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VII. *On the Embryogeny of Hippuris vulgaris.* By JOHN SCOTT SANDERSON, F.B.S.E., Member of the Royal Medical Society of Edinburgh.

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THE subject of the origin and development of the embryo has been lately brought before botanical readers so frequently in the various journals appropriated to vegetable physiology, and so much has been done by so many observers in the elucidation of the subject, that it must appear somewhat uncalled for to occupy your time with facts and observations which are only repetitions of what has been much better detailed by others in regard to other species, and by which therefore these results can only be corroborated.

As however the observations referred to are contained in foreign journals, and may have escaped the notice of many members whose attention has not been directed to this particular branch of botanical science, I trust that the following details will not prove wholly unacceptable, more especially as they will enable me to lay before you some of those highly important generalizations, which are to be obtained from the splendid researches of Hofmeister, Unger, Tulasne, and others, on the subject of embryogeny. We shall see as we proceed, that we are now enabled to construct a morphological type of development complete in all its parts, and applicable to all the hitherto investigated orders of phanerogamous plants.

Hippuris vulgaris belongs to the natural order *Haloragaceæ*, which contains only three British genera, *Myriophyllum*, *Hippuris* and *Callitriche*, all the species of which are water-plants with floating and submerged leaves. They appear to be distinguished by their submerged leaves possessing distinct bundles of spiral vessels, a fact which may be well seen in the common *Callitriche verna*, and has been lately shown by Barnéoud in those curious plants the *Trapas* which float on the rivers of Southern Europe, and are considered by many botanists as belonging to this order.

The ovary of *Hippuris* is one-celled, containing a single pen-

dulous ovule, attached nearly at its apex by a fleshy funiculus. In its earliest condition I have not had an opportunity of examining it. If however it be examined at a period considerably before that of impregnation and before the development of the solitary anther is completed, it is observed to have become completely anatropous. The nucleus lies loosely in the cavity formed by the envelopes, which completely surround it, attached to the chalaza. The envelope is not distinguishable into primine and secundine, and extends considerably beyond the apex. It consists of small hexagonal cells arranged in series, each containing a nucleus. On one side, the raphe, consisting of a bundle of imperfect spirals, is seen passing from the hilum to the chalaza.

The nucleus, the structure of which cannot be seen on account of the opacity of the envelopes without dissecting it out, consists of a large cell, the embryonic vesicle, extending from its apex to about two-thirds of its length, which is surrounded by a single layer of very transparent, gelatinous-looking nucleated cells, which are however deficient at the apex, at which point the embryo-sac seems to be totally uncovered.

Contained in this embryo-sac is seen the embryo-vesicle. This body consists of a single elongated cell attached to the free extremity of the embryo-sac. This cell (the embryo-vesicle) contains a granular protoplasm in which here and there globules are observed to float. It probably originates at a very early period from the micropyle-end of the embryo-sac, but I have not been able to trace it at any earlier stage than that represented. The form which it presents, of an elongated cell attached to the end of the embryo-sac next the micropyle, and smaller at its attached than at its free extremity, is prevalent throughout the *Scrophulariaceæ*, *Cruciferae*, and other orders.

From the fact that the embryo-vesicle is developed at so long a period before the bursting of the anther, little doubt can remain as to its existing prior to the act of impregnation, and not being, as supposed by Mirbel and Spach, a consequence of that act. Still less can it be supposed to be the end of the pollen-tube, according to the theory of Schleiden and his followers.

We now proceed to notice the changes which the embryo-vesicle undergoes subsequently to the act of impregnation. After impregnation, the granular protoplasm, which has accumulated at the larger extremity of the embryo-vesicle, becomes transformed into a spheroidal cell. A septum is then observable at the lower part, crossing it horizontally, by which it is divided into two cells. Of these the inferior is developed downwards by successive merismatic division, so as to form a confervoid filament, the suspensor. The upper assumes at the same time a

spheroidal form, and is distinguished from the rest by being filled with granules, exactly as occurs in the *Orchidaceæ*. Soon after it divides by a longitudinal septum, and subsequently by a transverse. These are followed by successive divisions, and the embryo with its suspensor is formed. While these changes are taking place, the embryo-vesicle, which in the early stage is adherent by one of its extremities to the micropyle-end of the embryo-sac, becomes correspondingly enlarged and elongated. It however never becomes completely filled with the cells of the suspensor, or at least not until a very late period. It seems to be narrowed at its apex, either by the absorption of its contents by the developing embryo, or by the pressure of the contiguous parts. Subsequently the round mass of cells described above, to which the term *embryo-globule* has been applied, undergoes further development, and the cotyledons and other parts being gradually formed, the embryo assumes its characteristic appearance.

