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XLVIII.—On the development of Chara

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XLVIII.—On the Development of Chara. By C. MÜLLER*.

[Concluded from p. 329.]

§ 6. Formation of the Fruit.

THE origin of the fruit must be sought for in the very youngest whorls of branches only. *It there exists as one of those external cells which surround the central cell*, and is either developed separately or in combination with the cells of the anther. It differs considerably from the latter, inasmuch as the latter is a cell produced by intercalary growth which is evolved from the articulations of the fruit-cell and is developed downwards, the former being directed upwards. Whilst at this period the other external cells are elongating to form branches, the cells of the anther and fruit merely become simply rounded, containing in their interior a yellowish white mass with defined globular outline (the cytoblastema, Plate VII. fig. 27). The development of the anthers always proceeds more rapidly than that of the fruit, when both occur together; for they may be absent in one and the same species, as *Ch. crinita*.

The next step in the further evolution of the fruit-cell consists in the subdivision of its cytoblastema into six parts. *It is exceedingly difficult to detect this*; I was only able to succeed by gently compressing the cell, whereupon all that I perceived was, that these globular masses had formed. These should be considered as so many cytoblasts, hence we have one central and five external cytoblasts. From these as many cells are formed by the process with which we are acquainted, during which however the cytoblasts are usually perfectly absorbed (fig. 28). These six cells are so arranged, that the apex of each is situated externally. This is the first stage at which anything definite can be perceived in the young fruit, and although another very small cell *constantly* exists beneath the central cell, I cannot state anything more regarding its formation. Suffice to say that it exists there, and is seen in figs. 28—32. It forms the commencement of that cell, which has been described above (§ 2), in the ripe fruit, and which is shown in figs. 1 and 2. The statement there made, that it might be of importance to the existence of the spores, is remarkably borne out by its so early and constant presence, which clearly shows that it is an essential organ of the fruit.

The five terminal cells which are arranged upon the spore-sac in the form of a crown are next formed, and also from cytoblasts, as may be most distinctly perceived in fig. 29. These here also become speedily absorbed, and the cells which are formed around them have become so firmly adherent to one another, that they

* Translated from the Botanische Zeitung for July 3, 1845.

completely inclose the central cell and prevent any access to it from without (figs. 30—35). As a proof I have given a figure (fig. 36) from these young fruits, which may be compared with § 2. fig. 35. from them when ripe. In it the existence of the central cell is distinct enough at the intercellular spaces. The preparation is placed upon its vertex, and thus the pressure of the five terminal cells against one another may be distinctly seen.

This central cell forms the commencement of the nucleus, and the five external with the five* terminal cells form the young sporal sac. The sporal membrane is not yet developed.

All parts of the fruit now become elongated, and as they increase, the cells of the sporal sac, which continue to become utricular, assume another position, *i. e.* they turn spirally around the nucleus, whilst in their youngest state they had merely an upright position.

When the fruit has arrived at the limit of its longitudinal extension it expands spherically, becoming at the same time filled with cells. These are again formed from cytoblasts, as may be seen in fig. 32, and it is probable that in the new cells thus formed *new* ones are again formed and so on, until the process of cell-formation ceases from the transformation of all the cells into starchy matter. This is a complete confirmation of Schleiden's observations on cell-formation in the embryo. I was not satisfied however by observing merely the true commencement of this formation (fig. 32); for the cells of the sporal sac become so speedily turbid, that the interior is rendered quite undistinguishable, nor could I succeed in extending my observations by dissections.

When the fruit has attained its proper dimensions the remaining cells become thicker; the primordial utricles, which were at first scarcely perceptible, now become distinct, and the contents of the cells are formed. These are at first of a reddish colour; they continue to become more intense, and subsequently become brownish yellow and green, which colour they retain. In the meantime the nucleal membrane has become thickened, and is now surrounded by another strong brownish membrane. This is the spore-membrane. It is merely the *internal membrane of the spore-sac thickened*, and may be subsequently completely separated from it. Thus are explained its perfectly homogeneous structure, flattened form, spiral windings and the interruption of this winding, the upper angles of which are always the most

