ON A VASCULAR SPORANGIUM FROM THE
STEPHANIAN OF GRAND 'CROIX.

[With Plate I.]

By F. W. OLIVER.

IN the course of an investigation into certain seeds contained in the well-known silicified 'magmas' of Grand 'Croix many fossilised fragments other than those forming the main subject of that inquiry have necessarily come under my observation. These include numerous fern-sporangia of varying affinity and preservation, for the most part detached, though in occasional instances showing continuity with the vegetative organs. In one instance a transverse section of a detached sporangium was obtained which revealed an organization of more than passing interest. The facts of its structure, which are novel and perhaps unique, give rise to the conjecture that we have in this sporangium a point not without morphological signification, and this quite apart from any confident attribution of the sporangium in question to its systematic position—which indeed for the present must remain a matter of opinion.

The preparation which forms the subject of the present communication showed a transverse section of a sporangium, the wall of which possesses a lining of unmistakeable tracheal elements. This section is represented in photograph 1, Pl. I., taken directly from the object. In outline the section is not quite circular, the diameter which coincides with the plane of symmetry slightly exceeding that at right angles to it. The dimensions are .65 mm. $\times$.53 mm. The wall of the sporangium is unequally developed on the two sides. Whilst for about half its perimeter the wall consists of a single layer of relatively small rectangular cells, its other half is two, and, at places, three cells deep, and the cells of this side are larger, thicker walled and rounded. This broad indurated band represents the annulus here, and suggests a comparison with the sporangium of *Botryopteris forensis*, B.R. which has been fully figured and described by Renault¹.

The interior of the sporangium appears filled with a mass of contracted and collapsed spores; the less deformed of these have an average diameter of .02 mm. Lying between the wall and the sporogenous mass is an interrupted ring of tracheal elements.

¹Ann. des Sci. Nat. (Bot.), sér. vi. vol. i. Flore fossile d'Autun et d'Épinac, pt. ii., p. 47

These tracheae are fairly thin walled and exhibit well-marked pittings of a reticulated type. It has been possible to recognise five groups of these tracheae adjacent to the sporangial wall and distributed at intervals, as represented by *t*, *t* in photograph 1. The largest number found in any group was six (*t*⁶)—close to the broken middle point of the thin side of the sporangium (*g*), whilst against the annulus at *t*³ the number was three, elsewhere generally fewer than three (the number in each case is indicated by the figure following the reference letter *t*).

Owing to their slight displacement most of the tracheae are seen a little obliquely, a fortunate circumstance, as it permits of the details of their thickening being studied. The high power photographs 2 and 3 and figs. 4, 5 and 6 give these details. Photo. 2 and fig. 4 represent the group of tracheal elements abutting on the fracture in the thin part of the wall (*g*), fig. 5, a group from the opposite side of the sporangium with a portion of the indurated sporangial wall (*w*). The oval pits are numerous and shew a very delicate bordering. The largest element (*t* in fig. 4) has a diameter of .045 mm. The tracheal elements were evidently delicate structures and it is not improbable that they were originally more numerous than is actually indicated by the number of those preserved in this specimen. At places they occur quite flattened against the wall (as at *t*, fig. 6), so that they may have formed during life a continuous lining to the sporangium. I attribute their preservation in this case to the early mineralisation of an immature sporangium. As the block of spores ripened and distended the sporangium the tracheae would be unrecognisably crushed against the wall. It is not possible to say definitely from inspection of this specimen whether the elements were tracheides or vessels, as they are shown only as short segments.

Though the position occupied by these tracheal elements corresponds with that usually associated with a tapetum, it is not possible to make any statement as to their origin, owing to the relatively advanced developmental stage of this sporangium. Were the data available, it would be interesting to know with what layers of the sporangium the tracheal zone is associated in development. Whether, like the endothecium of an Angiospermic anther, it arises in common with the tapetum, or whether some other relation obtains. In view of the unexpected complexity of the sporangium here described, attention might perhaps be profitably devoted to such immature Botryopteridean and other sporangia as may be available.

