, radiating, vertical laminæ of vessels, between which are numerous secondary medullary

* On the right hand of this figure the vascular zone has been removed from the interval between the two stars, showing the undulating outline, b, of the very thin medulla, which has adapted itself to the corresponding undulating contours of the medullary angles of the vascular wedges, c, the intervening primary medullary rays, a, and upon which the inorganic cast, fig. 1, of the medullary cavity, a, was moulded in its turn.

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rays. Now this very complicated arrangement of parts is admitted by all to exist alike in Calamites and Calamodendron, and the inorganic cast of the interior of the medullary cavity of a Calamite also reappears unchanged in the Calamodendron. This remarkably detailed identity in the morphological features of two plants, the former of which is admitted to be a Cryptogam, whilst the latter is assumed to be an Gymnospermous Phanerogam, is, in itself, sufficient to suggest the strongest doubt as to the accuracy of this assumption; but fig. 3 carries us further. Abundance of specimens in my cabinet prove the absence from the bark of all the nodal constrictions, as also of the longitudinal ridges and furrows, formerly supposed to be characteristic of the exterior of the bark of a true Cryptogamic Calamite. We possess little evidence respecting the bark of Calamodendron, but M. Brongniart inclined to the belief that it also had a smooth exterior.

There being such a remarkable identity in the general, as well as in the minute morphology of *Calamites* and *Calamodendron*, let us now see what value may be assigned to the differences of detail that are supposed to distinguish the two plants.

To facilitate an apprehension of this part of the subject, I have prepared diagrammatic outlines of three cubical wedges. One of these (fig. 4) is cut out of the stem of a Calamite, fig. 5 is from my so-called *Calamopitus*, and fig. 6 is from a *Calamodendron* from Chemnitz. Each of these blocks comprehends superiorly, a portion of the horizontal transverse section, and inferiorly, of a vertical tangential section. In like manner in each block the two outer portions, g, g, represent two primary medullary rays, and the central area, c, is part of a single vascular wedge. In each of these figures the further margin, c, of each cube is supposed to be the portion nearest to the medulla.

In fig. 4 (*Calamites*) we find that the cells of the broad medullary ends of the two primary medullary rays g, g, are larger in size and less regular in their arrangement than those of the narrower, more peripheral portion g', of each ray, where the cells are smaller in size and disposed in regular radial rows, parallel to those of the vessels of the vascular wedge, c. Turning to the tangential side of the block, we see that the vertical extensions of the same rays, g'', g'', are still composed of parenchyma, the component cells of which tend to assume an arrangement in vertical lines.

Between these two rays we have part of a vascular wedge, c, narrower at its medullary end than at its opposite one. It is composed, as is most usual, of barred vessels or tracheids, not always easily distinguishable in transverse sections from the cells of the more peripheral extremities of the primary medullary rays. In the tangential section, we see the secondary medullary rays, *l*, of the wedge, each being composed of variable numbers of cells arranged in vertical rows.

Turning to a similar diagram of a cubic block from my *Calamopitus*, fig. 5, we find the general arrangements to be identical with those of fig. 4. The differences between them are chiefly twofold. In this plant, the transverse section shows the cells g, g, of the two primary medullary rays to be more uniform in size and more regular in their linear, radial arrangement than is usual amongst the Calamites. This exceptional condition exists close to the medullary axis as well as more peripherally, as will be seen on contrasting fig. 4, g, g, with fig. 5, g, g. But the most striking feature in this second type is seen in tangential sections of these rays, as at fig. 5, g', g'. Instead of being composed of an aggregation of parenchymatous cells, these rays consist of a very marked prosenchymatous

form. At the same time these are merely fusiform cells, not lignified fibres. The difference between them and what are found in fig. 4, g'', g'', is merely a morphological one, probably of small physiological import; nevertheless we have here a true Calamite possessing one of the distinctive morphological features supposed by Brongniart to be characteristic of *Calamodendron*.

The vessels of the vascular wedge, c, c, are identical in their arrangement, and in the distribution of their secondary medullary rays, l, with what we find in ordinary *Calamites*. Structurally, however, these vessels present a peculiarity. Instead of their walls being transversely barred round their entire circumference, they are reticulated, and apparently only on those sides of each vessel that are parallel to the secondary medullary rays. There is, however, nothing in these reticulations, beyond their positions, to identify them with the true bordered pits of the Gymnosperms. These reticulated tracheids are very common in other Carboniferous Cryptogams.

