

DARWIN CHARLES

INSECTIVOROUS PLANTS

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CHAPTER I

DROSERA ROTUNDIFOLIA, OR THE COMMON SUN-DEW

Number of insects captured – Description of the leaves and their appendages or tentacles – Preliminary sketch of the action of the various parts, and of the manner in which insects are captured – Duration of the inflection of the tentacles – Nature of the secretion – Manner in which insects are carried to the centre of the leaf – Evidence that the glands have the power of absorption – Small size of the roots.

During the summer of 1860, I was surprised by finding how large a number of insects were caught by the leaves of the common sun-dew (*Drosera rotundifolia*) on a heath in Sussex. I had heard that insects were thus caught, but knew nothing further on the subject.¹ I gathered by chance a dozen plants, bearing fifty-six fully expanded leaves, and on thirty-one of these dead insects or remnants of them adhered; and, no doubt, many more would have been caught afterwards by these same leaves, and still more by those as yet not expanded. On one plant all six leaves had caught their prey; and on several plants very many leaves had caught more than a single insect. On one large leaf I found the remains of thirteen distinct insects. Flies (Diptera) are captured much oftener than other insects. The largest kind which I have seen caught was a small butterfly (*Caenonympha pamphilus*); but the Rev. H.M. Wilkinson informs me that he found a large living dragon-fly with its body firmly held by two leaves. As this plant is extremely common in some districts, the number of insects thus annually slaughtered must be prodigious. Many plants cause the death of insects, for instance the sticky buds of the horse-chestnut (*Aesculus hippocastanum*), without thereby receiving, as far as we can perceive, any advantage; but it was soon evident that *Drosera* was excellently adapted for the special purpose of catching insects, so that the subject seemed well worthy of investigation.

The results have proved highly remarkable; the more important ones being – firstly, the extraordinary sensitiveness of the glands to slight pressure and to minute doses of certain nitrogenous fluids, as shown by the movements of the so-called hairs or tentacles; secondly, the power possessed

¹ As Dr. Nitschke has given ('Bot. Zeitung,' 1860, p. 229) the bibliography of *Drosera*, I need not here go into details. Most of the notices published before 1860 are brief and unimportant. The oldest paper seems to have been one of the most valuable, namely, by Dr. Roth, in 1782. There is also an interesting though short account of the habits of *Drosera* by Dr. Milde, in the 'Bot. Zeitung,' 1852, p. 540. In 1855, in the 'Annales des Sc. nat. bot.' tom. iii. pp. 297 and 304, MM. Groenland and Trcul each published papers, with figures, on the structure of the leaves; but M. Trcul went so far as to doubt whether they possessed any power of movement. Dr. Nitschke's papers in the 'Bot. Zeitung' for 1860 and 1861 are by far the most important ones which have been published, both on the habits and structure of this plant; and I shall frequently have occasion to quote from them. His discussions on several points, for instance on the transmission of an excitement from one part of the leaf to another, are excellent. On December 11, 1862, Mr. J. Scott read a paper before the Botanical Society of Edinburgh, [] which was published in the 'Gardeners' Chronicle,' 1863, p. 30. Mr. Scott shows that gentle irritation of the hairs, as well as insects placed on the disc of the leaf, cause the hairs to bend inwards. Mr. A.W. Bennett also gave another interesting account of the movements of the leaves before the British Association for 1873. In this same year Dr. Warming published an essay, in which he describes the structure of the so-called hairs, entitled, "Sur la Diffrence entre les Trichomes," &c., extracted from the proceedings of the Soc. d'Hist. Nat. de Copenhague. I shall also have occasion hereafter to refer to a paper by Mrs. Treat, of New Jersey, on some American species of *Drosera*. Dr. Burdon Sanderson delivered a lecture on *Dionaea*, before the Royal Institution published in 'Nature,' June 14, 1874, in which a short account of my observations on the power of true digestion possessed by *Drosera* and *Dionaea* first appeared. Prof. Asa Gray has done good service by calling attention to *Drosera*, and to other plants having similar habits, in 'The Nation' (1874, pp. 261 and 232), and in other publications. Dr. Hooker, also, in his important address on Carnivorous Plants (Brit. Assoc., Belfast, 1874), has given a history of the subject.

by the leaves of rendering soluble or digesting nitrogenous substances, and of afterwards absorbing them; thirdly, the changes which take place within the cells of the tentacles, when the glands are excited in various ways.

