

Opening address to the Botanical Society of Edinburgh delivered in November 1878 : being a sketch of the present state of our knowledge regarding the digestion, absorption, and assimilation of animal food by *Dionaea muscipula* / by Thomas A.G. Balfour.

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OPENING ADDRESS

TO THE

BOTANICAL SOCIETY OF EDINBURGH

DELIVERED IN NOVEMBER 1878

BY

THOMAS A. G. BALFOUR, M.D., F.R.C.P.E., F.R.S.E.

PRESIDENT

BEING

A SKETCH OF THE PRESENT STATE OF OUR KNOWLEDGE REGARDING
THE DIGESTION, ABSORPTION, AND ASSIMILATION OF
ANIMAL FOOD BY *DIONÆA MUSCIPULA*

EDINBURGH

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1879

OF THE

BOTANICAL SOCIETY OF AMERICA

MEMORIAL VOLUME

R52255

ON
DIONÆA MUSCIPULA,

AS REGARDS

ITS POWERS OF DIGESTING, ABSORBING, AND
ASSIMILATING ANIMAL FOOD.

GENTLEMEN,—It is now my duty to demit the high office to which you did me the honour of electing me. Conscious of my inability to discharge its duties aright, I made a claim on your kind indulgence, and I have now to acknowledge the uniform kindness and sympathy which I have experienced at your hands, and to return you my most cordial thanks. I deeply regret, as I am sure you also do, the absence on this occasion of one (I refer to Mr M'Nab) for whom we entertain the highest respect and esteem, whose monthly communications were so valued by us, and who was ever ready to give us the benefit of his opinions, which had been matured by a large experience, of which he had fully availed himself. We do trust and pray that the Giver of all good may still spare him to us and to the science which he loves so well, and that we may yet again have the benefit of his presence among us.

On leaving this chair it has been, as you know, the custom for the retiring President to address you on some theme connected with our special science; but I must

confess the difficulty which I have experienced in fixing on a subject. At one time I thought of continuing in the strain of my remarks on taking the chair, and enlarging on the various fallacies, from incorrect reasoning and false analogies, which have crept into our modern science, and which have, I am sorry to say, been supported by some names of real weight and distinction, which have tended, especially among young and ardent promoters of science, to give a currency and acceptability to opinions which, if left to their own merits, could not for a day survive a strict logical scrutiny. Such a theme, however, though important in the highest degree in the interests of *true* science and *true* religion, I have been compelled to forego, as circumstances transpired which deprived me of the anticipated leisure which would have been necessary for me to do anything like justice to the subject. The same cause must serve as my excuse for the nature of the remarks which I may make to you to-night. I had chosen as a subject for original research the degree of force with which the leaves of the *Dionæa* close, and had I been successful I should probably have pursued the same subject into the domain of tendrils, &c.; but, unfortunately, the anticipated results did not follow, and much time was expended in varying the experiments and in endeavouring to find out the cause of failure, but hitherto without any satisfactory result. I am not, however, without hope that the object aimed at may yet be attained, as I propose, if spared till spring, to use a new instrument in the research. These are the instruments used, and this is that which I propose for future observations. At the end of our meeting I shall be happy to explain the method pursued, and shall be glad if any one can suggest a more satisfactory mode of securing the end in view. Some years ago, very shortly before the appearance of Darwin's classic work on "Insectivorous Plants," I had the honour of laying before this Society the results of some experiments which I had made on *Dionæa muscipula*. Darwin's work threw, of course, everything else into the shade, and from the careful way in which his experiments were executed, and the large number of facts from which his deductions were formed, I certainly thought that the question regarding digestion and, by inference at

least, of assimilation of animal food by *Dionæa*, &c., was for ever set at rest. But such is by no means the case, and the humble office which I have this night undertaken to perform is to present you with some of the researches which have been prosecuted since that time, and which seem to me, *directly* or by just and necessary *inference*, to support the conclusion of the similarity between the animal functions and those which the *Dionæa* performs. As a just knowledge of structure lies at the bases of a correct physiology, I had intended in the first place to have placed before you the anatomy of this plant as that has been very fully investigated by Kurtz, Casimir de Candolle, and Fraustadt. I then designed dealing with the causes of the closing and opening of the leaf, and, after having treated of the digestion, &c., to have concluded with a brief sketch of the valuable and instructive researches of Munk, Sanderson, and Page on the electrical conditions of the leaf both before and after excitement. I found, however, that the subject was so large that I was compelled to confine myself to the third topic, and to that accordingly I shall direct your attention to-night.*

The great question in regard to this plant and its allies undoubtedly refers to digestion, absorption, and assimilation. As I have already said, after all the care and patience which have been expended on the study of these plants and the cautious inductions from a large number of experiments which have been drawn, it is surprising to find that ridicule should still be one of the weapons with which this subject is assailed; nevertheless such is the case, as an article in an able botanical journal clearly proves. As it is somewhat lively and amusing, I shall make a quotation, though I shall not restrict myself to the *ipsissima verba* of the author. A London house fly had been leisurely enjoying a sip of porter in the early part of the day, and, unfortunately, becoming rather unsteady in his gait and dim in his vision, he falls a victim to the watchful *Dionæa*, and dies a lingering death. The report of the case is com-

* I intend to treat only of *Dionæa muscipula*, and hence any reference to other plants of the same class is simply by way of illustration, and, as the analogy is in many respects so striking, of inferring the similarity of the functions of the *Dionæa*.

municated to the authorities. No coroner's inquest is instituted, and hence no *post-mortem* examination of the body takes place; but it is known to a select circle of his friends that this liquor was in his body, and that immediately thereafter he was captured. Now, this is one of the liquids most likely to turn *acid*, and in this case the litmus-paper of the man of science tells the effect but not the cause, for the functions of the plant may be and doubtless are more or less deranged by extraneous applications. So far so well. But does not this facetious gentleman know that a perfectly sober fly—whether in London or elsewhere, one whose strict teetotalism has guarded him from even tasting this Circean cup—or, that a portion of white of egg will call forth an acid secretion; and again, I should like to ask our humorous friend whether sour porter, be it from London or Dublin, contains formic acid?

