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NEW PHYTOLOGIST.

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ON STIMULUS AND MECHANISM AS FACTORS IN ORGANISATION.[1]

BY J. BRETLAND FARMER, F.R.S.

I SUPPOSE it may be taken for granted that in the study of plants, as in other sciences, the ultimate aim of all enquiry is to establish a clear connection between cause and effect. The earlier stages in the enquiry consist in describing and classifying the effects or phenomena themselves, but there are probably few investigators who remain content with these efforts alone. In order to gain a wide comprehension of the phenomena it is essential that the factors that underly them shall be convertible into chemical and physical expressions, since in this way only is there any apparent chance of penetrating the temple in which the secrets of life are so securely guarded,

It must be confessed that most of the attempts in this direction have met with but scant measure of success. The hypotheses have often turned out to be erroneous and the theories destitute of any solid basis. But this circumstance does not affect the essence of the enquiry, nor indeed even its method. It is—or ought to be—a truism that the value of any hypothesis stands not in a necessarily direct relation to its final correctness, but rather depends upon the extent to which it welds together, even temporarily, cognate facts so as to suggest new lines of enquiry. No one doubts the value of the atomic theory, though of late there have not been wanting numerous assailants of this fundamental doctrine; and although perhaps few naturalists would be prepared to assert to-day with the same confidence that would have shown twenty years ago, that we have got to the bottom of the question as to the origin of species, nevertheless, history will assuredly preserve the great Darwinian Theory as one of the most precious landmarks in the advance of science and philosophy, whether it should ultimately turn out that

[1] A lecture delivered before Section K of the British Association, Southport, 1903.

comes to occupy a central position in the cell-cavity. At maturity of the cell this *primary nucleus* divides into two daughter-nuclei, each of which travels to one end of the sac. Then each divides by two successive divisions until four nuclei are formed at each end of the sac. One of these four from each end then travels to the centre of the sac, and, sometimes before, sometimes after, fertilisation takes place, these two *polar nuclei* fuse together to form the *definitive* or *secondary nucleus* of the embryo-sac. Meanwhile, each of the three nuclei at the micropylar end of the sac becomes invested with protoplasm enclosed by a delicate membrane; a pair of these cells, usually somewhat elongated, at the extreme end of the sac become the *synergidae*, while the third and larger cell becomes the *oosphere* or egg-cell. At the chalazal end of the sac three antipodal cells are formed, and these are often much more conspicuous than the cells at the micropylar end.

Hofmeister[1] considered that all the nuclei of the sac possessed primitively the same value and any one of them could develope into an embryo. The sole function of the antipodals was that of elaborating substances for the embryo.

Vesque[2] and Warming[3] both regarded the embryo-sac as the product of fusion of two cells, and the four nuclei finally formed at each end of the sac were the representatives of the spores resulting from the divisions of these two spore-mother-cells.

Guignard[4] held that all the cells in the sac were endosperm-cells; that the oosphere was a reduced archegonium; that the synergidae were endosperm-cells which had become adapted to a new function; and that the antipodals are either an organic residuum of the sac or a reduced prothallus; but he eventually regarded the prothallus as consisting of the sexual apparatus, antipodals and the two polar-nuclei.

Hartog[5] believed that, as a result of two successive divisions of

[1] "Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen"; (Abhandl. d. Königl. Gesellsch. d. Wiss.; Vol. v., p. 671).

[2] "Développement du sac embryonnaire des Phanérogames Angiospermes"; Ann. d. Sciences Nat. Bot., ser. 6, Vol. vi., 1878.
"Nouvelles recherches sur le développement du sac embryonnaire"; Ditto, ser. 6., Vol. viii., 1879.

[3] "Bemerkungen über das Eichen"; Bot. Zeit. 1874.
De l' Ovule"; Ann. d. Sci. Nat. Bot. ser. 6, Vol. v., 1878.
Bull. de la Soc. Bot. de France, Vol. xxviii., 1881.
Ann. d. Sci. Nat. Bot. ser. 6, Vol. xii., 1881.
Ann. d. Sci. Nat. Bot. ser. 6, Vol. xiii., 1882.