Thus we see in this plant—1st. That the embryo-vesicle exists at a period previous to the act of impregnation; 2nd. That after impregnation a number of cells are formed by an endogenous process in its cavity which assume a confervoid arrangement; 3rd. That of these one is selected to be developed into the embryo; 4th. That the rest undergo no further development, but seem to conduce to the nutrition of the embryo. These facts are in every respect conformable to what is known of the embryogenic process in the *Orchidaceæ*, *Onagraceæ*, *Scrophulariaceæ*, *Cruciferae*, and other natural orders.

Since the above observations were made, I have had the opportunity of seeing the results of two very important series of researches by Hofmeister, of Leipzig and Tulasne. These researches lead to the conclusion, that the mode of development above described in *Hippuris* is that which holds universally throughout phanerogamic plants. The results of Hofmeister, as detailed in his Monograph on the origin of the vegetable embryo, published at Leipzig last year, are as follows:—

A long time previous to the period of fecundation a certain number of free cellular nuclei are formed in the embryo-sac. These generally occur at the end of the sac next the micropyle. After this, free spherical cells are observed to be formed at the same part of the embryo-sac, which are usually three in number, an arrangement which probably depends on merely mechanical causes, and is well seen in the *Orchidaceæ*.

These cells are destined for the formation of the embryo itself, and are to be distinguished from those of a smaller size which are often observed at the same period at the opposite extremity of the embryo-sac, and conduce merely to the formation of the endosperm.

These cells are the embryo-vesicles, and from them the embryo is produced. One of them only remains active, while the rest abort. This being acted on by the fovilla at the period of fecundation, undergoes the development detailed below and becomes the embryo.

At the period of impregnation the pollen-tube arrives at the embryo-sac. Sometimes the sac-membrane is so firm as not to be indented by it. Sometimes it is considerably indented, and adherent for a longer or shorter period. At other times it appears, from its great tenuity, to be pierced by it. In all cases the embryo-vesicle remains perfectly closed, so that any communication between it and the end of the pollen-tube is impossible.

After impregnation the embryo-vesicle becomes divided into two cells by a transverse septum. These two cells are the first of those which form what Hofmeister calls the *pro-embryo*. The distal cell then in most cases divides by horizontal septa into a row of smaller cells. The terminal cell of this row then becomes more developed than the rest, and gives birth by an endogenous process to the embryo-globule. This then becomes developed into the embryo by the successive formation of new cells.

These results will be seen to harmonize perfectly with what has been already said with reference to *Hippuris*. They were obtained from the examination of a very great number of species belonging to various natural orders; among which may be mentioned *Orchidaceæ*, *Gramineæ*, *Liliaceæ*, *Iridaceæ*, *Amoryllidaceæ*, *Polygonaceæ*, *Caryophyllaceæ*, *Ericaceæ*, *Geraniaceæ*, &c., and there is every reason to depend on their accuracy.

In the last two numbers of the 'Annales des Sciences Naturelles,' which have only appeared in the course of last week, M. L. R. Tulasne has published the most complete and beautiful series of researches, as far as they go, among the many to which this controversy has given origin. The facts which are brought forward by this author are confirmatory in the most important particulars of what had previously been ascertained by Hofmeister, Unger, and others, but are distinguished by the author's inquiries having been carried to an earlier period in the development than had been arrived at by any previous observer in the families to which they refer, namely the *Scrophulariaceæ* and the *Cruciferaæ*.

In the *Scrophulariaceæ* generally, as in *Hippuris*, the embryo-vesicle assumes at an early period an elongated form, and its subsequent development is identical. Tulasne has traced it to its earliest origin in several species. He has shown that it is developed originally on the inner surface of the wall of the embryonal sac near its summit, but at a point quite separate from that at which the pollen-tube is applied. This vesicle, at first exceedingly minute, grows upwards in the cavity of the embryo-

sac, until it assumes a form similar to that seen in *Hippuris*. These facts are important, as serving to point out more distinctly the strict correspondence between the morphological modifications of the same development as observed in the *Scrophulariaceae* and other orders, with those possessed of distinct embryo-sacs, as the *Orchidaceae*.

The researches before us also derive an additional interest from their showing the total inaccuracy of the observations of Prof. Wydler of Berne, (which were made on the same natural order,) who in the year 1838 set himself to support the theory of Schleiden, and from whose alleged facts that physiologist derived some of the most powerful supports of his views.