It is necessary, in the first place, to describe briefly the plant. It bears from two or three to five or six leaves, generally extended more or less horizontally, but sometimes standing vertically upwards. The shape and general appearance of a leaf is shown, as seen from above, in fig. 1, and as seen laterally, in fig. 2. The leaves are commonly a little broader than long, but this was not the case in the one here figured. The whole upper surface is covered with gland-bearing filaments, or tentacles, as I shall call them, from their manner of acting. The glands were counted on thirty-one leaves, but many of these were of unusually large size, and the average number was 192; the greatest number being 260, and the least 130. The glands are each surrounded by large drops of extremely viscid secretion, which, glittering in the sun, have given rise to the plant's poetical name of the sun-dew.

[The tentacles on the central part of the leaf or disc are short and stand upright, and their pedicels are green. Towards the margin they become longer and longer and more inclined outwards, with their pedicels of a purple colour. Those on the extreme margin project in the same plane with the leaf, or more commonly (see fig. 2) are considerably reflexed. A few tentacles spring from the base of the footstalk or petiole, and these are the longest of all, being sometimes nearly 1/4 of an inch in length. On a leaf bearing altogether 252 tentacles, the short ones on the disc, having green pedicels, were in number to the longer submarginal and marginal tentacles, having purple pedicels, as nine to sixteen.

A tentacle consists of a thin, straight, hair-like pedicel, carrying a gland on the summit. The pedicel is somewhat flattened, and is formed of several rows of elongated cells, filled with purple fluid or granular matter.² There is, however, a narrow zone close beneath the glands of the longer tentacles, and a broader zone near their bases, of a green tint. Spiral vessels, accompanied by simple vascular tissue, branch off from the vascular bundles in the blade of the leaf, and run up all the tentacles into the glands.

Several eminent physiologists have discussed the homological nature of these appendages or tentacles, that is, whether they ought to be considered as hairs (trichomes) or prolongations of the leaf. Nitschke has shown that they include all the elements proper to the blade of a leaf; and the fact of their including vascular tissue was formerly thought to prove that they were prolongations of the leaf, but it is now known that vessels sometimes enter true hairs. The power of movement which they possess is a strong argument against their being viewed as hairs. The conclusion which seems to me the most probable will be given in Chap. XV., namely that they existed primordially as glandular hairs, or mere epidermic formations, and that their upper part should still be so considered; but that their lower part, which alone is capable of movement, consists of a prolongation of the leaf; the spiral vessels being extended from this to the uppermost part. We shall hereafter see that the terminal tentacles of the divided leaves of *Roridula* are still in an intermediate condition.

The glands, with the exception of those borne by the extreme marginal tentacles, are oval, and of nearly uniform size, viz. about 4/500 of an inch in length. Their structure is remarkable, and their functions complex, for they secrete, absorb, and are acted on by various stimulants. They consist of an outer layer of small polygonal cells, containing purple granular matter or fluid, and with the walls thicker than those of the pedicels. Within this layer of cells there is an inner one of differently shaped

² According to Nitschke ('Bot. Zeitung,' 1861, p. 224) the purple fluid results from the metamorphosis of chlorophyll. Mr. Sorby examined the colouring matter with the spectroscope, and informs me that it consists of the commonest species of erythrophyll, "which is often met with in leaves with low vitality, and in parts, like the petioles, which carry on leaf-functions in a very imperfect manner. All that can be said, therefore, is that the hairs (or tentacles) are coloured like parts of a leaf which do not fulfil their proper office." Dr. Nitschke has discussed this subject in 'Bot. Zeitung,' 1861, p. 241 &c. See also Dr. Warming ('Sur la Différence entre les Trichomes' &c., 1873), who gives references to various publications. See also Groenland and Trcul 'Annal. des Sc. nat. bot.' (4th series), tom. iii. 1855, pp. 297 and 303.

ones, likewise filled with purple fluid, but of a slightly different tint, and differently affected by chloride of gold. These two layers are sometimes well seen when a gland has been crushed or boiled in caustic potash. According to Dr. Warming, there is still another layer of much more elongated cells, as shown in the accompanying section (fig. 3) copied from his work; but these cells were not seen by Nitschke, nor by me. In the centre there is a group of elongated, cylindrical cells of unequal lengths, bluntly pointed at their upper ends, truncated or rounded at their lower ends, closely pressed together, and remarkable from being surrounded by a spiral line, which can be separated as a distinct fibre.

These latter cells are filled with limpid fluid, which after long immersion in alcohol deposits much brown matter. I presume that they are actually connected with the spiral vessels which run up the tentacles, for on several occasions the latter were seen to divide into two or three excessively thin branches, which could be traced close up to the spiriferous cells. Their development has been described by Dr. Warming. Cells of the same kind have been observed in other plants, as I hear from Dr. Hooker, and were seen by me in the margins of the leaves of *Pinguicula*. Whatever their function may be, they are not necessary for the secretion of a digestive fluid, or for absorption, or for the communication of a motor impulse to other parts of the leaf, as we may infer from the structure of the glands in some other genera of the *Droseraceae*.

