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XLIV.—On the Plurality and Development of the Embryos in the Seeds of Coniferæ

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but the bill, in addition to the feature pointed out above, is of a more slender and attenuated form than is observable in any other.

XLIV.—*On the Plurality and Development of the Embryos in the Seeds of Coniferæ.* By ROBERT BROWN, Esq., F.R.S., F.L.S., and Foreign Member of the Academy of Sciences in the Institute of France*.

[With a Plate.]

THE following short paper on a subject which I intend to treat at greater length, contains a few facts of sufficient interest perhaps to admit of its being received as a communication to the present meeting.

In my observations on the structure of the female flower in *Cycadææ* and *Coniferæ*, published in 1826†, I endeavoured to prove that in these two families of plants the ovulum was in no stage inclosed in an ovarium, but was exposed directly to the action of the pollen.

In support of this opinion, which has since been generally, though I believe not universally adopted, the exact resemblance between the organ until then termed ovarium in these two families, and the ovulum in other phænogamous plants, was particularly insisted on; and I at the same time referred, though with less confidence, to their agreement in the more important changes consequent to fecundation.

I noticed also the singular fact of the constant plurality of embryos in the impregnated ovula of *Cycadææ*, and the not unfrequent occurrence of a similar structure in *Coniferæ*. In continuing this investigation, in the course of the same summer in which the essay referred to appeared, it seemed probable, from the examination of several species of the Linnæan genus *Pinus*, namely, *Pinus Abies*, *Strobus* and *Larix*, that the plurality and regular arrangement of embryos were as constant in *Coniferæ* as in *Cycadææ*; for in all the species of *Pinus* here referred to, the preparation for the production of several embryos was equally manifest, and the points or areolæ of production were in like manner disposed in a single circular series at the upper extremity of the amnios.

From these observations, which I have since confirmed in the same and also in other species of *Pinus*, an additional and important point of resemblance is established between *Cycadææ* and

* Read before the British Association at Edinburgh in August 1834, and published in the *Annales des Sciences Naturelles* for October 1813.

† In the Appendix to Capt. King's Voyage.

Coniferæ; and it is worthy of remark, that while the female organ in these two families exists in a simpler form than in other phænogamous plants, the normal state of the impregnated ovulum is much more complex, and might even be considered as compound, or made up of the essential parts of several confluent ovula.

On considering the well-known œconomy of several *Coniferæ*, and especially of the genus *Pinus*, as at present limited, namely in their requiring (at least) two seasons to ripen their cones, it occurred to me that these plants, from the extreme slowness in the process of maturation, conjoined with the considerable size of their seeds, and also from the striking peculiarity already noticed, were probably the best adapted for an investigation into the origin and successive changes of the vegetable embryo.

With this view chiefly I commenced in the present summer (1834) a series of observations, intending to follow them up from the period when the enlargement of the impregnated cone begins to take place, to its complete maturity at the end of the second or beginning of the third year.

Pinus sylvestris was selected for this purpose, corresponding observations being also made on other species, particularly *Pinaster* and *Strobus*; and although the investigation is necessarily incomplete, the facts already ascertained appear to me of sufficient importance to be submitted to physiological botanists.

In an essay on the organs and mode of fecundation in *Orchideæ* and *Asclepiadeæ*, published in 1831, I have given some account of the earliest changes observable in the impregnated ovulum of the former family; and in noticing the jointed thread or single series of cells by which the embryo is suspended, I remarked that the terminating cell or joint of this thread is probably the original state of what afterwards, from enlargement, subdivision of its cavity, and deposition of granular matter in its cells, becomes the more manifest rudiment of the future embryo.

I had not indeed actually seen this joint in its supposed earliest state; the following observations on *Pinus*, however, will perhaps be considered as giving additional probability to the conjecture.

But before entering on my account of the origin and development of the embryo in *Pinus*, I shall state briefly the still earlier changes consequent to impregnation that take place in this genus; not only with a view of rendering the account of the embryo itself more readily intelligible, but also in confirmation of the opinion formerly advanced on the nature of the female organ in *Coniferæ* and *Cycadeæ*.