As late as last year in the French Botanical Society, a member, in answer to M. Heckel of Montpellier, threw doubt on the digestive nature of the secretions of these plants by asserting that there was nothing wonderful in an acid liquid, whether a glandular secretion or not, preserving animal matter from putrefaction, inasmuch as we constantly found sound vegetables preserved by being pickled in vinegar. Unfortunately for this member, the simplest experiment might have saved him from committing himself to such an unguarded and erroneous statement. In the paper to which I have referred I made that experiment by taking two pieces of meat, one of which was wrapped carefully round with sphagnum—which yields a thoroughly acid fluid—while the other portion was entrapped in the leaf of a *Dioncæa*. At the meeting of our Botanical Society both of these pieces of meat had been in their respective places for some time, and when submitted to the sense of smell of our distinguished President, Sir Robert Christison, he had no hesitation in declaring that the meat in the sphagnum was far gone in decay, while the other portion had no disagreeable smell whatever.

But the question regarding digestion and absorption has been opposed by abler advocates than these, even by those

holding high positions in the world of science. Thus Duchartre has objected to the idea of absorption on the ground that it was not in accordance with our knowledge of the functions of leaves, and of the whole course of the nutrition of vegetables, and therefore was not to be seriously entertained. In my previous communication to this Society I pointed out that this argument of his reminded one of the miserably fallacious arguments against miracles urged by Hume, and stated that in both cases it was a mere *petitio principii*. All plants are not constituted like the *Dionæa*, and if it has such a peculiarity in structure, why should it not have a similar one in function?

Bechamp declares that the idea of carnivorous plants is the product of an illusion,—the subversion of the best founded demonstrations of science.

You will at once perceive that these latter objections proceed on the assumption that the functions of these leaves are directly opposed to the whole course of nature. But is this the case? In another article which appeared in "The Garden" I attempted to show that there are links in creation appearing every here and there, and testifying that in structure and function animals are not everywhere separated from plants by a perfectly impassable barrier, but exhibit a striking unity in the Creator's plan. What, for instance, can be more clearly vegetable than the chlorophyll, which is the cause of the lovely and refreshing verdure which is everywhere exhibited by plants? And seeing that this product exercises a special reducing power on the carbonic acid of the atmosphere enabling the plant to fix the carbon and eliminate the oxygen, it seems only fitted to find a place in that kingdom which has been called an "apparatus of reduction;" yet it is not altogether alien to the animal world, for allied green granules have been found in the bodies of *Hydra viridis*, *Euglena viridis*, &c. And the chief pigment in the bile of herbivorous animals—the biliverdin—has been regarded by Dr Thudichum as somewhat analogous to this product of the vegetable world. Again, cellulose, of which the cell-walls of plants are almost, if not entirely, made up, is not exclusively confined to these, but is found also in the mantle of *Phallusia mammillaris* and in that of the *Cynthiæ*, &c.

As regards the liver of animals, no less an authority than Prout has declared that here the animal and vegetable kingdoms approximate in function. His words are—“ Long and repeated attention to the functions of the liver, both in health and disease, has satisfied me that this organ in its assimilative function is analogous to or identical with the assimilative functions of vegetables.” Such were the instances adduced to overcome in some measure an objection of that kind. But since that was written there has been discovered by Professor Hanstein of Bonn, and prosecuted by Professor Famintzin of St Petersburg, one of perhaps the most interesting proofs of the similarity in the two kingdoms as regards structure, seeing that he has shown that in the very origin of the structure in both cases there is a marvellous resemblance. Every one at all conversant with human or comparative embryology knows that, before the “ primitive trace ” of the embryonic structure appears, there are formed three distinct layers in the thickened oval portion of the germinal vesicle which are styled the three layers of the blastoderm or germinal membrane, and which have been named respectively the serous, vascular, and mucous layers, or, more correctly, the epiblast, mesoblast, and hypoblast. From these three layers the whole structures of the body are produced. From the epiblast arise the brain and spinal cord and the organs of the senses, also the epithelium of the skin, with the cutaneous glands. The mesoblast gives origin to the osseous and muscular systems generally, the spinal nerves, connective tissue, the urino-generative organs, &c. ; also to the heart and blood-vessels, the spleen, lymphatic glands, supra-renal capsules, &c. From the hypoblast or inner layer are derived the intestinal epithelium, together with that of the glands opening into the intestine and the glandular cells which they contain, also the lungs, the thymus and the thyroid glands, the liver, pancreas, and permanent kidneys. Now, Hanstein pointed out the existence of three distinct layers in the developing embryo of *Capsella bursa-pastoris*, and also in that of several *Compositæ*. The further development of these three initial layers or embryonic membranes “ has proved to be quite identical with the formation of the embryonic

