The Spores of Equisetum

The structure & the ~~history~~ development of the spores of Equisetum were very favourite subjects for study with the older botanists. Sachs, Sanio, Hofmeister, Russow, Tschistiakoff, & Leitgeb have all contributed to this subject whilst of living botanists none has given us so valuable an account as Strasburger.

All are now agreed that the mature spore of Equisetum possesses four layers to its wall. On the extreme outside there is the spirally cleft wall which constitutes that curiously hygroscopic structure — the Elater. Within this layer is a membrane which is usually spoken of as the "middle layer"; within this lies the "Exospore"(1) whilst the innermost & last formed layer of all is the endospore.

When, however, we turn to the literature for information

(1) according to the interpretation which is given to the "middle layer" the "Exospore" mentioned above corresponds to the whole or only to a part of the true Exospore. As will be seen below I regard it as the true Exospore in its entirety.

regarding the origin + interpretation of these four layers of the Spore-coat we find a surprising diversity of opinion.

Without describing the opinions + labours of the ~~in~~ different investigators in detail I may briefly summarise the views which have been expressed regarding the development of the wall of these spores in the following manner:—

(1) All four layers are formed by the Spore-protoplast in centripetal succession.

(2) The outer (forming the Elater) + middle layers are derived from the special-mother-cell wall, the exospore + endospore from the spore-protoplast.

(3) The outer layer is derived from the special-mother-cell wall, the middle layer, the exospore + the endospore are formed by the spore protoplast

(4) The outer layer is formed by the tapetal cytoplasm, the middle layer, the exospore + the endospore are formed by the spore-protoplast.

I have recently re-examined the development of the Spores of ~~Equisetum~~ two Species of Equisetum (E. arvense & E. limosum) with the principal object of attempting to decide which of the above accounts is the correct one.

After a careful study of my preparations I have come to the conclusion that none of them completely expresses the facts & in the present note I will briefly ~~express~~ state the results of my study of this & a few other points ~~in the development of the Spores.~~

The Spore-mother cells form a Solid mass of tissue in which the individual cells are separated from one another by delicate walls giving the reactions of pectic bodies. The tapetal cells form a continuous layer round the Sporogenous tissue. ~~The~~ Very soon the Spore-mother-cells begin to Separate from one another by the apparent Splitting of the delicate walls between them. This Splitting of the membrane first becomes noticeable at the angles between several mother-cells. In the meanwhile the tapetal cells have lost their separate individuality & have become fused into a plasmodium. This tapetal plasmodium ~~now~~ commences to penetrate into the interior of the sporangium making its way between the separating spore-mother-cells. It may be noted that ~~the~~ tapetal cytoplasm, free from nuclei first advances into the interior of the sporangium & that only after a short but appreciable interval the nuclei make their way along the cytoplasmic branches between the sporogenous cells. At about this stage the division of the spore-mother-cells takes place. I have been able to confirm Osterhaut's account of the development of the spindle during the prophases of the first meiotic division in Energy particular. The chromosomes proved too numerous & crowded to enable me to count them with any exactitude. The formation of these bodies from the Spirem can be followed with ~~unusual clearness~~ comparative ease & is particularly interesting in the light of present day cytological discussions regarding this subject. The Spirem can be seen from an early stage to be double, being composed of two parallel parts which usually lie very closely indeed together. This two-fold character of the Spirem although often obscured by the intimate approximation of the two component parts, ~~can~~ was, however, observed over & over again ~~be detected at almost every stages in the post-synaptic history of the Spirem~~ when the search was careful & thorough enough.

This double Spirem segments into the bivalent chromosomes in such a manner that the two constituent ~~elements~~ chromosomes lie side by side parallel with one another.

Although a ~~marked~~ certain polarity of the Spirem can be seen at one period during this division & the thread is then thrown into a number of loops no evidence could be found that the sides of these loops become approximated or that they ~~have~~ bear any direct relation to the pairs of chromosomes which subsequently develope. I think there can be no doubt that the pairs of parallel chromosomes which ~~are developed~~ can be quite clearly seen in the later stages of the prophase & during the metaphase are ~~derived from the segmentation of a spirem~~ which consists of two parallel halves.