The first and most evident change observable is the production or separation of a distinct body within the nucleus of the ovulum, which, before impregnation, is a solid uniform substance.

In this stage the upper extremity of the included body, or amnios, is slightly concave, and has a more or less rough or unequal surface; the inequality being in consequence of the laceration of the cellular tissue, by which it was in its early stage attached to the apex of the original nucleus, or rather to a short cylindrical process arising from it and corresponding in size and form with this concave upper extremity, from which it separates when the amnios has attained its full size.

On this concave upper extremity of the amnios a few minute points of a deeper colour, and disposed in a single circular series, are sometimes observable; in general, however, they are hardly to be distinguished.

Below the concave apex the amnios itself is slightly transparent for about one-fourth of its length, the remaining portion being entirely opaque.

On dividing the whole longitudinally it is found to consist of a pulpy cellular substance, in which no definite cavity is originally observable; the upper transparent portion is however of a looser texture, and on the included embryos becoming manifest, a cavity irregular both in figure and extent is formed in its centre.

But before the embryos themselves or their funiculi become manifest, the areolæ, or portions of the substance destined for their production, are visible.

These areolæ, as I observed them in the common larch in May 1827, are from three to five in number, of nearly cylindrical form, arranged in a circular or elliptical series, and are seated near the apex, with which they probably communicate by the similarly arranged points of its surface already noticed.

In the amnios of *Pinus sylvestris*, as observed in June and July last, the corresponding parts were found considerably more advanced. In the specimens then examined, the remains of the embryoniferous areolæ, from four to six in number, were still visible, but consisting of conical membranes of a brown colour, presenting their acute apices towards the surface, and at the base seeming to pass gradually into the lighter-coloured pulpy substance of which the mass of the amnios consists.

Corresponding and nearly approximated to each of these conical membranes, a filament, generally of great length, and either entirely simple or giving off a few lateral branches, was found. This filament or funiculus consisted generally of four series of elongated transparent cells or vessels, usually adhering together with firmness, but in some cases readily separable without laceration; and in one of the species examined, *Pinus Pinaster*, the transverse septa of the funiculus were either very obscure or altogether wanting.

The upper extremity of each funiculus was in all cases manifestly thickened and of a depressed spheroidal form; and in each of the four cells or vessels of which it consisted exhibited a small opaque areola analogous to the nucleus of the cell, so frequently observable in the tissue of Monocotyledonous plants, and which also exists, though less commonly, in Dicotyledones.

A lacerated and extremely transparent membrane was generally found surrounding and adhering to the thickened origin or head of the funiculus.

In the earliest state examined of *Pinus Pinaster*, the funiculus was found equally transparent through its whole length, and having no appearance of subdivision or any other indication of embryo at its lower extremity. In a somewhat more advanced state of the same plant, as well as in the two other species observed, namely *Pinus sylvestris* and *Strobus*, the lower extremity of the funiculus was subdivided into short cells, sometimes disposed in a double series, but more frequently with less regularity and in greater numbers, the lowest being in all cases the most minute and also the most opaque, from the deposition of granular matter, which is nearly or entirely wanting in the upper part of the cord. This opaque granular extremity of the funiculus is evidently the rudiment of an embryo. When the funiculus ramifies, each branch is generally terminated by a similar rudiment, and these lateral embryoniferous branches not unfrequently consist of a single vessel or cell, while the embryo of the trunk or principal branch is as generally derived from more than one.

That each of these opaque bodies terminating the trunk and branches of the funiculi are really rudimentary embryos, is proved by tracing them from their absolutely simple state to that in which the divisions of the lower extremity become visible, and those again into the perfect cotyledons.

The results of this investigation in its present incomplete state are, 1st, that the plurality of rudimentary embryos in *Pinus* (and probably in other *Coniferæ*) is not only constant, but much greater than could well have been imagined independent of actual observation; each impregnated ovulum not only containing several distinct funiculi, but each funiculus being capable of producing several embryos. In the ripe seed, however, it is a rare occurrence to find more than one of these embryos perfected.