* According to Meyen (Physiolog. vol. iii. p. 394) there are sometimes six sporal sac cells. I have never seen them myself. If however it be true, it is the same, as when we find the central utricle surrounded by six, seven, eight or more cells. Hence here the minimum is six, in the former case five.

acute (compare § 2), which evidently arises from their having been inserted in the intercellular passages between the nucleus and the spore-sac. In fig. 3 the ripe fruit, the internal membrane of the spore-sac cannot be any longer recognised. From what has been stated the simple deduction arises, that *the fruit is the metamorphosed bud of a branch or shoot*. Even as regards its function *it is nothing more than a bud*, which differs from the terminal bud of the stem merely in combining at the same time one character of the stem, *i. e.* the cortical layer. Hence the nucleus is nothing more than the perfect analogue of the central utricle or of the metamorphosed stem itself. *The sporal sac is the perfect analogue of the cortical layer of the stem. The contents of the nucleus agree perfectly with those of the internodal cells of Nitella.* The fruit of *Chara* differs from these buds only in its compound structure. Whilst the buds of the stem and branches were developed longitudinally, the buds destined to form the fruit remained at the grade of buds and concentrated their formative powers in themselves. *Finally, no impregnation takes place.* This deduction is evidently a consequence of the above; however it can do no harm to mention it again here in *italics*. Thus all artificial investigations on the so-called anthers are referred to a separate province, and their explanation becomes still more obscure.

The five terminal cells, like the other parts of the sporal sac, have to defend the young nucleus from injury; they therefore grow together over it and perfectly inclose it. The sporal membrane has to fulfill the same office as soon as the spores are deprived of their coating, the spore-sac, in order to prevent their development into new plants.

After the above remarks had been written, I found in Kützing's 'Phycologia,' p. 80, a similar comparison of the individual organs of the fruit. I add them here for comparison with my own: "The true fruit of the *Charæ* is nothing more than a branch, the evolution of which takes place in width instead of in length; the five cells which crown its apex are the verticil of branches*. The internal utricle has become transformed into the coats of the seed; the external tubes, which form the cortical layer in the stem, form the external coat of the seed †; the angular cell-contents ‡ be-

* From what has been stated this cannot be true, because branches are never formed from the cortical layer; we rather have a repetition and a confirmation of the development of new cortical cells in the older ones beautifully repeated in the cortical layer of the stem. Kützing regards this cortical layer as the elongation downwards of the cells of the branches. Hence the five terminal cells are new cortical cells.

† Older authors also believed this, as Meyen, Phys. 3 Bd. p. 395, where a similar morphological interpretation of the fruit of the *Charæ* is anticipated. I hope to have rendered the above extended interpretation useless by direct observations.

‡ From what has been stated this is incorrect.

come converted into pure amylum, in which state they partly exist in the utricular cells of the stem, only here they are coloured green by chlorophylle."

§ 7. Systematic Position.

This paragraph is not for the purpose of deciding upon the systematic position of the *Charæ*, for that has been already spoken of; I merely wish to notice a few special points.

It is evident from the above, that the formation of the fruit of the *Charæ* cannot be considered as a high grade of development. To what other cryptogamic family is it best comparable? I do not hesitate to state, the *Algæ*. Kützing, in his 'Phycologia Generalis,' has unconditionally referred them to this position, placing them near *Lemania*. We must here bear in mind the structure of the fruit before all things, and although we are but little acquainted with the fruit of those *Algæ* which are nearest related to the *Charæ* in habit, in examining the latter I at the same time met with another of the *Algæ* in which the most remarkable analogies to the fruit of the *Charæ* existed. I allude to *Chatophora tuberculosa*. In the 'Flora,' 1842, no. 33, I have published a small treatise on it, which unfortunately still remains very imperfect. The main point is, that in it the analogues to the anthers of the *Charæ* may be positively found. They are red globules, formed in a much more simple manner than the anthers of *Chara*. They also lie close to the fruit, which is also nothing more than metamorphosed buds. Kützing, who quotes my paper in the essay above mentioned, p. 325, denies *any* analogue of the anthers either of Phanerogamia or Cryptogamia, and asserts that the above red globules are nothing more than the more highly developed fruit! Having lately carefully moistened and again examined my dried specimens, by which they were not found altered in the least, *I must most decidedly protest against this statement!* When I look at the two cells of the anthers and fruit of *Chara* represented in fig. 27, I find, as it appears to me, the lowermost red, the contents of the upper being green,—a similar formation to the two organs in *Chatophora*. Unfortunately not having enough specimens, I cannot make any more remarks upon them than what I have already stated in my history of the development of *Chatophora*. I therefore strongly recommend those fortunate persons, who should again meet with them, to examine them most accurately and to compare them with the organs of fructification of *Chara*. As far as I know, no one has noticed the above red globules. However, as long as this remains so, we must regard the *Charæ* as a *familia incertæ sedis*, but must place them near the *Algæ*.