At fig. 5, g'' g'', we see traces of special parenchymatous rays passing outwards through the prosenchymatous tissue.

Turning to fig. 6, where we have a similiar cubic block from the *Calamodendron striatum* of Autun, we have further peculiar features of resemblance and of differentiation.

As before, the central division of the transverse section, c, is the vascular wedge, made up of numerous radial lamellæ consisting of very large vessels separated by very conspicuous secondary medullary rays, l, the latter usually consisting of two rows of cells which frequently separate isolated single vascular lamellæ from one another. A little less frequently we have two and occasionally even three such rows of vessels between each two medullary rays. Turning to the longitudinal section, c', we find the vessels

to be barred, as we have seen to be the case with those of ordinary Calamites; the medullary rays, l', consisting of parenchymatous cells, are as conspicuous here as they are in the transverse section. This greater development of these secondary medullary rays distinguishes *Calamodendron striatum* from ordinary Calamites, but this cannot be regarded as a generic feature, much less as an ordinal one.

On each side of this vascular wedge we have the two radial zones g, g, corresponding to the primary medullary rays of figures 4 and 5. The transverse section shows these rays to be composed of cells whose diameter is very much smaller than that of the vessels composing the vascular wedge on each side of which they are grouped. Their appearance in this section closely corresponds with that of a Coniferous wood. Turning to their longitudinal and tangential sections, g', g', we find that these cells are prosenchymatous and partially sclerenchymatous. They are long fibrous structures such as we find abundantly in many Equisetiform and other Cryptogamic plants. In the transverse section, g, we see some parenchymatous medullary rays, as at g', g', and at g'', g'', in the tangential surface, we see vertical prolongations of these rays as described by Brongniart (see page 257). These have a lenticular vertical section, and those near the centre of the fibrous zone are unquestionably longer and broader than those in its more lateral portions; but these central ones are far from being continuous though the internode, as they are described by Brongniart.

In my transverse sections of *Calamodendron striatum* the radial length of what I call the primary medullary rays (fig. 6, g) is much greater than is common amongst Calamites. In the latter plants these rays generally diminish rapidly in diameter as they proceed outwards, and their ultimate external prolongations become, in the most matured

stems, almost undistinguishable from those of the secondary medullary rays (fig. 3, g). At the same time ordinary Calamites vary extremely in the length of these primary rays, and I have transverse sections in my cabinet which, in this respect, approximate very closely to what I find in my sections of *Calamodendron*.

Comparing the three forms of organization illustrated by figs. 4, 5 and 6 we find them unmistakeably constructed upon a common plan, even as regards the most important of the details. The differences between the vascular or xylem elements of the three examples have no more than specific value. The chief distinctions between figures 4 and 6 are to be found in what I term the primary What in the ordinary Calamites we medullary rays. have seen to be entirely composed of parenchyma, in the Calamodendron consists of prosenchymatous fibres largely intermingled with radial parenchymatous laminæ. My numerous examples of very young and minute Calamites show me that, in them, these primary medullary rays originate in exactly the same way as they do in the first year's growth of any ordinary exogenous stem*; whilst, as is also the case in these Exogens, the peripheral ends of these primary rays become undistinguishable from the secondary medullary rays in the more external layers of older stems. These identities justify my designating both medullary rays. The only question of importance therefore to be asked is, Does the alteration of their composition seen in Calamodendron, compared with what we find in Calamites, materially alter the character of these organs? I conclude that it does not. In the first place, it is indisputable that fig. 5, my so-called Calamopitus, is but a very slightly

^{*} De Bary applies to these organs in Phanerogams precisely the same terms that I have for years applied to those of the Calamites. See 'Comparative Anatomy of the Phanerogams and Ferns,' English Translation, p. 235.

