

con abbondanti resti di conchiglie littorali, l'altra è una specie di conglomerato.

“Da tutto ciò ella vede non esser possibile basarsi sui caratteri litologici per segnare l'età di una formazione, perchè rocce di aspetto e di composizione identica si trovano spesso in terreni che spettano ad epoche svariatissime; dippiù potrei citarle rocce che sono attualmente in via di formazione e che pure presentano compattezza ed aspetto da confondersi con rocce di terreni molto antichi.

“La litologia non può servire che a sincronizzare terreni i quali geograficamente sono a non troppa distanza gli uni dagli altri; in caso contrario, il geologo si trova subito nell'impossibilità di fare a meno della paleontologia.

“Senza conoscere gli altri fossili che si troveranno nelle rocce da Lei presentatemi, e senza aver notizia delle loro condizioni stratigrafiche non oso pronunziare sull'età loro il mio giudizio, come ho fatto per il loro modo di formazione; *benchè per conto mio sia persuaso, come Ella, trattarsi di un terreno pleistocenico analogo a quello studiato da Lyell ad Ischia*: ivi pure sono argille turchine con conchiglie che vivono anche attualmente nel vicino mare.

“Mi creda, &c.

Londra, 10 Agosto, 1859.

“Dr. G. CAPELLINI.”

XXI.—*Researches on the Cellular Formations, the Growth, and the Exfoliation of the Radical and Fibrillar Extremities of Plants.*

By MM. GARREAU and BRAUWERS\*.

IN a series of researches undertaken by one of us, with the view of acquiring a knowledge of the causes which preside over the distribution of mineral matters in the different organs of plants, we had occasion to remark that when seeds germinated at a temperature of 68° to 78° Fahr., the points of the radicles, and subsequently the fibrillar extremities of the roots, frequently bore, very soon after their emergence from the axis, more or less marked traces of a cellular exfoliation, or a tear-shaped enlargement of a viscous consistence, although both were placed in media suited for the regular accomplishment of their physiological functions.

As these facts seemed therefore to depend on their normal development, it became interesting to examine them with care. Prof. Link, in an essay only too concise, distinguished by the accuracy of the optical observations it contained†, directed the

\* Ann. Sc. Nat. 4 sér. x. p. 181; translated by A. Henfrey, F.R.S.

† Ann. des Sc. nat. 3 sér. xiv. 5. Besides this work of Link, readers interested in this subject should refer to a memoir by M. Gasparrini (*Ricerche sulla Natura dei Succiatori e la Excrezione delle Radice, &c.*), published at Naples in 1856, and referring to the question which has been the object of the investigations of MM. Garreau and Brauwers.—*Note of Ed. of Ann. des Sc. nat.*



attention of botanists, in 1850, to the excoriation and the mode of increase of the radical fibres of the hyacinth, and the viscous thickening which is observed at the extremity of young adventitious roots of willows; but while the figures he gives of the objects represent faithfully what occurs at the seat of the elongation of the tissue, this is not the case with that part of his essay which refers to the elementary formations of these organs, since he states them to arise from an extra-cellular cambium. Moreover, the objects to which this botanist directed his investigations were too limited in number, and the conditions of the experiments were not sufficiently varied, for anything like a profound study of the subject. It may be added that in science, whatever the object attempted, it often happens that interesting facts escape even the most patient observers; and it may be imagined that, notwithstanding the merit of the author just cited, our researches are justified by the hope of adding some new facts to this important question.

For the greatest facility and success of observations of the facts relating to the cellular formation and growth of the radicle, it is of great importance to trace its development in the absence of contact of any foreign body capable of adhering to or affecting its surface. With this view, selected seeds of very diverse species were placed, moistened with rain-water, upon hair-sieves, and covered with a moist woollen cloth. These seed-beds, placed in pots which contained water at the bottom, kept the seeds in a constantly moist atmosphere; thus the radicles, whose development proceeded more or less rapidly according to the temperature (which could be adjusted at will), formed tufts, beneath the meshes of the sieve and above the surface of the water, in which the subjects of observation, equal in age and dimensions, afforded means both for multiplied examinations and control of the observed facts.

Seeds placed in these conditions germinated much more quickly, at equal temperature, than in the best-prepared earth,—a result which appears attributable to the free access of air. Thus, at a temperature of 78° F., the radicle of cress was protruded from the seed-coats in eight hours, those of *Camelina* in fifteen, and from the caryopsis of little millet in two days.