EXPLANATION OF PLATES V., VI. AND VII.

- Fig. 1.* Ripe fruit of *Chara vulgaris* cut through the axis, and exhibiting the internal structure.
- Fig. 2.* The same, showing the exterior.
- Fig. 3.* A portion of the spore-sac more highly magnified. The brown sporal membrane forms its internal border.
- Fig. 4.* The nucleus from *Chara vulgaris*.
- Fig. 5.* Starch-cells from the same nucleus. *Fig. 20.* A cell converted into cytotblastema, magnified 400 diameters.
- Fig. 6.* The germinating spores of *Ch. vulgaris*.
- Fig. 7.* The lowermost part of the germ, containing a distinct primordial utricle, cytotblasts, their fibres, and the cytotblastema deposited in the joints, after treatment with iodine.
- Fig. 8.* The same, exhibiting the formation of intercalary cells, treated with iodine.
- Figs. 9, 10.*—10. New plants of *Ch. vulgaris* formed by intercalary growth.
- 9.* The earliest stage of the last figure, after treatment with iodine; magnified 300 diameters.
- Fig. 11.* Terminal bud of the stem of *Ch. hispida*, 400 diameters. *Fig. 14.* The same seen from below.
- Fig. 12.* A portion of the same bud with perfect branches. The cells of the shoots are deposited along with their septa, but have not yet assumed their vesicular form.
- Fig. 13.* This has taken place here.
- Fig. 15.* A branch of *Ch. hispida* transversely divided.
- Fig. 16.* A branch with the cells of the shoots forming.
- Fig. 17.* A branch of *Ch. hispida* with the commencement of the cortical formation.
- Fig. 18.* The central cell of the internode, after treatment with nitric acid and iodine, 400 diameters.
- Fig. 19.* A branch of *Ch. hispida* cut through longitudinally. The internodal cells are distinctly seen.
- Fig. 21.* Apex of a branch of *Ch. crinita*, after treatment with iodine.
- Fig. 22.* Apex of a branch of *Ch. hispida* cut through longitudinally.
- Fig. 23.* Summit of a branch of *Ch. hispida* with a divided apex.
- Fig. 24.* A part of the apex of a branch of *Ch. crinita*, after the addition of nitric acid and iodine. The secondary membrane is distinctly seen internally. One end of the primordial utricle is separated from the transverse wall of its cell.
- Fig. 25.* The primordial utricle in the lowest articulations of the germ of *Ch. vulgaris*. Treated with nitric acid.
- Fig. 26.* The same from the apex of a branch of *Ch. hispida*, also treated with nitric acid.
- Fig. 27.* Apex of a branch of *Ch. crinita* with the cells of the fruit and anthers.
- Fig. 28.* Early state of the fruit of *Ch. crinita*, 400 diameters.
- Fig. 29.* The same, with the formation of the five terminal cells, 400 diam.
- Figs. 30 and 31.* The same, perfectly formed, 400 diameters.
- Fig. 32.* The same. New cells have become developed within the nucleus from cytotblasts: 400 diameters.
- Fig. 33.* The same. The cells of the spore-sac are arranged spirally around the nucleus: 250 diameters.
- Fig. 34.* The perfectly formed fruit of *Ch. crinita*, 250 diameters.
- Fig. 35.* Its five terminal cells, seen from above, 400 diameters.
- Fig. 36.* The same from the young fruit, 400 diameters.