As I have already said, this sporangium suggests a comparison with *Botryopteris*. I turn therefore to the Botryopterideae in the first instance with a view to determining how far the ascertained facts of their sporangial structure favour a reference of my sporangium to this group.

Zygopteris, Corda. Here the sporangium is large, being 2.5 mm. long by 1.3 mm. across its longer transverse diameter. The wall in Renault's figures¹ consists of a single cell-layer of well preserved cells with two indurated bands (the annulus) passing down the two opposed faces. A second layer or membrane is usually shewn retracted from the wall and enclosing the spore mass; Grand'Eury² figuring a similar form (*Schizostachys frondosus*) represents the wall as of several layers.

Solms-Laubach³ conjectures "that the inner layers were destroyed in Renault's specimens, and his figures show a sac-like envelope inclosing the spores, which I can only suppose to be a crushed cell layer." D. H. Scott⁴ in reproducing Renault's figures regards the sac-like envelope as a possible tapetum. A point of great interest is recorded by Renault⁵ in the statement that the pedicel of the sporangium in *Zygopteris* is traversed by a flattened, bi-polar, vascular band which extends to the base of the sporangium, being accompanied by a tissue which he regards as phloem. The spores of *Zygopteris* have a diameter of .08 mm.

Botryopteris dubius, B.R.—The sporangia of this plant have been fully described and figured by Renault⁶. The walls of the sporangia were relatively massive and consisted of several series of cells. In the best preserved specimens two layers were distinguishable in the wall:—an outer layer three or four cells deep, limited externally by an epidermis; and an inner, some three cells deep, the elements of which were elongated in the sense of the chief axis of the sporangium. There was an indurated band (annulus) passing down one side of the sporangium. The dimensions of the sporangium and of the spores are essentially the same as those

¹ Ann. des Sci. Nat. (Bot.), sér. vi., vol. iii., pl. i., figs. 1 to 3.

² Flore carbonifère du dép. de la Loire, p. 201, and tab. xvii., *d* and *d'*.
This author comments on the thickness and complexity of the wall, which he states to be formed of an outer cellular and an inner fibrous layer. He suggests a comparison with the pollen-sacs of *Cycas*.

³ Fossil Botany, Eng. Edn., 1891, p. 150.

⁴ Studies in Fossil Botany, p. 287.

⁵ Flore fossile d'Autun et d'Épinac, pt. ii., p. 43.

⁶ Ann. des Sci. Nat. (Bot.), sér. vi., vol. i., pl. x., fig. 24 and pl. xi., figs. 25, 26, 27.

given above for *Zygopteris*. In his later writings Renault¹ recognises *B. dubius* as a *Zygopteris*, though in a note in his *Zygopteris* paper² he had expressed a doubt as to the possibility of such a reference. I am unaware whether the evidence upon which this change of opinion is based has been published. Whilst agreeing with *Zygopteris* in the position, form and dimensions of the sporangia, *B. dubius* seems to have but a unilateral annulus, whilst in the complexity of its wall it much surpasses that which has been described for *Zygopteris*.

Botryopteris forensis, B.R.—The sporangia are smaller than in either of the foregoing, the length of the sporangium being 1.5—2 mm., its diameter .7—1.0 mm., whilst its spores attain a diameter of .06—.07 mm. The wall is described as being two-layered,³ *i. e.*, an outside limiting layer one cell thick, enlarged on one side to form the annulus, and a thin-walled, often indistinct, lining.