When the radicle begins to sprout, it is usually smooth all over its surface, and presents no mark of exfoliation when the germination takes place in the ordinary thermometrical conditions of the atmosphere in the climate of Lille; but at a temperature of 68° to 78° F., the exfoliation begins very early in plants with feculent perisperm or cotyledons; and this more precocious tendency to exfoliate coincides, as we shall soon see, with a peculiar mode of dislocation of their elementary organs.



The radicle of wheat (*Triticum sativum*) when it originates in the ordinary conditions of the atmosphere, presents itself in the form of a cylinder conical at its apex, and in the centre of this latter region exhibits a portion of a sphere formed of quadrilateral cells, which, coloured of an amber tint, taken as a whole, differ distinctly from the more elongated and colourless cells which cover them. The former constitute what, for the better comprehension of the facts, we will call the summit of the radical axis, and the latter that of the cortical layer.

Taken in these conditions, and at the outset of the germination, all the cells of the cortical layer, including those of its apex, are smooth and coherent, and the most external are longer than those which they immediately cover.

In proportion as the organ grows, it is observed that the epidermal cells, which are of larger size according as they are placed nearer to the base of the radicle, contain an animal matter which is coloured pale rose by deutonitrate of mercury, and dark brown by iodized iodide of potassium. This substance, which contains extremely fine granules, accumulates in the middle region of the cells into a little heap, above which the wall of the cells becomes rounded externally in the form of a slight hernia, into the cavity of which the same matter passes; and in proportion as it accumulates there, this appendix becomes developed, until it acquires a length equal to twice or three times the diameter of the radicle; so that each epidermal cell with its absorbing appendix (radical hair, A. H.) presents the form of a cross with an excessively long shaft.

It is not possible to trace the mechanism by which this substance determines the elongation of a portion of the wall of the cell into this appendix; but we may conjecture that, as the essential agent of all cellular formations, it is this which secretes and coordinates the materials.

In proportion as the radicle is developed, and usually when it has attained a length of 1 to 3 centimetres, it may be observed that its apex is swollen, and has assumed the form of a tear. This region, which is viscid to the touch, readily becomes softened when immersed in water, communicating to it a consistence like that of white of egg, and a very marked sweet taste.

The radical extremities of 500 grammes of wheat, immersed in distilled water, gave a solution which, when heated to 140° F., presented flocculent coagula of azotized matter (caseine, albumen); and when this matter was separated, and an excess of alcohol of 0.815 spec. grav. added to the liquid, there was produced a pulverulent deposit in a grumous mass of pasty consistence and sweet taste, formed of a mixture of dextrine and sugar. The substance precipitated in a state of powder, saccharified starch in the same



manner as diastase; but, however great the number of successive dilutions and precipitations which it was made to undergo, it always retained a notable quantity of dextrine, which could be estimated, by Fehling's solution, at a third of its weight. A portion of the viscid matter in solution in water, filtered, gave by evaporation a transparent residue, scarcely coloured, very prone to decomposition, turning brown at 194° F., and which, when calcined to whiteness, left a small quantity of ashes, in which analysis proved the presence of phosphates of potash and lime. According to this, the substance possesses exactly the composition of a farina saccharified by diastase. This substance, which is also found diffused throughout the proper tissue of the radicle, may serve for the development of this organ; and this supposition gains a certain degree of probability from the fact that it is accumulated in largest proportion in the extremity of the radicle, the seat of the formation and enlargement of the cells.

It is true that, being soluble in water, it may, in case of heavy rains, escape in part from this destination, in which case it would have to be supposed that the excess of this aliment is lost to the plant, and diffused through the soil, to form, as we shall endeavour to show hereafter, what have been called the excretions of roots; but, though there seems to be some foundation for this last conjecture, there is no doubt that this material serves for the development of the central cells which are to exfoliate, since the latter are suspended and grow for some time in the viscid medium, which alone retains them united to the rest of the tissue.

When the radicle of wheat, in the condition just indicated, is examined with a sufficient magnifying power, the moment it is moistened, and under the slight pressure of the covering glass, the outermost coat is seen to fall away; the disjointed cells of which it is composed separate from one another, and float completely isolated in the viscid matter. The cells, as we have seen, are clearly distinguished, by their forms and larger dimensions, from those which constitute the apex of the axis, appearing more elongated the further they are placed from the curved line which bounds this region,—a fact which indicates that they must necessarily originate at the confines of that line.