[5] "Some Problems of Reproduction: a Comparative Study of Gametogeny and Protoplasmic Senescence and Rejuvenescence." (Quart. Journal Microx. Science, Vol. xi., 1891).

the primary nucleus of the sac: "four prothallial cells are formed; of these two in the mean position [the mother-cells of the oosphere and upper polar-nucleus and of the uppermost antipodal and lower polar-nucleus respectively] are gametogonia, which by a mitotic division form four gametes, three functional, one arrested. The apical cell [of the original four] forms an archegonium reduced to a two-cellular neck [synergidae]; the basal cell forms two cells constituting a barren archegonium or mere prothallial cells" [the two lower antipodals]. The definitive or endosperm-nucleus he regards as a zygote formed by fusion of two gametes: the two polar nuclei.

Nawaschin in 1898 published the following epoch-making observations: that whenever a pollen-tube was seen in contact with the embryo-sac *both* male nuclei were observed in the latter, were seen to have an almost cylindric long-club-shaped appearance, and to exhibit a worm-like contortion; they lay free in the sac and so close together as to appear like a single body. One of these two nuclei travelled to the ovum, the other to the upper polar-nucleus, to which latter it became applied; both nuclei retained their worm-like character. During the time that the one male nucleus was becoming more and more closely applied to the ovum, the polar-nucleus, along with the second male nucleus with which it was in contact, travelled to the other polar-nucleus and became attached to the latter in the middle of the sac. All the nuclei remained separate and distinct until the prophases of their division. The second male nucleus, which by this time had lost its worm-like shape, was smaller, richer in chromatin, and possessed a coarser chromatin net-work than the polar nuclei, the lower of which latter is considerably larger than the upper. The character of the separate nuclei and composition of the nuclear groups were observed in a great number of fertilised ovules, so that there can be no doubt of the phenomenon being a constant one. Fusion of the three nuclei took place only after the prophases of division were completed; the same being true with regard to the fusion of the other male nucleus with that of the ovum. The formation both of the embryo and the endosperm was normal; in *Fritillaria tenella* the embryo, after reaching one-third of its size, died away, and the endosperm became absorbed. The ripe seed of *Lilium Martagon* contained a normal embryo. Nawaschin believed that, from the peculiar shape of the two male nuclei in these plants, they possess an independent movement like that of worms.

His theoretical conclusion with regard to these phenomena is that we have before us in these plants a species of *polyembryony*, in the form of a pair of twin-embryos exhibiting a very dissimilar and unequal development, the one remaining thallus-like, in the form of the endosperm, and becoming eventually absorbed by the other. His view is based on the fact that the normal endosperm arises as the result of the fusion of one of the male nuclei with the *sister-cell of the ovum, i.e.*, with one of the female nuclei; and that therefore we have as much right tospeak of this fusion as a *sexual act* as in the case of the actual process of fertilisation itself. At a somewhat later date Nawaschin[1] observed "double fertilisation" in certain Dicotyledons. In the case of *Helianthus* the male nuclei were seen greatly to resemble spermatozoids, the polar nuclei were observed to fuse *before* fertilisation of the ovum, and the product of this fusion—the embryo-sac-nucleus—after copulation with the second spermatozoid was seen to divide rather earlier than was the case with the fertilised oosphere. In *Rudbeckia* similar phenomena occurred. Fusion of the polar-nuclei before fertilisation of the ovum was also observed in *Delphinium elatum*. It is an interesting fact that Merrel found elongated, spirally-twisted bodies (=spermatozoids) in the pollen grain of the Composite, *Silphium*.