~~I have still, however, to determine ~~however~~, the very important point of whether the two ~~halves of the spirem parallel elements of the s~~ halves of the spirem are derived from the splitting of an originally single thread or by the approximation of two separate & distinct threads. It is not unlikely that the latter alternative will prove to be ~~the~~ the correct one~~

The very important point, however, still remains to be determined, ~~of~~ whether the two parallel halves of the Spirem are derived from the splitting of an originally single thread or by the approximation of two separate + distinct threads.

In the light of what has been observed in other plants in which the chromosomes have been seen to originate from a double Spirem + from certain, as yet not very conclusive, indications in Equisetum itself, we may expect the latter ~~alternative to prove the correct one although it is~~ a point which is exceedingly difficult to determine in the present instance.

So far as they go, therefore, ~~&~~ my observations speak very decidedly against the ~~development~~ ~~occurrence of~~ origin of the chromosomes of this plant from the approximated sides of loops + they ~~[illegible]~~ agree much more nearly with the views of the Bonn + Louvain Schools.

~~[illegible]~~.

~~although this is a point which is exceedingly difficult to determine in the case of ~~those~~ ~~nuclei~~ Equisetum.~~
~~So far as they go, therefore, my observations distinctly favour the views held by the Bonn & Louvain Schools of Cytology regarding the development of the heterotypic chromosomes.~~

Another interesting feature which is very nicely shown in these nuclei is the fate of the chromosomes during the telophase of the division.
It will be recollected that until recently ~~the~~ most cytologists believed that ~~the~~ during the telophase of division the chromosomes became joined end to end & that the filament which was thus formed became gradually thinner & longer & coiled ~~through the~~ in every direction through the nuclear cavity. The coils anastomosed with one another so that finally the chromatic contents of the nucleus formed a reticulum.

Grégoire & his pupils have, however, shown that in several cases at any rate there is no such end to end arrangement of the chromosomes ~~at~~ during the reconstruction of the daughter nuclei. but that the chromosomes become united by lateral branches which are spun out between them & that at the same time they become more & more vacuolated. ~~So that the daughter nucleus the becomes~~ The resting daughter-nucleus, therefore, possesses an alveolar-reticulate structure.

The series of changes which the chromosomes undergo ~~in these cases~~ during the reconstruction of the daughter-nuclei in <u>Equisetum</u> are quite like those described by Grégoire. At the conclusion of the anaphase the chromosomes are seen to be very closely packed together. After the nuclear membrane is formed the chromosomes begin to separate from one another but at certain points their soft semi-fluid ~~solid~~ substance appears to remain adherent & branches or connecting arms are drawn out ~~present~~ between

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them at these spots. As the nuclear cavity enlarges & the chromosomes become more & more widely separated from one another the branches between them become proportionally longer & gradually the substance of the chromosomes appears to be lost in the series of reticulations which are in this manner spun out.

From what has been said it will be seen that there is a complete reconstruction of the daughter-nuclei at the conclusion of the first meiotic division. The second division calls for no special notice in this brief communication. It may be mentioned here that I can find no sufficient evidence of the degeneration of sporogenous tissue to possess any theoretical significance. It is true that in a few sections one or ~~[illegible]~~ perhaps two degenerating cells could occasionally be found but I am inclined to attribute their occurrence to peculiarities in the penetration of the fixing agent & I do not

~~(1) I have found nothing to compare with the extensive degeneration of sporogenous tissue described by Prof. Bower.~~

consider that any importance can be attached to them.(1) At the conclusion of the second meiotic division the spore-tetrads are completely separated from one another & are enveloped in the massive tapetal plasmodium.

~~In the~~ The young spores (or pollen-grains) of the ~~large~~ majority of plants which have ~~been~~ hitherto been examined are enclosed in temporary walls, ~~which~~ often of a mucilaginous nature, which the older botanists called the "special-mother-cell walls" & which ~~S~~ Strasburger has more accurately & concisely named the "special-walls".

~~It has given me no little trouble to decide whether these walls occur round the spores of Equisetum~~ Although the plasma-membrane limiting the spores of Equisetum often stains ~~&~~ rather deeply & (to some extent) simulates a membrane I have come to the conclusion, after a very careful examination of my preparations, that no special-~~membrane~~ wall is developed in this plant.