The cells, transparent and full of granules which are coloured yellow by iodized iodide of potassium, are pushed forward and to the sides by the new formations. In proportion as they are removed from the point where they are formed, they grow in all dimensions, the nitrogenous granules they contain becoming more rare; then they increase in length, and remain applied upon the persistent portion of the epidermis, or more or less



speedily exfoliate. These elongated cells, taken in the adult condition, are devoid of large granules; but their living substance presents itself then in the form of a nucleus connected with the internal membrane by filaments in which exist rapid currents conveying granules of extreme tenuity. Subsequently, when the cell has acquired its full size, the substance of the currents and the nucleus becomes divided, in each cell, into two or three masses, of oval form, which soon constitute two or three cells placed end to end, but which ultimately separate from one another.

The radicles of millet, barley, buckwheat, beans, clover, lentils, vetch, wild chicory, *Crepis virens*, and hollyhock, taken in the same conditions, present exactly the same mode of growth and exfoliation of their cortical layer, with this exception only—that the exfoliable layer of the radicle of the hollyhock is comparatively very abundant, rich in viscid matter, and the cells of which it is composed more closely packed than those of wheat, although loosely connected, in the manner of an epidermis, by the interposed viscid substance.

The radical extremities of wild chicory, of cultivated lettuce, of *Crepis virens*, of *Papaver somniferum*, black mustard, and cultivated *Camelina*, allowed to exfoliate in distilled water, gave solutions which, on evaporation *in vacuo*, left residues scarcely coloured, of a gummy aspect. Those obtained from the radicles of chicory and *Crepis virens* exhaled a poisonous odour, and had a bitter taste analogous to that of lactucarium. That furnished by the radicles of poppy has the odour and taste of opium, and those derived from black mustard and *Camelina* have a saline sulphurous taste, and emit an unbearable alliaceous odour.

These matters, which, in the ordinary course of vegetation, are abandoned to the soil, seem to afford an explanation of the antipathies of certain plants towards others, since direct experiment has proved that they are always hurtful when they are absorbed by the plants in sufficient quantity.

That portion which, for the better comprehension of the facts, we have called the axis of the radicle, presents greater difficulties in its study, depending in part on the fact that its summit is masked by the adhering cortical zone not yet exfoliated, and in part that some of the cells of this latter region are loaded with very fine feculent granules, which interrupt the passage of light. But by removing the point of the radicle to the extent of about a quarter of a millimetre, and moistening its apex with a drop of phosphoric acid diluted with twice its weight of water, the still adherent cortical cells may be made to exfoliate, and the extremity of the axis of the root is set free, while the feculent granules of its cells are dissolved, and leave the tissue conveniently transparent.



These cells, which are united so as to form an axis or cylinder, whose free extremity ends in a hemisphere, have the form of quadrangular prisms enlarged about the middle; they decrease from the base of the organ towards its apex, so as to become cubical or tubular in that region, where, by the aid of a sufficient number of preparations, it may be ascertained that those cells which bound the hemispherical portion of the axis, devoid of feculent granules, are furnished with proteinous substances collected in each cell into two or four distinct masses, such as are observed in the later phases of the development of pollen-cells.

Very soon each of these masses, which continues the symmetry of a row of cells, becomes a new cell, so that the multiplication takes place by a binary or quaternary formation in the interior of mother cells, and not, as Link supposed, at the expense of an extra-cellular cambium. We have not been able to determine whether these new cells result from the formation of simple septa in the mother cell, or by double septa produced by the application together of the lateral walls of two young cells formed around the masses of proteinous substance; however, we incline to believe that they originate in this latter manner, because the most superficial layers of these cells are those which, when pushed forwards, constitute the cortical zone, and, as we have said, they exfoliate as complete isolated cells, which could not be the case if there were only a simple septum formed in the middle.

The cells observed immediately above those which are in course of multiplication, at first square and full of feculent granules of extreme minuteness, become a little elongated in the direction of the axis; and while this elongation takes place, the feculent granules disappear, and the living proteinous matter, then visible, becomes condensed in each cell into two or three irregular heaps, between which septa soon appear. These new cells, whose smaller diameter is then parallel with the axis, in part enlarge without undergoing change, and in part multiply by binary divisions parallel to the axis, becoming wider and larger like the former, forming with them linear series resembling those which are formed by the grains of maize on the axis of the spike. One fact worthy of note is, that in proportion as the cells of the radical axis multiply, we perceive, between the parallel rows they form, dark lines (intercellular passages) produced by the presence of air or some other gas which penetrates to within a short distance of the apex of the axis. This mode of multiplication may be observed in the extremity of the axis of millet, where it is even more easily traced than in that of wheat. It is found also in the radicles of buckwheat, barley, hollyhock, and the *Leguminosæ*: everything leads to the



supposition that this kind of development occurs in the generality of plants. Very frequently, when the medium in which they vegetate stands at a rather low temperature, the extremities of the radicles on the fibrils are tardy in exfoliating; and then their elementary cells, instead of becoming detached singly, exfoliate in sheets like an epidermis, strips of which they in fact are.