2ndly. That an embryo in *Coniferæ* may originate in one or in more than one cell or vessel even in the same cord; and it also appears that the lower extremity of the funiculus, the seat of the future embryo, is originally in no respect different from the rest of its substance.

The greater part of the appearances now described are represented in the accompanying Plate.

April 20, 1844.

POSTSCRIPT.—It is necessary to notice the recent publication of a very important memoir by MM. de Mirbel and Spach on the development of the embryo in *Coniferæ**.

These excellent observers confirm the principal statements of the preceding essay, with the brief abstract of which only they were acquainted.

They have also extended the investigation to *Thuja* and *Taxus*, two genera which I had not examined, and in which, especially in the latter, the structure appears to be remarkably modified; and they have ascertained some points in *Pinus* itself that I had overlooked.

In this memoir M. de Mirbel refers to his early observations on the structure of the seeds of *Cycas* which occur in an essay read before the Academy of Sciences in October 1810, and soon after published in the 'Annales du Muséum'†.

These observations and the figures illustrating them clearly prove M. de Mirbel's knowledge of the plurality of embryos in *Cycas* at that period. And in his recent memoir on *Coniferæ* he regards them as giving the earliest notice of that remarkable structure; stating also that my first publication on the same subject was in 1835.

But as the 'Prodromus Floræ Novæ Hollandiæ' was published before M. de Mirbel's essay in the 'Annales du Muséum,' which appears from his references to that work in the essay in question, he must have overlooked the following passages:—

"In Cycadi angulata puncta arcæ depressæ apicis seminis totidem canalibus brevibus respondent gelatina homogenea primum repletis et membrana propria instructis, unico quantum observavius embryonifero, quo augente reliqui mox oblitterati sunt."—*Prodr.* p. 347.

"Structura huic omnino similis haecenus absque exemplo nec ulla analoga (nempe embryones plures in distinctis cavitatibus ejusdem albuminis) nisi in Cycadi et nonnunquam in Visco cognita sit."—*Prodr.* p. 307.

I may add, that this structure of *Cycas* was ascertained in living plants on the east and north coasts of New Holland in 1802 and 1803.

The earliest observer of the principal fact, however, was probably the late Aubert du Petit Thouars, who in a dissertation on the structure and affinities of *Cycas* published in 1804‡, distinctly notices the points on the surface and the corresponding corpuscula within the apex of the albumen, into which corpuscula he

* Annales des Sc. Nat. 2 série, November 1843.

† Annales du Muséum d'Hist. Nat. tom. xvi. p. 452. tab. 20.

‡ Histoire des Végétaux des Iles d'Afrique, p. 9. tab. 2. n.

hazards the conjecture that the grains of pollen enter and become the future embryos. This, in regard to *Cycas*, might be considered the revival of the general hypothesis advanced by Morland in 1703*, and some years afterwards adopted, but without acknowledgement, by C. J. Geoffroy†, and which seems to have entirely originated in the discovery by Grew of the existence of a foramen opposite to the radicle of the embryo in the ripe seeds of some Leguminous plants‡.

But as M. du Petit Thouars had evidently no intention of extending his hypothesis beyond *Cycas* and probably *Zamia*, it can hardly be said to anticipate the general and ingeniously supported theory of Dr. Schleiden, respecting which physiological botanists are at present almost equally divided. On this theory it is not my intention at present to express an opinion; nor did the question of the mode of action of the pollen form any part of my object in the preceding essay. I shall only here remark, that according to the latest statements of Dr. Schleiden with which I am acquainted§, although he admits that his investigation is not in all points complete, he seems to have no doubt that his theory of the origin of the vegetable embryo in the pollen tube is applicable to *Coniferæ*. He has in the first place ascertained the existence of my areolæ or corpuscula, which he denominates large cells in the embryo-sac or albumen, in all the European genera of *Coniferæ*||; and in *Abies excelsa*, *Taxus baccata*, and *Juniperus Sabina*, he states that he has succeeded in preparing free the whole pollen tubes from the nucleary papillæ to the bottom of the corpuscula. But as (if my observations are correct, and they seem to be confirmed by those of M. de Mirbel) the corpuscula are not developed in *Pinus*, as the genus is at present limited, until the spring or even beginning of summer of the year after flowering, and if Dr. Schleiden's statement be also correct, the pollen must remain inactive for at least twelve months.

