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XXXVI.—Reports on the progress of physiological botany. No. 5

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permission. The natives said the egg was found in the jungle, and observed that such eggs were *very very rarely* met with, and that the bird which produces them is still more rarely seen."

The value of such a statement of course depends on the character of the narrator, and on this head Mr. Joliffe observes—"M. Dumarele is a French merchant of Bourbon, a very respectable gentlemanly man, about sixty years of age, who has for years been trading with his own vessels along the coasts of Madagascar, and is well-acquainted with the different races of natives and with the resources of the country. His very unassuming and quiet manner, and intelligent conversation, much prepossessed us in his favour, and we believed everything he told us to be worthy of credit as far as his judgement and good intention went."

Mr. Joliffe's own opinion seems to be, that M. Dumarele was imposed upon in some way by the roguery of the natives. He judiciously adds however—"M. Dumarele's story should not be despised or discredited in these times, when such extraordinary discoveries are constantly made in every branch of science, but publicity should be given to his statement, that persons visiting Madagascar may, if possible, collect fresh information on the subject, and clear up the mystery. The sight of one sound egg would be worth a thousand theories."

It is a singular circumstance, if nothing more, that Marco Polo refers the *Roc*, of Arabian-Night celebrity, to the island of Madagascar; but as the *Roc*, however gigantic, was decidedly not *brevipennate*, a discussion of its history would be irrelevant to our present subject.

XXXVI.—*Reports on the Progress of Physiological Botany.*

No. 5. By ARTHUR HENFREY, F.L.S. &c.

On the Phenomena accompanying the Germination of the Spores of Ferns.

IN the year 1842, Nägeli discovered on the pro-embryo (the cellular expansion fruit produced from the spore in germination) of Ferns, peculiar organs which he considered to be analogous to the antheridia of the other Cryptogamic plants.

In the account he published of these structures* he describes them as gland-like organs growing on the under surface, near the margin, very rarely upon the upper surface. They frequently appear as if composed of a single cell; but it may mostly be

* Bewegliche Spiral-faden (Saamenfaden?) an Farren; Schleiden und Nägeli's Zeitschr. für Wiss. Botanik, Heft i. 168. Zürich, 1844.

recognized that the organ is a sac formed of a single layer of cells. This sac is filled with contents which appear granular and opaque. It bursts at the apex and allows a quantity of minute, round cellules to escape. These cellules move about actively in water. Each contains a spiral fibre, which by tearing the membrane of the cellule becomes free, and then exhibits a motion similar to that of the spermatic filaments of the Mosses, Liverworts and Charas.

The course of development of these organs is detailed, and is to the following effect :—Certain cells of the pro-embryo grow out by their free surface into processes which are gradually elongated and become divided by transverse septa, so as to resemble in some measure short and thick confervoid filaments ; the number of superposed cells varies from two to five. Then these cells become multiplied by the formation of vertical septa, so that each is divided into five cells, four forming a peripheral layer inclosing one in the centre. The central cells of all the articulations become confluent into a canal running up the middle of the organ which thus becomes a sac, closed below by the cell of the pro-embryo and above by the four cells of the uppermost articulation. This structure is usual, but slight modifications occur, not only in the number of articulations formed, determining the length of the organ, but in the development of the particular joints, the uppermost and the bottom one sometimes remaining in the state of simple cells.

The organs when fully formed have the central cavity so densely filled with the moving cellules, that they sometimes appear like mere double or even simple sacs, the cells forming the walls being compressed by the internal expansion.

The central canal at first presents an opaque granular appearance ; subsequently the contents are converted into the above-mentioned cellules. The mode of development of these is discussed by the author, and the analogous process in the antheridia of other Cryptogamia referred to ; he concludes that it is most probable that they are formed by a succession of developments from parent-cells, the central cell of the five of each articulation being the primary parent-cells.