Guignard essentially confirms Nawaschin's observations. He states as a result of his own labours on *Lilium Martagon* that union of both polar nuclei may precede their fusion with the vermiform sperm-nucleus and that the latter may subsequently become applied to *both* polar nuclei, but in some cases the sperm-nucleus was observed to fuse primarily with the antipodal polar-nucleus; more frequently however, copulation with the egg-polar-nucleus is the first process, because the latter is the first of the two met with by the sperm-nucleus as it passes down the sac. Guignard regards, in contradistinction to Nawaschin's view, the union or fusion of the sperm-nucleus with the polar nuclei as a case of *pseudo-fertilisation*, on the following grounds. In *true* fertilisation both sexual nuclei have the same reduced number of chromosomes, whilst the lower polar nucleus, as at any rate is known to be the case in *Lilium*, contributes a larger number of chromosomes to the fusion, with the result that the product of copulation of sperm and polar-nuclei possesses a greater number of chromosomes than does the fertilised ovum.

[1] "Ueber die Befruchtungsvorgänge bei einigen Dicotyledoneun" (Berichte der deutsch. Bot. Gesellschaft, vol. 18, 1900).

Some further observations by Guignard[1] on *Tulipa Celsiana* and *T. sylvestris* revealed the fact that the various nuclei of the embryo-sac in these two plants were very irregularly arranged and more or less similar in appearance. The lower polar nucleus, which is morphologically different from the upper one, being often larger and with denser granulations, is situated at the base of the sac, below the antipodal nuclei. The antherozoids are elongated, but not spirally twisted, and are both equivalent. The oosphere is first fertilised. The second sperm-nucleus was seen fusing with the upper of the two polar-nuclei, hence union between these latter is a late occurrence in these plants. The second sperm-nucleus and the two polar nuclei fuse together as three distinct individualities, which gradually become less and less marked and finally vanish. He observed that at the moment of division of the fertilised ovum the sac contained four endosperm-nuclei. The phenomena above described hold good for the two species mentioned; but the different races of cultivated Tulips, on the contrary, agree in this respect with the Lily and *Fritillaria*.

This author further observed[2] "double fertilisation" in several other orders of plants, such as Compositae, of which five or six genera were investigated, with the result that his obervations largely coincided with those of Nawaschin on *Rudbeckia*. In Ranunculaceae[3] the genera *Caltha*, *Ranunculus*, *Helleborus*, *Anemone*, *Clematis* and *Nigella* were examined. The two male-nuclei in these plants are spindle-shaped while within the pollen-tube, becoming elongated as they pass into the sac; they rapidly fuse with the two nuclei of the sac. In *Nigella damascena* the larger size of the male nucleus which fuses with secondary nucleus of the sac is correlated with the fact that the latter divides *before* the fertilised ovum. At the time of endosperm-formation the fusion of the male and female nuclei in the oosphere is not completed, and even after fifty endosperm-nuclei are formed in the sac the ovum remains still undivided. The same phenomenon was observed in *Anemone nemorosa*. Quite recently[4] the order Cruciferae revealed the same

[1] "L'appareil sexual and la double fécondation dans les tulipes" (Annales des sciences naturelles, ser. 8, vol. xi., 1900.

[2] "Nouvelles recherches sur la double fécondation chez les végétaux angiospermes" (Comptes Rendus de l'Acad, des Sciences, vol. 131, 1900).

[3] "La double fécondation chez les Renonculacées" (Journal de Botanique, Dec. 1901).

[4] "La double fécondation chez les Crucifères" (Journal de Botanique, Nov. 1902).

phenomenon of "double fertilisation" which is probably of universal occurrence in Angiosperms. In *Capsella* fusion of the polar-nuclei was observed to take place at a very late period, yet division of the fertilised secondary nucleus was sometimes seen to be well-nigh complete while the other antherozoid is still in contact with the nucleus of the oosphere. Division of the ovum occurs after formation of the first four endosperm-nuclei. In *Lepidium* there is a slightly earlier fusion of the polar-nuclei.