membranes in animals. Before any trace of cotyledons, while the embryo is very small, the *Pleroma* forms an axile cylindrical cord sheathed in two layers of cells, the periblem and dermatogen. Soon divisions appear in the dermatogen at the lower end of the embryo (near the suspensor), and the periblem increases to several layers on the sides of the embryo, but remains one-layered at both ends. These cell-divisions give rise to the root-cap and the primary bark. In the more developed embryo, where the cotyledons appear as two symmetrical projections, three membranes or layers of tissue (if the tissue be rendered transparent) are as clearly distinguishable in the cotyledons as in the axile portion of the embryo, &c." Professor Famintzin summarises his chief results as follows:—"In the earliest stages of the formation of the vegetable embryo, three morphologically distinct layers of tissue appear, which, during the complete development of the embryo, and most likely during the whole life of the plant, retain, with few rare exceptions (the embryonic vesicle for instance), their independence, and only certain defined tissues are formed from them. In other words, they correspond exactly to the embryonic membranes of the animal kingdom." Gorup Besanez and Will made known that in the seeds of the vetch a ferment is contained which, on being abstracted by glycerine, can dissolve albuminous substances, such as fibrin, and render them capable of absorption. But while this was going on slowly but surely, Professor Morren of Liege rushed into the field, and, by his lucid and able work on "Vegetable Digestion," entirely removed the ground on which his opponents were standing by showing that the whole course of nature bore out the conclusions regarding digesting and absorbing plants. "In fact," he exclaims, "I see no difference between the alimentation of the plant and that of the animal; it seems to me necessary to characterise the process in plants by the same name. In other words, digestion has either no existence at all or it is common to all living beings." And again he says, "There is no ground for astonishment in all this, for, in my opinion, the facts observed among carnivorous plants are in perfect harmony with the general theory of the nutrition of plants;" and yet

again, "Digestion is common to all vegetables,—it seems to be the necessary condition of assimilation."

These are *bold* statements, but they are no less *true*; and the whole of his able article on vegetable digestion is devoted to its proof. Not long ago in this Society we had an admirable digest of this work of Morren's, so that it would be superfluous for me to dwell at any length upon it. At the same time, as it is so well fitted to meet some of the most frequent scientific objections, I must cursorily recall some of the most salient points. Digestion is essentially a process of fermentation, whereby substances which would otherwise be insoluble are rendered soluble, and so fitted to be taken into the system. In the animal economy we have various ferments playing an important part in the process of digestion. Thus the saliva contains ptyalin, which effects the change of starch into dextrin, and ultimately into glucose or grape-sugar. This is called the amylolytic action of saliva, and a small quantity of the ferment, under favourable circumstances, is capable of effecting the change in an almost indefinite amount of starch. Should this ferment fail in accomplishing the whole result desired, we have in the pancreatic fluid, which is poured into the intestine immediately below the hepatic secretion, one kind of ferment which acts as powerfully as ptyalin and for a similar object, so that any residual starch becomes transformed into grape-sugar. Now, in the vegetable kingdom we have a fine and familiar instance of a similar ferment in the germination of barley. Diastase is the name applied to it, but in its action it is identical with ptyalin and one of the ferments in the pancreatic juice, as it acts on the insoluble starch in the seeds, and by changing it ultimately, by means of hydration, into grape-sugar, secures its becoming available for the nutrition of the embryo. Now, diastase is also found in potatoes in the neighbourhood of its buds, where it effects a similar change. In connection with this, it is an important fact that chemists can establish no distinction between animal and vegetable diastase.

There is another ferment found in the mucus of the stomach and also in the *succus entericus*, which changes cane-sugar into grape-sugar; for though cane-sugar is

soluble, it is not absorbed nor assimilated by animals, and hence it must be digested. Now this ferment exists in the sugar-cane and beetroot; and when these plants are about to flower there is a great demand for nutritive material, the cane-sugar is accordingly transformed into glucose, and after the flowering it is found that the sugar has disappeared, part of it having been burned off in respiration, and the remainder having given rise to cellulose, as has been experimentally proved by Durin ("Comptes Rendus," July 3, 1876, p. 355).

The next digestive fluid which we shall consider is the gastric juice, which contains pepsin as its ferment, which changes the insoluble proteids into soluble peptones, and so renders them capable of being absorbed. And here again the pancreatic juice, by another ferment, which has been named trypsin, materially aids, and though there are differences between the effects of the *two* ferments, yet for our present purpose it will suffice us to regard them both as rendering soluble albuminous bodies which would otherwise have remained incapable of absorption. In the vegetable world we have a similar process; thus, in the grains we have stored up albuminoid materials under the form of gluten, legumin, and farina to supply the first necessities of the germinating period. These substances are insoluble in the cotyledons, but as the little plant is developed they are dissolved and are assimilated by the active protoplasm. We have already referred to the experiment of Gorup Besanez and Will, in which a ferment was extracted from the vetch which had the power of dissolving fibrin and of transforming it into peptones, thus resembling trypsin, for as this pancreatic ferment produces leucin and tyrosin, so in the case of legumin we have leucin and asparagin appearing; and not only so, but in the same *Vicia sativa* Will has shown the still greater resemblance to the pancreatic juice by obtaining another ferment which transforms starch into grape-sugar.*

* There is an interesting circumstance in connection with this double digestive agent in the case of yellow elastic tissue, or at least of elastin, which is its chemical basis. We know that this substance is insoluble by pepsin, and though Darwin declares that it is insoluble also in *Drosera*, yet in one instance I observed its solution in a leaf of *Dionæa*. On June 8, 1878, a small piece of *ligamentum nuchæ* was placed at 4 P.M. on a leaf of *Dionæa*. On

But we have yet to consider further changes effected in digestion by the bile and the pancreatic juice, which act on the fatty articles of food, the *former* slightly emulsifying them, and the *latter* both emulsifying and saponifying them, this last process being the splitting them up by means of hydration into glycerine and fatty acids. Oleaginous grains, when pounded in water, give a well-known emulsion, soon followed by glycerine and fatty acids; a similar action occurs during germination. Now we have accumulations of oils and fats stored up in the seeds of Cruciferæ, Papaveraceæ, Linaceæ, &c.; also in bulbs of onion, &c.*

This vegetable digestion is generally manifested in the depôts of nutriment which occur in seeds, tubercles, certain roots, bark, and pith. It occurs when vegetation begins, and the tissues are impregnated with water, &c.