In the *Cruciferae* M. Tulasne has also accomplished all that can be done to perfect our knowledge of the embryogeny of the order. In particular he has described and figured distinctly the embryonal sac, the existence of which was doubted in that order, and has traced the embryonal vesicle from its earliest condition, that of a minute cellule attached to the micropyle extremity of the embryo-sac, up to that of a cylindriciform cell filled with a granular protoplasm, at the period at which it should seem that fertilization takes place.

Numerous other points of great importance might be mentioned as illustrated by this admirable series of researches. They will well reward the perusal of all who take any interest in vegetable anatomy and physiology, and they are illustrated by drawings, which exceed in beauty and detail all their predecessors, although many of these have been beyond all praise.

From the accurate knowledge of the facts connected with the origin and development of the vegetable embryo, into the possession of which the researches of Unger, Hofmeister, and Tulasne have put us, we need be at no loss to arrive at certain general conclusions as to the order in which the various steps of the embryogenic process are brought about, and the laws by which it is governed. We shall therefore occupy the remainder of this paper in enumerating as shortly as possible the most important of these generalizations.

In order to facilitate description, we shall divide what seem to be the essential phenomena of the embryogenic process in the higher plants into three classes, in the first of which we shall consider the process of development of the embryo-sac; in the second the changes which take place within the embryo-sac before, and in the third, after the act of impregnation.

We shall first speak of the development of the embryo-sac, or the individualization of a cell of the female organ for reproductive purposes.

At a very early period a constituent cell, of what is called in

descriptive language by a singular misnomer the *placenta*, gives rise by successive division to a cylindrical body, which consists of a central series of cells surrounded by others of smaller size. This, by another equally obvious misnomer, is called the *ovule*. From the central series of cells just mentioned one is separated and set apart for reproductive purposes, while the rest are variously developed so as to form coverings to this one. It enlarges at the expense of the rest, and receives the name of embryonal sac, and is strictly analogous to the animal unimpregnated ovum.

We next consider the changes which take place in the cavity of the embryo-sac previous to impregnation.

At a period considerably prior to impregnation a vesicle is developed, always at the micropyle-end of the embryo-sac, and probably always from a cytoblast. This vesicle enlarges more or less, and contains a fluid granular protoplasm. To this the name embryo-vesicle is assigned. It is analogous to the germ-vesicle in animals, both in its production and subsequent development.

Besides the embryo-vesicle other cells are frequently developed at this period, which are destined to conduce to the nutrition of the future embryo.

Lastly, we have to consider the changes which take place in the embryo-sac after impregnation.

At this period a cell belonging to the male organ (the pollen-grain) becomes so developed that its membrane and that of the embryo-sac are brought in contact; in consequence of which an interchange of their contents takes place, and under the peculiar influence of the one upon the other, the embryo-vesicle begins to develop within it two cells divided from each other by a transverse septum, in the same way as the first change observed after animal impregnation is the development of two cells in the germ-vesicle. These cells then multiply to a greater or less extent by transverse division so as to form a confervoid filament. At last, either at the centre or termination of this filament, one cell becomes developed by an endogenous mode of cell-production into a body to which the term embryo-globule is applied, and which is in fact the future embryo, while the rest perform a subordinate function, being probably merely subservient to the nutrition of the embryo. This last process corresponds in animals to the successive divisions of the two cells previously referred to, what is called the "*cleaving of the yolk mass*," on the surface of which the embryo is subsequently developed.

The foregoing sketch of what may be considered as the morphological type of the embryogenic development in the higher plants will, it is believed, include all those modifications which occur in those families which have been hitherto investigated. And consi-

dering that of late years, since the means of research have been so much more complete than formerly, there has been such a remarkable consonance in the results obtained by different observers, there is little reason to apprehend that any new facts are likely to arise, which will render it necessary to modify our generalizations to any great degree. We may therefore consider the controversy for the present settled. The doctrine of Schleiden is now only a matter of history, and as such possesses very great interest. When in 1837 he first brought forward his splendid discoveries as to the previously unknown nature and functions of cells, he founded upon them another doctrine, according to which the existence of sexes in plants was denied, and the so-called male organ alone was supposed to originate the germ. The history of this celebrated doctrine exemplifies in a remarkable manner the truth of the observation, that, although false facts may do an infinity of mischief in science, false theories are often productive of the greatest benefit.

The numerous researches which have been set on foot within the last ten years with a view to the refutation of the doctrines of Schleiden, have not only established the utter baselessness of these last, but have furnished us with a series of details more complete and more conclusive than any which we possess in connection with any other subject in the whole range of vegetable anatomy.