Of the forms just detailed our sporangium approaches most nearly in dimensions to *B. forensis*, but its spores have a diameter of only one-third (.02 mm. as compared with .06—.07 mm.), a disparity perhaps explicable in view of the immature condition of the sporangium and the collapsed condition of the spores. With *B. dubius* it has a point of contact in the lining of elongated cells which that sporangium possesses. Finally, the little vascular bundles which Renault has traced into the pedicels of *Zygopteris* render the assumption that this sporangium may have possessed a vascular coat not a very hazardous one. Indeed if *B. dubius* be really a *Zygopteris* with a well preserved wall, the elongated cells of the lining may have been tracheal in nature, a remark likewise applicable to the inner layer of *Schizostachys*. Hence it would appear as not wholly improbable that a tracheal layer in the sporangial wall of Botriopterideæ may have been a common character. As yet the evidence is lacking, and in any case can only be expected to accrue slowly from occasional and exceptionally preserved specimens.

But there is another group, the Marattiaceæ, that should not be omitted from consideration as affording a possible resting place for our sporangium. Of the numerous Pecopteroid and other fructifications that have been attributed to this order, several show the rudiments of an annulus. Such a form with unmistakeable

¹ Flore fossile d'Autun et d'Épinac, pt. ii., p. 42.

² Ann. des Sci. Nat. (Bot.), sér. vi., vol. iii., p. 23.

³ Flore fossile d'Autun et d'Épinac, pt. ii., p. 54.

annulus is *Sturiella*, Weiss (*Pecopteris intermedia* of Renault), the sporangia of which Solms-Laubach¹ says are especially distinguished "by the presence in their wall of an apical group of abnormally thick-walled cells which extend some way down on the outer side of the sporangium; these cells have quite the appearance of an annulus." But in addition to this character there is a supposed peculiarity of the cells of the annulus, which Renault places on record² in his original description of the specimen. He says "Les cellules qui composent le connecticule [*i. e.* the annulus] sont irrégulières; leurs parois fortement incrustées présentent des stries transversales ou des réticulations (fig. 10)." The figure in question³ is a somewhat tangential longitudinal section of a sporangium, and in the position at which an inner layer to the wall (did such exist) would be exposed, three spindle-shaped cells are shewn with transverse striate markings. Without examining the original preparation, I should, however, hesitate to put any interpretation on these appearances other than that sanctioned in the passage quoted from the text.

Whilst admitting the possibility that my sporangium might be placed near this last type—should it bear the interpretation just suggested—I am inclined to associate it with the *Botryopterideæ*, indeed, it may be a sporangium of *Botryopteris forensis*, B.R., revealed in a new light owing to a fortunate accident of fossilisation. Such an attribution would receive a certain measure of corroboration from the fact that throughout the small block from which the preparation was obtained, the very characteristic equisetiform hairs of *B. forensis* are sparsely scattered. That the dimensions of the cross-section (.65 mm. $\times$.53 mm.) are somewhat below the normal for this species may be due to the fact that our section is not across the broadest portion of the sporangium, or possibly, it may not yet have attained its full dimensions. The smallness of the spores (.02 mm. diameter) is also susceptible of explanation in view of their immaturity and of the contraction which they have undergone.

The biological significance that may be attached to the tracheal mantle may well be that of an organ for the conveyance to the maturing spores of adequate supplies of water. That such a provision has not been more generally recognised is not on the

¹Solms-Laubach, *Fossil Botany*, Eng. Edn., 1891, p. 145.

²Renault, *Cours de botanique fossile*, tom. iii., p. 123.

³Loc. cit., plate xxii, fig. 10.

whole surprising in the case of fossil Ferns, for these tracheae are very delicate structures and liable to obliteration on the maturing of the sporangium. In the fossil seeds of Gymnosperms—*Stephanospermum*, and others—the presence of tracheal elements at the periphery of the nucellus of the seed, passing from the chalaza to the pollen-chamber, was a common feature. Not improbably, in these cases, adequate physiological requirements connected with important functions were operative and led to the retention of the tracheal tissue to a late stage in development.