But Miss Ethel N. Thomas[1] distinguished herself through being the first to publish an account of the process of "double fertilisation" in Dicotyledons, an undertaking to which she was prompted by Miss Ethel Sargant, who had, by her own original observations, confirmed the work of Nawaschin and Guignard on the Liliaceae. Miss Thomas found that in *Caltha palustris* the two polar-nuclei were usually completely fused before the entrance of the pollen-tube. The generative nuclei when emitted are very minute and are either oblong, or lens,-dumb-bell-, or straight S-shaped. She received the impression that the first generative nucleus emitted was the one which fertilised the polar-nuclei, for the latter process always appeared to be much more advanced than that of the fertilisation of the oosphere, and she suggests that this may partly account for the fact of the phenomenon being overlooked for so long. The vermiform nucleus which fertilises the polar nuclei, increases greatly in size, while this is not the case with the other sperm-nucleus.

The epoch-making experiments on the *hybrid fertilisation of endosperm* conducted by De Vries[2] in 1898 afford a most striking illustration of the reality, and, in certain cases, the far-reaching consequences of the phenomenon of "double fertilisation," this latter, indeed, alone affording an explanation of the facts involved in those experiments. De Vries in 1898 possessed forty specimens of the variety of the Maize-plant whose grains contain a *sugary* endosperm; in the following year he obtained from these grains a second generation of sixty plants producing sixty-seven spikes full of grains all containing sugar only. It is therefore clear that the plants destined for his experiments, being the offspring of the same original lot, would, if fertilised with their own pollen, have yielded pure spikes of sugared grains. The hybrid fertilisation took place in August, 1898. At the beginning of the month, before flowering

[1] "On the Presence of Vermiform Nuclei in a Dicotyledon." — "Double Fertilisation in a Dicotyledon—*Caltha palustris*" (Annals of Botany, Sept. 1902).

[2] "Sur la fécondation hybride de l'endosperme chez le Mais" Revue générale de Bot., vol. xii, 1900).

took place, he cut off the greater part of each male infloresence. On emergence of the stigmas from their bracts he powdered them at intervals with pollen of a variety of Maize possessing grains with *starchy* endosperm, yet without entirely preventing fertilisation by the pollen emanating from the lower branches of their own male inflorescences. The result was ten large spikes full of grains. Each spike bore two kinds of grains, the greater number being starchy like the father, the remainder sugary like the mother. These last were largely due to auto-fertilisation, which was proved by sowing a portion of them in 1899, when they reproduced the sugary variety of the mother. The starchy grains were *hybrids, as well in their endosperms as in their embryos.* The endosperm exhibited entirely the character of the father, being well filled with starch and containing no visible trace of sugar, being a chalky-white within, and having a smooth external surface, without the wrinkles so characteristic of the grains of the sugary variety. It was clear that these paternal characters had been communicated by the second spermatozoid of the pollen-tube. In order to prove the hybrid nature of the *embryos* of these grains he sowed a portion of them in 1899 and allowed the plants to be fertilised by their own pollen. He obtained a crop of thirty-two plants yielding thirty-five spikes, rich in grains All these spikes were of mixed nature, about a quarter of the grains were sugary, the three remaining quarters being starchy; the former had reverted to the character of the grandmother, the latter exhibited that of the father and grandfather. The starchy grains of his crossed spikes of 1898 were therefore hybrids, capable of reproducing the types of their two parents. In all these spikes there occurred no grains of intermediate character, half sugary, and half starchy.

W. O. Focke, in his great work "Die Pflanzenmischlinge," which contains a résumé of all the experiments conducted by Körnicke, F. Hildebrand and De Vries, proposed the term "xenia" for all cases in which an influence of the pollen on the hereditary characters of the fruit or grain *outside the embryo* has been either determined or presumed. About the same time as, or a little later than De Vries' work, some detailed investigations and experiments were carried out by Correns,[1] as a result of which he established several valuable and important corollaries for which we have no space here. He at first imagined that xenia was due to a fusion of *half the generative nucleus* (as a result of division of the latter) with

[1] "Untersuchungen über die Xenien bei *Zea Mais*" (Berichte der deutsch. bot. Gesellschaft, 1899), etc.