The extreme marginal tentacles differ slightly from the others. Their bases are broader, and besides their own vessels, they receive a fine branch from those which enter the tentacles on each side. Their glands are much elongated, and lie embedded on the upper surface of the pedicel, instead of standing at the apex. In other respects they do not differ essentially from the oval ones, and in one specimen I found every possible transition between the two states. In another specimen there were no long-headed glands. These marginal tentacles lose their irritability earlier than the others; and when a stimulus is applied to the centre of the leaf, they are excited into action after the others. When cut-off leaves are immersed in water, they alone often become inflected.

The purple fluid or granular matter which fills the cells of the glands differs to a certain extent from that within the cells of the pedicels. For when a leaf is placed in hot water or in certain acids, the glands become quite white and opaque, whereas the cells of the pedicels are rendered of a bright red, with the exception of those close beneath the glands. These latter cells lose their pale red tint; and the green matter which they, as well as the basal cells, contain, becomes of a brighter green. The petioles bear many multicellular hairs, some of which near the blade are surmounted, according to Nitschke, by a few rounded cells, which appear to be rudimentary glands. Both surfaces of the leaf, the pedicels of the tentacles, especially the lower sides of the outer ones, and the petioles, are studded with minute papillae (hairs or trichomes), having a conical basis, and bearing on their summits two, and occasionally three or even four, rounded cells, containing much protoplasm. These papillae are generally colourless, but sometimes include a little purple fluid. They vary in development, and graduate, as Nitschke³ states, and as I repeatedly observed, into the long multicellular hairs. The latter, as well as the papillae, are probably rudiments of formerly existing tentacles.

I may here add, in order not to recur to the papillae, that they do not secrete, but are easily permeated by various fluids: thus when living or dead leaves are immersed in a solution of one part of chloride of gold, or of nitrate of silver, to 437 of water, they are quickly blackened, and the discoloration soon spreads to the surrounding tissue. The long multicellular hairs are not so quickly affected. After a leaf had been left in a weak infusion of raw meat for 10 hours, the cells of the papillae had evidently absorbed animal matter, for instead of limpid fluid they now contained small aggregated masses of protoplasm, which slowly and incessantly changed their forms. A similar result followed from an immersion of only 15 minutes in a solution of one part of carbonate of ammonia to 218 of water, and the adjoining cells of the tentacles, on which the papillae were seated, now likewise contained aggregated masses of protoplasm. We may therefore conclude that when a leaf

³ Nitschke has elaborately described and figured these papillae, 'Bot. Zeitung,' 1861, pp. 234, 253, 254.

has closely clasped a captured insect in the manner immediately to be described, the papillae, which project from the upper surface of the leaf and of the tentacles, probably absorb some of the animal matter dissolved in the secretion; but this cannot be the case with the papillae on the backs of the leaves or on the petioles.]

Preliminary Sketch of the Action of the several Parts, and of the Manner in which Insects are Captured.

If a small organic or inorganic object be placed on the glands in the centre of a leaf, these transmit a motor impulse to the marginal tentacles. The nearer ones are first affected and slowly bend towards the centre, and then those farther off, until at last all become closely inflected over the object. This takes place in from one hour to four or five or more hours. The difference in the time required depends on many circumstances; namely on the size of the object and on its nature, that is, whether it contains soluble matter of the proper kind; on the vigour and age of the leaf; whether it has lately been in action; and, according to Nitschke,⁴ on the temperature of the day, as likewise seemed to me to be the case. A living insect is a more efficient object than a dead one, as in struggling it presses against the glands of many tentacles. An insect, such as a fly, with thin integuments, through which animal matter in solution can readily pass into the surrounding dense secretion, is more efficient in causing prolonged inflection than an insect with a thick coat, such as a beetle. The inflection of the tentacles takes place indifferently in the light and darkness; and the plant is not subject to any nocturnal movement of so-called sleep.

If the glands on the disc are repeatedly touched or brushed, although no object is left on them, the marginal tentacles curve inwards. So again, if drops of various fluids, for instance of saliva or of a solution of any salt of ammonia, are placed on the central glands, the same result quickly follows, sometimes in under half an hour.