The organs containing the spiral filaments discharge their contents when placed in water, even before they are fully developed. In an undeveloped condition they appear as round vesicles $\cdot 004$ to $\cdot 005$ of a line in diameter, containing homogeneous, or finely granular, colourless mucilage. Sometimes chlorophyll globules present themselves. Many possess a parietal nucleolus. The perfect cellules contain only a spiral filament. This usually has two turns ; sometimes only one and a half, sometimes two and a half or three. The filament has one broad and obtuse end,

while the other is attenuated. The author in some cases distinctly detected a long filiform appendage, like that described by Meyen in the Charas. The thickened end is sometimes quite clavately thickened. When the filament is clearly seen, it is evidently a band with a flat surface applied against the wall of the cellule. The bursting of the cellules allows the filaments to escape, but sometimes the whole or a fragment remains adherent to it and is carried about by it. While the spiral filaments are contained in the cellules in which they are produced, the convolutions are closely approximated; as soon as they become free, they generally extend themselves and become like the turns of a screw.

When the cellules are evacuated from their sac, they often lie from one to ten minutes unmoved; then some of them begin to move. At first they turn around their own axes without change of place. As yet nothing is seen of the emergence of the spiral filament. By degrees they begin to move from their place, at first slowly, then more and more rapidly. The cellule still continues to rotate on its axis. Next, a portion of the filament is seen to protrude from the cellule, which then tears quite open, and the filament thus comes in contact with the water in its entire length. The motion is then considerably accelerated. The cellules frequently begin to move directly they emerge from the sac; sometimes they rotate while still inclosed in it and before it has opened; this happens when they are not in very close contact.

M. Nägeli describes five or six kinds of movement of the spiral filaments which he endeavours to define mathematically, but he states that besides these, the motion often appears quite irregular, especially in being suddenly arrested, diverted to one side or reversed. But he does not consider these irregularities beyond what may be accounted for by interfering influences occurring in the fluid. He considers the motions as by no means voluntary; being much too regular and mechanical for this. He says also that a careful comparison of them with those of the Infusoria shows that they are totally different.

The fundamental type of the movement of the filament is the revolution round the axis, as Schleiden (*Grundz. der Wiss. Bot.*) has explained it in the rest of the Cryptogamia. That this revolution round the axis is proper to it as a primary peculiarity, free from the other motions, is shown by these round and closed cellules, which, with their inclosed filament, revolve merely around their axis in water, or even while still within the organ of the plant. This peculiarity must, from the fact, be at once attributed to the spiral filament; all the other movements may

then be deduced from it. That there is an advancing movement follows from the heliacal shape. That it exhibits various deviations from the straight line is quite as natural a result of the inequilateral construction, since both the thickness of the filament and the diameter of the convolutions, as well as their distance from each other in the same spiral filament, alter successively from one end to the other.

They differ in chemical composition from the spiral fibres of the spiral tissues of plants, as they give with iodine the characteristic reaction of mucilage (a compound which contains nitrogen); the membrane of the cellule remains uncoloured.

After a comparison of these organs with the antheridia of the other Cryptogamia, from which the author arrives at the conclusion that they are to be regarded as identical in their nature, he briefly discusses their import and probable function in the following terms:—

“The antheridia have been compared with the anthers, a misconception which is only applicable by an ignorance or misapprehension of the morphology of the elementary organ. I believe no refutation of this view is now necessary. The antheridia have not been compared with other organs of plants: they do not exhibit even a distant analogy to any of them. The only remaining analogy for the antheridia is with the male organs of reproduction of animals. In favour of this speaks the similar course of development of the spermatic filaments in plants and animals, since even in many of the Mammalia, the spermatozoa originate wound spirally in cellules; further, the resemblance of the motion of the filaments in plants and animals, and, finally, the circumstance that in the Cryptogamia these spermatic filaments are the normal elementary parts of an organ, which, from its situation, must evidently have a relation to the reproduction. These reasons certainly appear to me to have great weight; and if they do not absolutely warrant the assumption that the antheridia are the male organs of the Cryptogamia, they may yet excite further investigation on this ground.

“The most important objections are: 1. that no organ analogous to the antheridia has been found in the Phanerogamia, and that they are themselves wanting in certain Cryptogamia with true spores; 2. that, as the preceding observations show, the antheridia of the Ferns occur upon the pro-embryo; so that it is almost impossible to conceive what relation they can here have to the spore-cells, which are formed not merely at a much later period, but first make their appearance long after the pro-embryo has altogether disappeared.”

The figures illustrating this memoir are taken from *Aspidium*

augescens, Link, *Asp. concinnum*, Link, *Asplenium dissectum*, Link, and other species not specified; but the author states that the phenomena are constant in all the Ferns he has examined.