Morren gives a table containing the proximate elements in the nutriment provided for the young plant, and he also gives one with the proximate elements in the nutriment provided for the young animal which afford a fine illustration of the similarity of composition; and if so, why should there not be a similarity of digestion?

Farina of Wheat.		Cow's Milk.	
Starch, . . .	780	Sugar of milk, . . .	347
Fatty matter, . . .	20	Butter, . . .	258
Gluten, . . .	170	Casein, . . .	242
Albumen, . . .	20	Albumen, . . .	97
Salts, . . .	10	Salts, . . .	56
	1000		605
			339
			1000

June 10th, leaf was open, the fibre was wet, and the leaf again closed. Next day (11th), leaf was partially open, spikes slightly crossing X. June 13th, at noon, warm sunshine, distal half of leaf open, so that at the point the spikes are separate / \, and the tissue is seen of a white colour. Proximal end is quite closed. It continued so till 17th. On June 19th it was quite closed throughout the whole extent. On opening it the piece of elastic tissue was found in it. It remained closed till July 1st, when, at 3.15 P.M., it was again examined, and the elastic tissue was found nearly dissolved. It was again closed, and was so on July 3, but, unfortunately, no further examination was made.

* In the case of *Drosera* and *Dionæa* we know from Darwin's statements, and from our own observations, that fat is not digested by the secretions of these plants; but this circumstance, in their case, can be no disadvantage, for in the ordinary food of such plants, which consists of insects, there cannot be much danger of the fatty elements disturbing their digestion.

Hence, then, in all vegetables the embryo and buds during the first stages of germination digest the nutritive stores in their neighbourhood. When chlorophyll, however, is developed a new feature is manifested, for under the influence of light the plant becomes an instrument of reduction, and acts an intermediate part between the mineral and animal worlds, but the starch, oil, and albumen thus stored up are rendered soluble by digestion, and by absorption and assimilation made to contribute to the plant's own maintenance as well as to serve for the nourishment of animals. These views of Professor Morren are not peculiar to him, but express the opinions which the most eminent scientific observers now hold. I shall only refer to one, viz., Van Tieghem, whose ability and skill are everywhere acknowledged, and whose prolonged attention to this subject entitles him to speak with authority; and in his latest paper on the digestion of albumen* we find him thus expressing himself—"All living things digest." He speaks of digestion being the act of a living being, by which it transforms by the aid of an active liquid produced by it, and renders soluble a substance formerly insoluble. It is in his view either *external* if the substance is *outside* the organism, and in this case is followed by absorption, or *internal* if the substance to be dissolved is in the cells of the body, and in such a case is not followed by absorption. "Infusoria and free vegetable aquatics, living exclusively on dissolved aliments, appear to be destitute of an *external* digestion; they are, nevertheless, like all the others, the seat of the internal digestive phenomena. It is by the free surface of the body that in certain regions the *external* digestion acts in their case, but similar digestive regions can be met with together or separately upon each of the three fundamental organs of vegetable apparatus—the *roots*, the *twigs*, and the *leaves*." One of the most interesting facts experimentally determined was that the digestion was in some cases completely effected by the cells of the albumen itself quite independently of the embryo, which in such a case performs simply the office of *absorption*. His experiments in proof were of two kinds. In the first case the albumen was carefully

* Comptes Rendus, tome 84, p. 578.

removed from the embryo and integuments and placed in the ordinary conditions of vegetation, and careful observations were made to see whether there were signs of activity and solution of the solid contents of the cells. In such a case the power of digestion must certainly be in the albumen itself. But as in this case the normal condition of the albumen could not be said to have been preserved, another kind of experiment was made with the view of controlling the first. In this second case the embryo was left inside the albumen, and the attention was directed to the fact whether the solution began from *without* or from *within* (centripetally or centrifugally). If centripetal, it must be from the *albumen*, but if centrifugal it must be from the *embryo*. He divided albuminous contents of seeds into three kinds, which he names, 1st, Fleshy or oleaginous or corn albumen; 2d, Amylaceous or farinaceous albumen; 3d, Cellulosic or horny albumen; and as instances of these three he chose for experiment *Ricinus communis* as an illustration of the first class. The second class was represented by *Mirabilis longifolia* and *Canna aurantiaca*; whilst *Aucuba japonica* and *Phoenix dactylifera* represented the third kind, where the reserve matter consisted essentially of the thickenings of the cellular membranes.

It was in the first of these classes alone that he found the digestive power existing in the cells of the albumen. At first it measured in length 12 mm., and in breadth 8 mm., and at the end of the month it was in length 22 mm., and in breadth 16 mm., and also somewhat thicker, so that two great dimensions were doubled, the constituent cells were much enlarged, and the air-passages separating them were also developed. The fleshy or corn albumen had here absorbed oxygen and disengaged CO₂ in equal volumes—*i.e.*, it had respired like an animal. One of the most curious results of this experiment was that starch was formed by this isolated albumen, without, of course, the presence of any chlorophyll; and this starch increased so much that it tended to transform the fleshy albumen into the amylaceous kind.