The presence of vascular tissue in close proximity to the sporangium in Pteridophytes generally is not very common. In the sporangiophore of *Sphenophyllum Dawsoni* a small bundle runs to a point just short of the sporangium, where it ends in a somewhat bulb-like enlargement consisting of reticulated tracheides. Something of the same kind is indicated in *Helminthostachys* and *Botrychium*, and occasionally in *Lygodium*,¹ whilst in *Tmesipteris* little bundles run within the margin of the synangial septum. Amongst the Cycads I find that strands of well-developed spindle-shaped tracheides penetrate the pedicels of the pollen-sacs in *Bowenia spectabilis*², where they may be found reaching up to within a distance of six cells of the actual sporogenous mass. To these instances may be added that of the pollen-sacs in *Cordaianthus Penjoni* and *C. Saportanus*, to the base of which delicate vascular ramifications penetrate³. Finally, presenting some analogy with the foregoing we have certain instances amongst the Amentales⁴—*Casuarina*, *Castanea* and *Corylus*—in which spindle-shaped tracheides occur right amongst the sporogenous tissue of the nucellus, though in a manner suggesting that they are vestigial in nature.⁵

But the chief interest in the observation here put on record seems to lie in the recognition in a sporangium of one of the palaeozoic Ferns of a condition which is recognised as normal in so many of the fossil gymnosperm seeds. If my conjecture that the sporangium belong to one of the Botryopterideae be confirmed,

¹Scott, *loc. cit.*, p. 289.

²I am indebted to my friend Mr. A. C. Seward, F.R.S., for kindly placing at my disposal a series of sections through a cluster of pollen-sacs of this plant.

³Cf. Renault—Structure comparée de quelques tiges de la Flore Carbonifère. Pl. xvi, fig. 14, g, and Pl. xvii, fig. 3, f.

⁴M. Treub, in *Ann. du jard. bot. de Buitenzorg*, vol. x. M. Benson, "Contrib. to the Embryology of the Amentiferae." *Trans. Linn. Soc. 2nd ser.*, vol. iii., Bot. S. Nawaschin, *Bull. de l'Acad. Imp. des Sc. de St. Petersburg*, 1899, vol. x., No. 4, p. 375.

⁵M. Benson, *loc. cit.*, p. 421.

then the observation has a certain, if unimportant, bearing upon current views regarding the phylogeny of the Cycadales. Scott¹ in his interesting discussion of the Botryopterideae correlates the French and English representatives of the group and shows how they are to be regarded as representing the more simply organised stock of the primitive Ferns, the polystelic Marattiaceae being the more complex. On purely anatomical grounds the Botryopterideae seem to have a claim to affinity with the stock from which the Cycadofilices arose, and in our present lack of knowledge concerning the manner of fructification of this group, the suggestion that the vascularity now found in the sporangium of an apparent Botryopterideae may be homologous with the tracheal tissue which we recognise as so characteristic and well marked a feature in the early Gymnosperms does not appear wholly unreasonable. Whilst in our sporangium, and in the Botryopterideae generally perhaps, if my surmise be well founded, the tracheal sheath served the simple end of conveying water to the ripening spores (perhaps under xerophilous conditions), in the early Gymnosperms it has undergone a marked advance and specialisation, in harmony with the modified fate and enlarged functions of the macrosporangium; and at the same time has come to discharge functions more complex than the mere supply of water to a sporogenous tissue.

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¹*Loc. cit.*, pp. 277 and 507.

EXPLANATION OF THE PHOTOGRAPHS* AND FIGURES ON PLATE I.

Illustrating F. W. OLIVER'S paper on "A Vascular Sporangium."

PLATE I.

Photograph 1.—Transverse section of the sporangium ($\times 110$).

*t*¹ solitary tracheal elements.

*t*³ and *t*⁶ groups of three and six tracheal elements.

Photograph 2.—View of the tracheal group *t*⁶ (of photo. 1) under higher magnification ($\times 290$).

t-t tracheal elements (six in all).

g gap in wall.

Photograph 3.—View of the tracheal group *t*³ (of photo. 1) under higher magnification ($\times 290$).

w thick part of sporangial wall.

t tracheal group.

*I am indebted to Mr. W. Tams, of Cambridge, for the trouble he has taken in obtaining the photographs reproduced here.

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