Nothing further appeared on this subject until December 1847, when Dr. J. Münter communicated to the Berlin Naturforschende Freunde*, the observations of Count Leszczic-Suminski; in January 1848 Prof. Ehrenberg also laid these before the Berlin Academy, and in the same year they were published in detail in a special memoir†.

These researches are in the highest degree curious, and if the facts related prove to be correct, must importantly affect the received views of analogies in the generative processes of plants. As the account scarcely admits of compression, we will give the important passages in the author's own words:—

The Sexual Organs of the Ferns.

"In the year 1846 M. Nägeli‡ made the interesting discovery that the pro-embryo of Ferns exhibits analogues of the antheridia of the Mosses, Hepaticæ and Charas. That observer described these antheridia or spiral-filament organs accurately and completely enough, but he was led away by a false principle in his researches, and thus regarded as differences in the stages of development what were actually different organs; since both in their anatomical structure and physiological import, they are to be distinguished as two completely separate groups.

"In the earliest condition of the pro-embryo are found on its under face, more rarely on the borders, peculiar gland-like cells projecting in a globular form from the surface. In more mature age they increase in number, and occupy more particularly the region among the radicle fibres. Some species, especially *Pteris serrulata*, are remarkable for their great number. These organs originate by a sac-like elongation of particular cells of the pro-embryo, forming globular protuberances from its surface. Each at first contains chlorophyll, but by degrees a free cell is formed, the contents of which exhibit homogeneous mucilage, transparent globules, or distinct nuclei with nucleoli. As soon as this cell has increased in size sufficiently to fill up the original projecting sac, it is parted by a septum from the cell of the pro-embryo. Thus the organ becomes independent. A third cell is often formed between these, flattened above and below, constituting a kind of peduncle to the upper cell. The contents

* A report by Dr. Münter appeared in the 'Botanische Zeitung,' Jan. 21, 1848, to which I shall allude presently.

† "Zur Entwicklungsgeschichte der Farrnkräuter;" by Count Leszczic-Suminski; Berlin, 1848.

‡ *L. c.*

of this latter display, often at a very early period, new minute cellules filled with a granular substance, occurring in an indefinite number and sometimes appearing very regularly arranged. They become more and more distinct, and in the mature condition generally fill up the parent-cell, so that this appears like a sac distended with round granules. By reciprocal pressure they acquire a parenchymatous aspect. When an organ of this kind has reached the proper stage of maturity, it bursts spontaneously at the apex and discharges an indefinite number of minute round cellules enveloped in mucus. In some cases I have observed an uniformly distributed, rhythmical motion of the whole discharged mass. But the cellules usually exhibit a motion round their axis very soon after their emergence; each of them unfolds a spiral filament, which generally remains connected with the delicate cellule by its posterior extremity, and advances with an active revolution round its axis.

“As Nägeli has well described the very various movements of these spiral filaments, it appears to me unnecessary to discuss this subject here. But I must observe that I have seen on the clavately swollen, anterior extremity of the spiral filament, delicate motile cilia of considerable length, which however are only to be perceived distinctly with the help of the strongest artificial illumination. They are best observed when the rapid revolution of the filament is slackened. Then about six such cilia may be observed on each, which after the cessation of the motion of the spiral filament also gradually cease to move, and either stiffly surround this or become in part so applied upon it that it is almost impossible to detect them. The motion of the cilia endures longer than that of the filament, and not unfrequently shortly recommences. The form of the spiral filament cannot be perceived distinctly either during active motion or after this has ceased, because in the first case the form is altered by the continual change of the convolutions and the motion of the cilia,—in the latter by the cessation of the revolution, as the filament then contracts in irregular curves. It is necessary therefore to seek out a moment when the spiral filament, sufficiently mature, still remains in its cellule, and occurs on a free space in the preparation. In such cases it exhibits either two or three convolutions, or appears wound in a semicircle with the swollen extremity applied to the wall. The cilia are not then perceptible. This position often gives a very well-defined figure. It is distinctly seen that the spiral filament incloses a longish vesicle in the above-mentioned clavate thickening of the anterior extremity. The thick end diminishes gradually down into a filiform tail which bears a slightly swollen knob at the end.