The great point, however, with which we have here to do is with the fact that in certain circumstances, not merely the living embryo, but also the dormant living

substance containing the reserve store around it, has itself the power of digesting the contents of its own cells when roused to activity.

But you must have noticed that the objection of Duchartre was specially directed to the subject of *absorption* by leaves, as not being in accordance with our knowledge of the functions of leaves, and of the whole course of the nutrition of vegetables. Now, as regards the power of absorption in leaves generally, we have the admirable and exact experiments of Boussingault, establishing it as a fact that, in so far as the physical function of leaves is concerned, they can replace the roots of a plant as absorbing agents. A lilac was chosen, whose forked branch, with an equal superficies of foliage on each fork, was so adjusted that the one fork was immersed in water, while the other was subjected to the ordinary atmospheric influences. The transpiration from the leaves of the latter was of the same amount as under normal circumstances, and at the end of a fortnight the leaves were as fresh as at the beginning of the experiment; which showed that the submerged leaves had supplied the place of roots, so far, at least, as regards water. In his experiments on the branches of vine, oleander, and artichoke, where in all of them apparently the end of the cut branch was submerged with the leaves, he seems to me to have laid himself open to the objection that possibly the open end of the stalk admitted the water to permeate the tissues; but then, on the other hand, the time during which the healthy condition of the atmospheric leaves was maintained (a month in the case of the vine-shoot, and four months in that of the oleander) show clearly that the immersed leaves must, at least, have played the *most important* part in the absorption of water. But while in all these an equal proportion was maintained between the surfaces of the submerged and of the atmospheric leaves, in the case of the artichoke it was necessary that the surface of the leaves below the water should be four times that of the aerial ones.

But yet another function of the root can be discharged by leaves, and that is the absorption of solutions of mineral matter. Boussingault employed for this experiment a solution of sulphate of lime, containing a $\frac{1}{1000}$ of solid

matter, and the leaves of many plants of different kinds were chosen, and these plants placed in circumstances favouring absorption. Drops of the above solution were placed on the leaves and covered by watch glasses, with greased edges, so as to avoid evaporation. Absorption of the whole mineral matter and fluid took place in most of the instances. The under surface of the leaf absorbed much more rapidly than the upper side. Other salts were tried, such as sulphate and nitrate of potassium, with like results; but when solutions of chloride of sodium and of nitrate of ammonia were employed, the absorption was not so complete. The leaves of a plant, then, are seen to be able to supply it with probably a considerable amount "of its saline constituents by means of the ammoniacal salts found in the air, and of the alkaline and earthy salts suspended there which are deposited on the surface of the leaves by rain and dew."

There is one other observation which the same high authority has made, which has a special bearing on *Dionæa*. He found that in certain cases where *pressure* was employed, the absorption of water took place to such an extent that it even more than replaced the water lost by transpiration. As an example, he gives a chestnut branch dipped in water, which transpired 16 grammes *per horam* for every metre of foliage; it was then placed in a tube of water, and subjected to a pressure of a column of water $2\frac{1}{2}$ metres high, and it was found that under these conditions the evaporation rose to 55 grammes hourly, and that at the end of five hours the branch weighed more than at the beginning. The force with which the *Dionæa* leaves press upon their contents must thus, it would appear, exercise a considerable influence on their absorbent power. In my paper previously referred to, I inferred that absorption had taken place by the *Dionæa* leaf, because I had from time to time observed the gradual solution of the animal matter enclosed, and also that none of the solution had in ordinary instances escaped outwardly, and that when the leaf opened at last nothing or only the merest trace of the substance was found; and I remarked that, if these considerations did not shut us up to the conclusion that absorption had taken place, I feared we must have an equally great difficulty in

establishing the fact of absorption by the roots of plants or by the lacteals and lymphatics of animals. I at that time, however, attempted to prove *directly* that absorption did take place, and for that purpose I used insects and pieces of beef, which I had stained red or blue by steeping them in a solution of cochineal, or in one of sulphate of indigo, and I hoped that by the colours in the cells I might have been able to trace the course of the absorbed material. Probably my infusions were too strong, but at any rate my expectations were disappointed, as the coloured fluid was actually squeezed out from between the leaves. But I observe that Fraustadt has since then made similar experiments, and with a successful result. He used small pieces of white of egg, coloured by aniline-red. After eight days the contents of the leaf had disappeared entirely, and the surface of the leaf was quite dry and covered with numerous red points, while previously to the experiment it had been of a uniformly green colour, as the glands had originally possessed colourless cell contents. Besides, after the experiment a large round body, probably a cell granule or nucleus, was in every cell coloured in a lively manner, and this could be seen distinctly fourteen weeks afterwards only slightly changed in colour from being preserved in glycerine. The only other parts affected by the colour were some peripheral vessels from the large middle vascular bundle of the petiole, which were also coloured red, but had a yellowish shade over against the glands. His experiment with saffron was not so successful, though the gland cells were thoroughly yellowish, yet the colour was not so intense.