~~It is interesting to observe that a certain relation~~

(1) I have seen nothing to compare with the extensive (however) degeneration of sporogenous tissue described by Prof. Bower in Equisetum. I will discuss this matter ~~[illegible]~~, more fully ~~when I publish~~ in ~~a later com~~ a future communication when illustrations will be given.

This fact is of some interest because several other instances occur in which a very massive tapetal plasmodium is associated with the feeble development or entire absence of the special walls. The Ophioglossaceae furnish excellent examples of this relation between the two structures. *Arum maculatum*, among pollen-bearing plants, is another instance of the association of an exceptionally massive tapetal plasmodium with comparatively feebly developed special-walls.

In those plants, on the other hand, in which a secretion-tapetum occurs the special-wall is ~~[illegible]~~ seldom found wanting & is usually well developed. ~~Lycopodium & Isoetes among the Pteridophyta & Ipomaea~~

Lycopodium, *Isoetes* & *Ipomaea* are all rather striking examples ~~of this co-relation~~. in which a secretion-tapetum is accompanied by massive special-walls.

~~The~~ I believe that the explanation of this relation is to be found in the necessity for ~~protecting the spores in the case of~~ providing protection for the young spores in those cases in which a secretion-tapetum exists.

The soft mucilaginous special-walls, which usually form a more or less massive investment to the spore-elements in sporangia provided with secretion-tapeta, ~~form~~ serve as a moist packing round & between the spores which shield these bodies from mechanical shocks & jars & which, above all, protect them from ~~desiccation~~ too great a loss of water.

Moreover, whilst they carry out this protective function, ~~they~~ the special-walls are sufficiently extensible ~~not~~ to ~~interfere with~~ permit of the growth of the spore-protoplast & they do not interfere with the passage ~~through the~~ of the nutrient materials required ~~for the~~ by the developing spores.

In those sporangia in which a tapetal-plasmodium is ~~produced~~ formed at an early stage in development this ~~body~~ protoplasmic ~~naturally~~ investment ~~fulfills this protective function~~ sufficiently protects the young spores from mechanical injuries ~~or~~ & desiccation to render the additional formation of a massive special-wall unnecessary.

The young spores of the tetrad separate from one another & lie, still without any cell wall round them, ~~still without any cell wall round them~~ completely enveloped in the tapetal plasma.

After a short time a ~~delicate~~ cell-membrane is developed round the spore-protoplast & later ~~almost~~ ~~[illegible]~~ a delicate lamellum ~~pectic layer~~ is seen to line the tapetal vacuole in which the young spore lies.

The future history of these walls shows that the membrane round the spore is the exospore whilst the ~~tapetal~~ membrane ~~layer or pectic layer~~ formed by the tapetum is the "middle layer".

I differ from my predecessors, therefore, in ascribing the "middle layer" of these spore-walls to the secretory activity of the tapetal

-plasma. I can find absolutely no evidence to ~~show that a super~~ support the view that a superficial lamellum of the exospore is split off to form a "middle layer" or that this layer has any relation to the spore-protoplast. Neither can it be derived from the transformation of the special-walls, as some botanists have supposed, since this membrane does not occur in Equisetum.
Following the subsequent history of these spore-walls we find that the tapetal activity produces another layer of cell-wall which is formed on the outside of the "middle layer" & which now separates this from the protoplasm of the tapetum. We can, with the greatest certainty observe that this new layer becomes the elater of the mature spore. The final layer of the spore-coat to develope is the endospore which is produced within the exospore by the spore-protoplast.
It will be seen, therefore, that the conclusion

to be drawn from these observations is that the exospore & endospore are both products of the spore-protoplast whilst the "middle layer" & the elater are successively formed by the tapetal cytoplasm.

In conclusion I may point out that the ripe spore contains a very considerable quantity of chlorophyll in its protoplast & also that when these spores are heated with concentrated ~~sulphuric acid on a cover glass~~ very pretty silicic ~~skelef~~ skeletons are left behind.

I have given above a brief outline of some ~~of the~~ features in the development of these spores but a fuller account with illustrations will be published ~~shortly~~ later. ~~This study~~ These observations ~~for a portion of the~~ were greatly facilitated by a Government Grant.

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