"In addition to these spiral-filament organs, we find on the under side of the pro-embryo near the notch of the border, on the cellular protuberance lying in the middle of the frond, other larger and not less important structures. These are hollow, ovate bodies, and consist of a papilla formed of ten to twelve cells, while the other organs seldom exhibit more than one. Their number is indefinite, since there are often only three upon one pro-embryo, while upon another of the same species appear eight or more. They differ from the above-mentioned organs not only in these points, but in their mode of origin and their structure. It is clear from the course of development that they are not spiral-filament organs in a more perfect condition. In the origin of these organs the cellular layer becomes thickened by the formation of new cells; in the course of this process a large globular intercellular space is formed having a contracted orifice at the outer end. This latter is usually hexangular, and is immediately surrounded by green, usually quadrangular cells. The cells further from it are larger and contain less chlorophyll. From the borders of this cup-like orifice arise four largish cells, containing merely a clear fluid, often with nuclei, and arranged in a circle; these leave a square intercellular space between them varying in size. From each of these cells three more are, as a rule, developed vertically one above another, so that the square space becomes elongated into a canal leading to the interior of the organ. The cells at the apex are usually applied together so as to close the orifice. The early origin of the canal causes the still uncovered cavity to be rarely met with.

"These structures, so different in anatomical character, which were formerly regarded as antheridia in a different stage of development, also assume a distinct physiological import.

"By continued observation I have succeeded in discovering in them the sexual apparatus of the Ferns, hitherto regarded as Cryptogamic. In the above-described hollow, ovate organs occurring on the middle of the pro-embryo, I have recognized the female apparatus; a circumstance, the establishment of which claims for the spiral-filament organs the import of male apparatus. The former, which is an ovule without envelopes, therefore a simple naked nucleus, is to be divided into two parts; one, the larger and upper portion projecting from the pro-embryo, the nuclear papilla (*mammilla nuclei*), and the other smaller, buried in the pro-embryo, the cavity for the embryo-sac (*antrum nuclei*). In the former we have again to distinguish: the orifice at the apex, the foramen of the nuclear papilla (*ossiculum mammille nuclei*); and the prolongation of it leading into the cavity for the embryo-sac, the canal of the nuclear papilla (*canalis mammille*

nuclei seu nuclei). The orifice of the latter is directed toward the base of the pro-embryo.

"Before the formation of the nuclear papilla, there arises at the bottom of the cavity for the embryo-sac a minute transparent cell, the embryo-sac. This is seated like a tubercle on a particular point as its suspensor. Already at this period we find in the cavity containing the embryo-sac from two to five, or even more free spiral filaments, never inclosed in their cellules. For at this period the spiral filaments move by the help of their cilia from the burst spiral-filament organs to the cavity for the embryo-sac, and penetrate into it. In this motion they are assisted by the mucus evacuated with them, and by the moisture always present on the under side of the pro-embryo. It requires some acquaintance with the form and different positions of the spiral filaments to recognise them in the cavity. The still wide opening of the cavity at this period facilitates their entrance (the borders of the organ scarcely project yet above the surface of the frond). At this period of the impregnation it sometimes happens that we notice a quantity of dead spiral filaments around the cavity of the nucleus; they then appear curved like an S, or else wound circularly or spirally. But I have seldom observed this phenomenon. As the embryo-sac grows and thus displaces the spiral filaments, the canal of the papilla of the nucleus is formed, in the manner above described, and receives into it one, two or more, rarely several of them; the rest decay in the bottom of the cavity. Before their entrance into it they exhibit with advancing growth an evident expansion, which occurs especially in those subsequently received into the canal. In the mean time the embryo-sac, filled with blastema, has produced in its interior a parenchyma composed of several cells (endosperm), appears green, and has advanced so much in growth that it almost fills the cavity in which it is contained. One of the spiral filaments penetrates by one end into the part of the embryo-sac turned toward the canal. The penetrating end is that at which the smaller enlargement exists, which at the same time exhibits a greenish tint; the larger, clavate, granular end projects out into the canal; this usually incloses a minute pyriform cellule. An obstacle of no slight importance interferes with the observation here also; the delicate filiform connection of the two ends of the spiral filament is usually torn by the pressure of the covering glass upon the preparation, and thus we see only the separated ends, one in the canal, the other in the cavity for the embryo-sac, totally unconnected. As soon as the smaller expansion has reached the middle of the embryo-sac, it separates from the spiral filament and now forms a closed globule, the germinal