The quiescent state of pollen for so long a time is indeed not altogether improbable on considering the analogous œconomy in several tribes of insects, in some of which the male fluid remains inactive in the female for a still longer period¶; and in plants, though for a much shorter period, I may refer to *Goodenoriæ*, in which the pollen is applied to the stigma a considerable time before that organ is sufficiently developed to act upon or transmit its influence**. But the supposed protracted state of inactivity

* Philosophical Transactions, vol. xxiii. part 2. n. 287. p. 1474.

† Mém. de l'Acad. des Sc. de Paris, 1711, p. 210.

‡ Anat. of Plants, p. 2. § Schleiden, Grund. der Bot. 2 Theil, p. 374.

|| Op. cit. pp. 354 et 357.

¶ Herold. Entwickel. der Schmetterl. &c. 1815, et Siebold in Müller's Archiv, 1837, p. 392.

** Append. to Flinders's Austral. p. 560.

in the pollen of *Pinus* does not necessarily lead to the adoption of Dr. Schleiden's theory. With respect to *Cycadeæ*, whatever opinion may be adopted as to the precise mode of action of the pollen in that family, it is certain that the mere enlargement of the fruit, the consolidation of albumen, and the complete formation of the corpuscula in its apex are wholly independent of male influence, as I have proved in cases where pollen could not have been applied, namely, in plants both of *Cycas* and *Zamia* (*Encephalartos*) producing female flowers in England at a time when male flowers were not known to exist in the country.

EXPLANATION OF PLATE VII.

Fig. 1. A scale of the cone of *Pinus sylvestris*, with its winged seeds, one of which is abortive: natural size.

N.B. The remaining figures are more or less magnified.

Fig. 2. An unripe seed, of which the testa, in this state cartilaginous, is cut open, partly removed and thrown back to show the included body, which is the half-ripe original nucleus with its sphacelated apex and the free portion of the inner coat, extending from the apex to about one-third of the length of the nucleus, below which it is intimately connected with and inseparable from the outer coat.

Fig. 3. The amnios or albumen, with the coats opened and laid back.

a. The body of the albumen, with its slightly concave upper extremity: in this stage separated from *b*, the apex, which is conical above, below cylindrical, and which was suspended from the top of the original nucleus.

Fig. 4. A plan rather than actual representation of a longitudinal section of any one seed examined, but the parts accurately copied from the calyptraform membranes, the funiculi or suspensors, and the nascent embryos of seeds of *Pinus sylvestris*.

In this stage the funiculi are distinct from the calyptraform membranes within which they originated.

Fig. 5. is also a plan of the slightly concave apex of the amnios or albumen, with its semitransparent points or pores circularly arranged; in this species (*Pinus sylvestris*) seldom exceeding five, and not unfrequently being only four or even three.

Fig. 6. One of the funiculi or suspensors, with its dilated upper extremity, to which the lacerated remains of a thin transparent membrane adhere: the funiculus itself ramified, each of the two lateral branches consisting of a single elongated tube or cell terminating in a rudimentary embryo: the trunk of the funiculus composed of several (apparently four) tubes or cells terminated by a single embryo, which is already slightly divided, the divisions being the commencement of its cotyledons.

Figs. 7 and 8. Two other funiculi belonging to the same seed less advanced, but both ramified.

Fig. 9. A funiculus of *Pinus pinaster* with its thickened head, in which the nuclei of its component elongated cells or tubes, and its adhering lacerated membrane are visible. The figure is given particularly to show that in this (the only one observed) there is no opaque granular portion of the compound funiculus; in other words, no indication of a nascent embryo.

Fig. 10. A funiculus of *Pinus Abies*, Linn., with its rudimentary embryo and thickened head, still partly inclosed in the calyptraform membrane.