modified form of a Calamite; yet, in it, the parenchymatous constituent cells of these primary rays are replaced by prosenchymatous ones, without disturbance of any of the other Calamitean features of the plant; the further modifications of these prosenchymatous cells merely involve questions of size, and of a slight degree of lignification in Calamodendron, which are surely not features of any ordinal De Bary, speaking of the difference between value! parenchymatous and prosenchymatous structures, says, "We find cells whose protoplasm and contents are reduced relatively to the strongly thickened and often lignified membrane, and which accordingly, without giving up the properties of typical cells, or their part in the process of assimilation, obviously participate in the mechanical functions, i. e. the strengthening of the parts to which they belong" (op. cit. p. 28). In accordance with the clear common sense of the above quotation, I conclude that the substitution of a mixture of parenchymatous and prosenchymatous elements in the primary medullary rays of Calamodendron for the solely parenchymatous ones constituting the same organs in the commoner Calamites, is utterly insufficient to justify the separation of these two plants into Cryptogamic and Gymnospermous groups. My plant, represented in fig. 5, which is obviously an intermediate form connecting these two extremes, reduces yet further the value of the small differences that distinguish them, and at fig. 5, g''g'', we already find traces of the same combination of parenchymatous and prosenchymatous elements that appears to be characteristic of the primary medullary rays of Calamodendron.

But one more point yet remains to be dealt with: M. Renault considers that he has obtained clear proof that *Calamodendron* was a Gymnospermous Phanerogam, inasmuch as he believes that he has obtained its male, or antheridial organs, and that its supposed anthers are filled with true pollen-grains. To this I make but two answers: first, even supposing it true that these objects were polleniferous structures, we have no evidence whatever that they belong to *Calamodendron*. Their doing so is a pure assumption. But even could it be proven that they were so related, I deny altogether that these objects are either antheridial or polleniferous.

My friend Mr. Cash, of Halifax, has received from M. Renault two sections of these objects, which he has kindly allowed me to examine. These sections being inscribed, in the handwriting of the French savant, "Epi de Calamodendron, Pollen divisé," there is no doubt as to their being really the objects to which I have just referred. I have no hesitation in saying that these are nothing more than sections of a very distinct form of Calamostachys, of which the supposed pollen-grains are merely the spores, enclosed within their mother-cells, exactly as I have figured similar ones from the sporangia of Calamostachys Binneyana, in my memoirs "On the Organization of the Fossil Plants of the Coal-measures," Phil. Trans. pt. ii. plate 15, fig. 17. From all these combined facts I once more conclude that Calamodendron striatum is an Equisetiform plant, closely allied to the true Calamites*.

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PLATE XIV.

Fig. 1. Inorganic cast of the medullary canal (fig. 2, a) of a Calamite, with the transverse nodal constrictions, a, produced by the projection inwards of the nodal tissues at that point. The longitudinal furrows produced by the similar inward projection of the inner angles of the longitudinal vascular wedges (fig. 2, c).

* I need scarcely remind Palæo-botanists that in 1881, Vom c. M. D. Stur, of Vienna, arrived at the same conclusion, in his valuable memoir "Zur Morphologie der Calamarien." Aus dem lxxxiii. Bande der Sitzb. der k. Akad. der Wissensch. I. Abth. Mai-Heft, Jahrg. 1881.

Fig. 2. Diagram of a young decorticated Calamite. a, medullary canal; b, thin layer of medullary parenchyma; c, circle of vascular wedges, each commencing internally at the internodal canal, d; e', longitudinal extensions of these wedges through each internode; f, a node; g, g', primary medullary rays; h, external orifices of the vertically elongated variety of infranodal canals; i cellular, and probably also vascular, extensions, apparently connected with a verticil of leaves.

PLATE XV.

- Fig. 3. Diagram of an older stem of a Calamite. a, medullary canal; b, b', exterior of the medullary cellular layer; c', radial section through a vascular wedge; c, exterior surface of the vascular zone; f, the node; g, primary medullary rays; h", an infranodal canal extending from the exterior of the medulla (b) to the inner surface of the bark, k; i, i', verticil of radial organs identical with i of fig. 2.
- Fig. 4. A diagram of a cube cut out of a stem like fig. 2. c, portion of a vascular wedge; g, g, portions of two primary medullary rays; l, secondary medullary rays.

PLATE XVI.

- Fig. 5. Similar cube to fig. 4, from a rare form of Calamite, in which the primary medullary rays, g g, consist of prosenchyma instead of parenchyma. c, vascular wedge. l, secondary medullary rays.
- Fig. 6. Similar cube, from a stem of a *Calamodendron*. c, vascular wedge; g, g', tissues occupying the positions of the primary medullary rays. g'', g'', vertical layers of parenchyma separating some of the prosenchymatous layers which represent the primary medullary rays of *Calamites*.

Botanical Laboratory, Owens College, Oct. 1st, 1886.



Williamson, William Crawford. 1887. "On the Eelations of Calamodendron to Calamites." *Memoirs of the Literary and Philosophical Society of Manchester* 10, 255–271.

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