The seed of black mustard, germinating at 54° F., produces radicles in which the cells of the apex of the axis, and those of the exfoliable layer which clothe it, are filled with granules whose opacity renders the most persevering investigation fruitless. But if we wait until adventitious roots are formed, we may find among these some not more than a fifth of a millimetre in diameter, and perfectly transparent. A fibre of this kind placed on a slide shows, without the necessity of injuring it, its axis with its spiral vessels and its cortical layer, which, instead of exfoliating like that of wheat, becomes detached in the form of a cap, formed by the union of several superimposed layers. A remarkable point is, that these caducous layers cease to be so when the radicle and cotyledon are kept in a sufficiently moist atmosphere, if the saturated atmosphere is only allowed access to the apex of the root. In that case, we see the most external cells of the cortical layer emit absorbent appendices, like those on the epidermis of the base and middle portion of the root, and the spiral vessels, which in ordinary cases terminate at a certain distance from the apex of the radical axis, present themselves quite close to the extreme limit of this region, which shows that there exists an intimate correlation between the functions of the absorbing appendices and those of these vessels, as was supposed by Link. This faculty possessed by the epidermal cells, of emitting absorbent appendices to counteract the deficient supply of water or humidity, has a no less remarkable influence upon the direction of the radicle.

If we moisten the meshes of a sieve with distilled water containing a trace of chloride of calcium, so that the cloth may not become completely dry in the open air, and then scatter over the outside of the cloth seeds of *Camelina*, the latter will adhere readily on account of the mucilaginous film they form when brought in contact with water. If the inside of the cloth of the sieve is then covered with a thick layer of Swedish filtering-paper saturated with water, the seeds germinate, and their radicles, instead of taking a direction perpendicular to the horizon, creep along the outside surface of the cloth, and remain attached to it by the aid of their absorbent appendages\*.

\* In like manner we often find an extensive felted mass of fine radical fibres adhering firmly to pieces of bone, shell, or porous stone buried in



From this description it is seen that the exfoliation of the cortical zone varies according to the conditions of humidity and temperature under which the radicles are placed; but we must recognize, side by side with these causes, that it is also subordinate to an individual predisposition, since it does not take place always in the same manner when the subjects are placed in identical conditions.

In the radicles of wheat, barley, millet, vetches, clover, pease, lentils, hollyhock, buckwheat, &c., it takes place by complete disunion of the cells in the midst of a viscid layer.

In the poppy, *Camelina*, black mustard, colza, purslane, chervil, corn-salad, &c., it takes place in the form of a hood, composed of cells but slightly adherent, and impregnated with the viscid substance.

In *Enanthe Phellandrium* the exfoliation takes place in strips composed of epidermal cells, which adhere strongly to the subjacent tissue.

In *Glyceria* it takes place in the form of a hood composed of very firmly coherent cells; in *Lemna* the exfoliable cortical layer forms a sheath, which adheres by its base to the hemispherical portion of the axis of the radicle; and it is remarkable that this hood already exists while the radicle is still enclosed in the coleorhiza. If *Lemna* is examined at the epoch when its radicle is beginning to sprout, this organ will be found in the form of a little cylinder, of a darker colour than the surrounding tissue, and it is contained in a groove existing in the inferior surface of the leaf. This cylinder, now measuring about the fourth of a millimetre, is covered by a membrane in the shape of a sheath, composed of cells contiguous to those which bound the inferior surface of the leaf (coleorhiza).

When the whole is compressed gradually between glass, the sheath is seen to burst at its apex, and allow the exit of the radicle already enveloped in that persistent hood which is observed at the extremity of the root when this is examined in the adult condition\*. This layer or hood, which, as we have said, adheres to the apex of the radical axis, grows for a long time after the radicle has ruptured the summit of the coleorhiza; for

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the soil, or to the sides of earthen pots where these are kept moist.—A. H.

\* This firm hood-like body, the *pileorhiza*, placed on the point of the root like the head upon an arrow, seems to occur on all nascent adventitious roots, before they have broken out from the cortical layer of the stem. Originating in the cambium-region, they push the cortical or epidermal tissue before them, and absolutely rupture the latter, the ragged edges of which stand up round the base like a collar, forming the so-called *coleorhiza*.—A. H.









Garreau, Lazare and Brauwers. 1859. "XXI.—Researches on the cellular formations, the growth and the exfoliation of the radical and fibrillar extremities of plants." *The Annals and magazine of natural history; zoology, botany, and geology* 4, 201–209.

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