The actual occurrence of absorption in the case of *Drosera* has been proved by a chemist, who fed the plant on flies which had been soaked in chloride of lithium, and after several days he found traces of the metal in all the tissues of the plant. But Mr Lawson Tait, who has so zealously and successfully prosecuted the subject of insectivorous plants, instituted experiments to prove that absorption of water and of ammoniacal salt does take place by the leaf of *Drosera rotundifolia*. They were of the following kind :—He deprived some silver sand of all organic matter, and with this he filled three pots, say A, B, C, and

in each of these pots he placed a number of plants of *Drosera* under the following conditions—1st, plants perfectly uninjured, but repeatedly washed all over with distilled water; 2d, plants similarly washed, but with all the roots pinched off close to the rosette: the leaves in this case were all buried, the budding flower-stalk alone appearing above the sand; 3d, plants similarly washed, with the roots and the flower-stalk left on, the former being buried in the sand, but all the leaves pinched off; 4th, plants similarly washed, roots left on, four leaves buried in the sand, two leaves, flower-stalk, and roots left above the sand, and protected against receiving anything from the sand. All were carefully watched, and no flies caught. The three pots were treated in the following way:—The plants in pot A were treated with pure distilled water; those in pot B had a strong decoction of beef given them, while those in pot C had $\frac{1}{2000}$ per cent. solution of phosphate of ammonia. Seventeen days elapsed, and the following results were obtained:—In pot A all plants growing and looking healthy. Though those with leaves buried and roots exposed looked sickly for a few days, yet at the end of the experiment they were putting forth new leaves. So were those plants with the leaves pinched off and the roots buried. Those with the roots pinched off, and all the leaves buried, were bursting into flower. In pot B all were greatly damaged, the food seemed to be too strong, and proved disastrous to all. The pot smelt strongly of ammonia. In pot C the appearance was much the same as in pot A, only the growth was much more active, for some of the plants with the roots off and leaves buried have pushed up new leaves through the sand. Those with only four leaves buried have put out numerous new leaves; the roots here are quite dry. In one of those latter Mr Tait cut away roots five days after the plant had been put into the pot, and it was as vigorous as the rest.

One of his conclusions is—It is, therefore, perfectly certain that the sundew cannot only absorb nutriment by its leaves, but that it can actually live by their aid alone, and that it thrives better if supplied with nitrogenous material in small quantities.

Mr A. W. Bennet has given us good grounds for be-

lieving that "absorptive glands" exist in the leaves of *Drosera rotundifolia* and *Pinguicula vulgaris*, and that bodies more or less analogous to these glands are found in all the other plants which have to the present time been regarded as carnivorous. Thus, they exist in *Nepenthes* and *Dionæa*, and the "quadrifids" of *Utricularia* strongly resemble them. The interesting fact is also stated by Mr Bennet that, with the exception of *Callitriche verna*, these absorptive glands do not occur in the leaves of any other than insectivorous plants. Though further researches on this subject are desirable, yet the above observations by so able and competent a botanist strongly confirm the views just stated, and point to the provision of special organs by which the process of absorption of animal food is accomplished.

We now proceed to consider the third great question—viz., that of assimilation. It is the part of the process to which probably most objections have been taken, even Professor Morren refusing to commit himself at once to it. I mentioned in my previous paper a fact communicated to me by Mr Lindsay, a very careful observer, that *Dionæas* covered with glass jars did not thrive so well as those which were fully exposed. This seemed to me to prove satisfactorily that the absence of insects was prejudicial to the healthy life of this plant. We determined, however, to put this to the test of fresh experiment. We had plants placed under large wide-mouthed jars, one of which was left open, while the other two were so arranged that water and air were freely admitted, but no insect could obtain access to the enclosed plants. (I show you the apparatus employed). For months they were left in the same greenhouse, and no difference was apparent in the general appearance and growth of the two sets of plants; and even at the end of two or three years the plants excluded from insects appeared as healthy and strong as the others. I always felt, however, that mere appearance was not a sufficient guide in a matter of this kind, and hence I never communicated the results to this Society. Besides, when I considered the wonderful structure of the *Dionæa*, the admirable adaptation of all its parts for their allotted functions, I could not but regard it as highly im-

probable that such complicated contrivances were not designed for the nourishment of the organism. Casimir de Candolle has more recently asserted that the opinion regarding digestion and absorption in the case of *Dionæa* can only be regarded as an *hypothesis* until direct experiments have proved that the substances so digested and absorbed are assimilated—*i.e.*, are utilised for the formation of new tissue. To test this De Candolle performed experiments similar to my own. One set of plants were fed with pieces of meat and white of egg, as well as insects, while the other two plants had only what they got from the soil. After six weeks' careful study of them he could detect no difference in their general appearance, or in the number and size of the new leaves which had been produced during the experiment. By many direct measurements he was satisfied that the different parts of the same leaf did not increase through animal food being digested. He owns that his experiments were too few, and I do not know that he has ever carried out his resolution to prosecute the subject further.

The fallacy of these experiments has, however, very recently been shown by Mr Francis Darwin, who, by most careful observations on *Drosera*, has proved that assimilation does undoubtedly occur, though, as its more marked indication is to be found in the organs of reproduction, it is easy to understand how other observers have been led into error. As I am not aware of any very exact experiments having been made on *Dionæa* in proof of assimilation, I shall refer to those where *Drosera* was chosen as the subject of experiment, and considering the many essential points of resemblance between that plant and *Dionæa*, we may feel justified in attributing like qualities to the latter.