vesicle, in the interior of the embryo-sac. The other end, projecting into the canal, dies away. This phænomenon must not be confounded with the forcible tearing of the spiral filaments just alluded to. Through the union of the germinal vesicle and the embryo originates the embryonary globule, which is only attached below to the bottom of the cavity containing the embryo-sac by a very delicate filiform suspensor. With the growth of the embryonary globule the colourless nuclear papilla dies, dries up, and the canal in particular becomes coloured brown. In this condition it persists for a long time upon the now expanding cavity of the nucleus. Usually only one of the numerous naked ovules produced upon the pro-embryo develops its embryo. This need not appear wonderful, since similar examples are not wanting in the vegetable world, as in many Palms one alone of the three original cavities is regularly perfected. A special reason may be looked for here in the minute size of the pro-embryo, which does not afford sufficient nutriment for several embryos. With the further development of the one embryo the other rudimentary ovules die. In these the foramen of the papilla expands, and allows the dead spiral filaments and the rest of the contents to escape. The canal, and especially the cavity for the embryo-sac, then exhibit a brown colour. The latter may be most distinctly recognized in this condition. In vegetating ovules, on the contrary, this part can only be observed by a most careful extraction of the single organ. For while on the one hand it is covered by the still erect nuclear papilla, the detection of it is on the other hand rendered impossible by the want of any peculiar colour or otherwise distinguishing outlines. Of all the species which I have examined, *Polypodium aureum* is, next to *Pteris serrulata*, the best-adapted. The impregnation follows exactly the above-described type in all families, genera and species; an exceptional occurrence is the appearance, on the margin of the pro-embryo, even in its earliest stage, of a spiral-filament organ differing somewhat in structure, as it loses its uni-cellular aspect. Five or six parietal cells are formed which inclose in the middle a space either filled with spiral filaments, cellulose or hollows. These structures must be regarded as monstrosities of the spiral-filament organs, since they occur abnormally and on individuals which never produce an embryo. Such an infertile pro-embryo either decays soon after its origin, or, passing into a succulent state of growth, appears much larger than is natural. In this condition it acquires a resemblance to a *Marchantia*, and usually produces a great number of abortive ovules."

This extract has reached such a length that we have not space to give an account of the author's description of the develop-

ment of the embryonary globule into an embryo. It must suffice to state, that by the multiplication of cells it gradually enlarges and acquires a definite form, producing a frond at one end and a radicle at the other, bursts through the cavity in which it was developed, and grows up, producing new fronds, into the characteristic form of its species. These ulterior stages of the germination from the pro-embryo have been described by other authors, although not so minutely, and our chief business is with the new doctrine of the generation which has already been critically examined and contested.

It must be mentioned here that the terms of Dr. Münter's report * are rather different from the above, which is important, as he gives the facts as witnessed also by himself and Prof. Link. He says with regard to the act of impregnation :—"Persevering observations of these two essentially different organs gave the following results. The spiral filaments emerged from the spontaneously opened hemispherical cells, two or three of them moved rapidly toward the cup-like cellular protuberance, penetrated through the orifice into the still very short blind canal, and then *were converted into a little heap of mucus* (schleimklümpfchen) after their motion had ceased. After *this (often-observed) process* the quadratic orifice closed, and it was seen that, in the blind end, *one of the cells lying on the inside of the wall of the semi-canal* enlarged, and in it new cells originated."

This cell is said to be the embryo, which, elongating in a direction at right angles to the canal, breaks through in two places, one end producing a frond, the other a root.

In the early numbers of the 'Botanische Zeitung' for the present year is contained a long memoir on this subject by Dr. Albert Wigand, who, after extensive investigations, arrives at the conclusion that the above-described process of impregnation does not occur, and that the views of Count Leszczic-Suminski and Dr. Münter are based on errors of observation. His criticisms would occupy too much space for the present article ; I shall therefore reserve them for a future notice, and add to them some observations of my own.

In the 'Annales des Sc. naturelles' for January 1849, M. Thuret describes the antheridia or spiral-filament organs of Ferns, but he does not appear to have detected the so-called ovules. He also mentions that he has found similar spiral-filament organs on the pro-embryo of the *Equiseta*.

* Bot. Zeitung, Jan. 21, 1848.