These experiments of Mr Francis Darwin were conducted with great care, all likely sources of fallacy having been avoided, so that I need not detail the plan followed farther than to say that the soup plates in which the plants were placed were divided into two equal portions, on the one side of which were the *unfed* plants and on the other the *fed* ones. Roast meat was used as the diet of these last, $\frac{1}{50}$ of a grain being placed on the secreting glands. The

experiments began on June 11th of last year, and ended on August 25 of same year. The first difference observed was on July 17, when the *fed* side, taken as a whole, was decidedly greener than the *unfed* side. This change was manifest in all the plates. The tentacles on the *unfed* side were of a redder colour than those of the fed plants, hence chlorophyll was more developed in the latter; and it was proved, by drying and weighing, that a much greater amount of cellulose was formed by the fed than by the unfed plants; because chlorophyll is associated with an increased assimilation of carbonic acid, and thus permits more cellulose to be formed. An average leaf from fed and unfed sides was examined on July 18, and a marked difference was observed both by the naked eye and by the microscope; in the former case it was evidenced by the dark purple hue of the fed leaf, and in the latter by the large and numerous chlorophyll grains crowded with starch, with which its cells were filled. He attributes the absence of appreciable increase of starch on August 16, 17, and 21, either to its having migrated to the root-stocks and flowering stems, or to its having been used up in larger quantity for the formation of the greater amount of cellulose, which we have seen was found.

To these experiments we shall immediately return; meanwhile we give his final results, which are that the carbohydrates are formed in far greater amount in the *fed* plants. The body of the chlorophyll grain, he adds, is protoplasmic, and hence an increase of nitrogen will favour formation of chlorophyll, and increase the starch-producing powers of the plant. Fraustadt, however, had come to an opposite conclusion regarding the starch, for he had found that it diminished in *Drosera* with absorption of organic matter by the leaves. Darwin's reply is simply—"This result may be perhaps attributed to over-feeding;" but this is by no means satisfactory, for the plant, which had caught an insect, on which he made his first and third experiments, was found deficient in starch. In the first instance the transverse sections through the middle of the petiole, where he found only about five or six cells containing starch, and these lying in the neighbourhood of the middle, largest vascular bundles. In the third experiment, where the

transverse section was through the leaf, there was not a trace of starch. Fraustadt's first experiment at least seems to have been made on a leaf which had not been fed artificially, but which had *naturally* caught an insect, small pieces of whose skeleton were all that remained, so that he could determine no more regarding it; and as his other experiments were with leaves subjected to the same condition, it is not likely that over-feeding would occur, for it has always appeared to me that this misfortune rarely if ever occurs in a state of nature. But Darwin seems to forget that the experiments were in pairs, the second referring to those leaves which had never had organic matter, in which the contents of the cells in the petiole wholly, or for the most part, gave the distinct reaction of starch. Fraustadt's fourth experiment was a transverse section of the midrib of the same plant which was used in his second one, and he found there that the cells were very abundantly filled with starch.

Darwin attempts to explain the deficiency on August 16, 17, and 21, as above stated, by two considerations; the first of these is, that the starch had migrated to the root-stock and flowering stems. Now as to the root-stock, it is a significant fact that the little ears of the base of the petiole, which embrace the rhizome, were, according to Fraustadt, to an extraordinarily abundant degree filled with starch, and this condition exists equally in cases where the leaves have absorbed animal or more general organic food, as where they have had none, and Fraustadt's conclusion is that, since where organic matter is given the starch grains disappear only in the portions above ground where the cells contain chlorophyll, the assimilation or the production of carbohydrates by chlorophyll and the absorption of organic matter exclude each other: but, he adds, that the *presence* of chlorophyll does not exclude the reception of organic substances.

With such diametrically opposite opinions before us, we must conclude either that *Drosera* and *Dionæa* are differently affected by organic matter absorbed by the leaves, which would be in the face of all sound analogy, or we must accept F. Darwin's other suggestion, that the starch had gone to form the increased amount of cellulose which,

as we have already seen, he found in his fed plants. We must, however, never forget that chlorophyll is not essential to the production of starch (if not also of other carbo-hydrates), as the experiments of Van Tieghem have shown.

But let us now look at some of F. Darwin's tables, and we shall be forced to the conclusion that real nutrition of the plant, and especially of some portions of it, is effected by the absorption by the leaves of organic matter. Table 3 gives the number of flower-stems on each side in the six plates on August 7, and the proportion is seen to be, for unfed to fed, as 100:149.1.

Table 5 again exhibits the number of healthy leaves (as shown by their having secretion on their glands) on each side of three of the six plates, and here the proportion of unfed to fed is as 100:136.9. Experiment about middle of August.

From Table 6, among other things, we learn that the total weight of unfed and fed plants (without flower-stems) dried at from 80° to 90° C. was in the proportion 100:121.5.

In Table 7, among other items, the total *number* of stems (including those bearing flowers as well as those bearing capsules) from all the plates gave the proportion of unfed to fed as 100:164.9; and the *weight* of these was as 100:231.9; the *average weight per stem* being as 100:141.3.

In Table 8 we have the *total number* of capsules, which gives the proportion of 100 unfed to 194.4 fed; *average number* of capsules for each stem, 100:121.6; *total weight* of capsules unfed to fed, as 100:130; *total number* of seeds in capsules, as 100:122.7; *average number* of seeds *per capsule*, as 100:122.7, same as above.

Table 9 furnishes us with the *average weight* of each seed, which was in proportion of 100:157.36; *total number* of seeds from all the plants in all the plates gave the proportion of 100:241.5; *total weight* of seeds from all the plants in all the plates was in proportion of 100:379.7.

It is very striking that the greatest disparity in the proportions is in the instance last cited; on this Mr F. Darwin remarks, that "the special advantage which nitrogenous food, given to the leaves, yields is the power of producing

a vastly superior yield of seeds;" *i.e.*, that the reproductive system is that specially affected by an animal diet.

After the flower-stalks had been removed, three plates of plants were allowed to rest in a greenhouse during winter, and in the middle of January more plants were springing up on the fed side than on the other; and on April 3, when picked out of moss and cleansed, Darwin was struck by the fact that the fed plants had a decidedly greater amount of root-stock. The fed plants had thus laid past a much larger store of material than the unfed ones, for the *total weight* of plants was in the proportion of 100:251·6, and the *average weight* per plant was as 100:213·0.

While Mr Francis Darwin was performing these most interesting and valuable experiments, Drs Kellermann and Raumer were, all unknown to him, prosecuting almost identical inquiries, and reaching almost exactly similar conclusions. The utmost care and exactitude characterised their whole proceedings, so that the results of these most competent observers being so exactly alike, must be regarded as settling the question as to the actual nutriment derived from the leaves, so far at least as the *Drosera* is concerned. They kept accurate notes of the number of leaves at beginning of experiment, as well as the mean number of leaves at time of experiment, &c.; the number of flower-stalks, the number of capsules, the average weight of seeds from one capsule, the weight of plants, the side buds, the winter buds, the number of feedings, the number of creatures given for food, for in their case they used aphides, and not roast beef, as Darwin had done. One of these cases contained young plants, which were fed eight times, from June 16 to September 1. The other case contained somewhat older plants, which were ten times fed, from May 4 to September 1.

These experiments proved that the totality of *fed* plants was superior to that of the *unfed*. This superiority showed itself specially in the number of flower-stalks and ripe capsules, the weight of seeds, and in the weight of the winter buds when dried. The percentages in some of these cases are given as follows:—

The flower-stalks in unfed 100:152 in fed plants.

The ripe capsules in unfed 100:174 in fed plants.

The collected seeds' weight in unfed 100 : 205 in fed plants.

Dried substance of winter buds in unfed 100 : 173 in fed plants.

And now, gentlemen, it only remains for me to congratulate you on the present state of our Society, and to remind you that our past session has been by no means an unproductive one, as several papers of great merit have been communicated to us. But as these can be perused in our "Transactions," it is needless to allude further to them. There is one circumstance, however, which has only recently occurred, to which I may for a moment call your attention. The meeting of the Cryptogamic Society will ever be remembered as an eventful incident in this city. The enthusiasm of the members, the ability of the papers read, and the fine collection of fungi, whose judicious arrangement, both æsthetically and scientifically, called forth the admiring plaudits of all, cannot fail to have awakened a fresh interest in this department of botany, and to have given a new stimulus to its more extensive cultivation amongst us ; and I do trust that when phanerogamous plants have mostly disappeared with the approach of winter, our Society may be enlivened by frequent exhibitions of cryptogamous vegetation, which no less than its more aspiring brother exhibits in its exquisite structure and marvellous functions the wonderful skill and matchless wisdom of Him who chooses the weak things to confound the mighty, yea, and the things that are not to bring to nought things that are ; for it is certainly from the study of these lowly organisms that we may expect to obtain the solution of some of the most difficult problems of vegetable physiology.

The subject of the present paper is the
 study of the properties of the
 function $f(x)$ defined by the
 equation $f(x) = \frac{1}{2} [f(x+a) + f(x-a)]$
 where a is a constant. It is well known
 that this function is harmonic and
 that it satisfies the differential equation
 $f''(x) = -\frac{1}{a^2} f(x)$. The general
 solution of this equation is
 $f(x) = A \cos \frac{x}{a} + B \sin \frac{x}{a}$
 where A and B are constants. It is
 easy to see that this function
 satisfies the given equation. In fact,
 $f(x+a) = A \cos \frac{x+a}{a} + B \sin \frac{x+a}{a}$
 $f(x-a) = A \cos \frac{x-a}{a} + B \sin \frac{x-a}{a}$
 and therefore
 $\frac{1}{2} [f(x+a) + f(x-a)] = A \cos \frac{x}{a} + B \sin \frac{x}{a} = f(x)$
 as required. It is also clear that
 this function is periodic with
 period $2a$. The function $f(x)$ is
 also harmonic in the sense that
 it satisfies the mean value property
 of harmonic functions. In fact,
 if C is a circle of radius a with
 center at x , then
 $f(x) = \frac{1}{2\pi} \int_0^{2\pi} f(x+a \cos \theta) d\theta$
 which is the mean value of f over
 the circle C . This property is
 characteristic of harmonic functions
 and is one of the reasons why
 they are so important in physics
 and engineering. The function
 $f(x)$ is also the real part of a
 complex-valued function $F(z)$
 which is analytic in the complex
 plane. In fact, if we set
 $F(z) = A e^{iz/a} + B e^{-iz/a}$
 then $f(x) = \operatorname{Re} F(x)$ and $F(z)$
 is analytic in the whole complex
 plane. This is another important
 property of harmonic functions
 and is the basis of the theory of
 conformal mappings. The function
 $f(x)$ is also the solution of the
 Dirichlet problem for a strip in
 the complex plane. In fact, if
 we consider the strip $0 < \operatorname{Im} z < a$
 and prescribe the values of f on
 the boundary, then the function
 $f(x)$ is the unique harmonic
 function in the strip which
 takes the prescribed values on
 the boundary. This is a special
 case of the more general theory
 of conformal mappings and
 harmonic functions. The function
 $f(x)$ is also the solution of the
 Laplace equation in a strip in
 the plane. In fact, if we
 consider the strip $0 < y < a$
 in the xy -plane and prescribe
 the values of f on the boundary,
 then the function $f(x)$ is the
 unique harmonic function in the
 strip which takes the prescribed
 values on the boundary. This is
 another special case of the more
 general theory of harmonic
 functions and conformal mappings.