The tentacles in the act of inflection sweep through a wide space; thus a marginal tentacle, extended in the same plane with the blade, moves through an angle of 180°; and I have seen the much reflected tentacles of a leaf which stood upright move through an angle of not less than 270°. The bending part is almost confined to a short space near the base; but a rather larger portion of the elongated exterior tentacles becomes slightly incurved; the distal half in all cases remaining straight. The short tentacles in the centre of the disc when directly excited, do not become inflected; but they are capable of inflection if excited by a motor impulse received from other glands at a distance. Thus, if a leaf is immersed in an infusion of raw meat, or in a weak solution of ammonia (if the solution is at all strong, the leaf is paralysed), all the exterior tentacles bend inwards (see fig. 4), excepting those near the centre, which remain upright; but these bend towards any exciting object placed on one side of the disc, as shown in fig. 5. The glands in fig. 4 may be seen to form a dark ring round the centre; and this follows from the exterior tentacles increasing in length in due proportion, as they stand nearer to the circumference.

The kind of inflection which the tentacles undergo is best shown when the gland of one of the long exterior tentacles is in any way excited; for the surrounding ones remain unaffected. In the accompanying outline (fig. 6) we see one tentacle, on which a particle of meat had been placed, thus bent towards the centre of the leaf, with two others retaining their original position. A gland may be excited by being simply touched three or four times, or by prolonged contact with organic or inorganic objects, and various fluids. I have distinctly seen, through a lens, a tentacle beginning to bend in ten seconds, after an object had been placed on its gland; and I have often seen strongly pronounced inflection in under one minute. It is surprising how minute a particle of any substance, such as a bit of thread or hair or splinter of glass, if placed in actual contact with the surface of a gland, suffices to cause the tentacle to bend. If the object, which has been carried by this movement

⁴ 'Bot. Zeitung,' 1860, p. 246.

to the centre, be not very small, or if it contains soluble nitrogenous matter, it acts on the central glands; and these transmit a motor impulse to the exterior tentacles, causing them to bend inwards.

Not only the tentacles, but the blade of the leaf often, but by no means always, becomes much incurved, when any strongly exciting substance or fluid is placed on the disc. Drops of milk and of a solution of nitrate of ammonia or soda are particularly apt to produce this effect. The blade is thus converted into a little cup. The manner in which it bends varies greatly. Sometimes the apex alone, sometimes one side, and sometimes both sides, become incurved. For instance, I placed bits of hard-boiled egg on three leaves; one had the apex bent towards the base; the second had both distal margins much incurved, so that it became almost triangular in outline, and this perhaps is the commonest case; whilst the third blade was not at all affected, though the tentacles were as closely inflected as in the two previous cases. The whole blade also generally rises or bends upwards, and thus forms a smaller angle with the footstalk than it did before. This appears at first sight a distinct kind of movement, but it results from the incurvation of that part of the margin which is attached to the footstalk, causing the blade, as a whole, to curve or move upwards.

The length of time during which the tentacles as well as the blade remain inflected over an object placed on the disc, depends on various circumstances; namely on the vigour and age of the leaf, and, according to Dr. Nitschke, on the temperature, for during cold weather when the leaves are inactive, they re-expand at an earlier period than when the weather is warm. But the nature of the object is by far the most important circumstance; I have repeatedly found that the tentacles remain clasped for a much longer average time over objects which yield soluble nitrogenous matter than over those, whether organic or inorganic, which yield no such matter. After a period varying from one to seven days, the tentacles and blade re-expand, and are then ready to act again. I have seen the same leaf inflected three successive times over insects placed on the disc; and it would probably have acted a greater number of times.

The secretion from the glands is extremely viscid, so that it can be drawn out into long threads. It appears colourless, but stains little balls of paper pale pink. An object of any kind placed on a gland always causes it, as I believe, to secrete more freely; but the mere presence of the object renders this difficult to ascertain. In some cases, however, the effect was strongly marked, as when particles of sugar were added; but the result in this case is probably due merely to exosmose. Particles of carbonate and phosphate of ammonia and of some other salts, for instance sulphate of zinc, likewise increase the secretion. Immersion in a solution of one part of chloride of gold, or of some other salts, to 437 of water, excites the glands to largely increased secretion; on the other hand, tartrate of antimony produces no such effect. Immersion in many acids (of the strength of one part to 437 of water) likewise causes a wonderful amount of secretion, so that when the leaves are lifted out, long ropes of extremely viscid fluid hang from them. Some acids, on the other hand, do not act in this manner. Increased secretion is not necessarily dependent on the inflection of the tentacle, for particles of sugar and of sulphate of zinc cause no movement.

It is a much more remarkable fact that when an object, such as a bit of meat or an insect, is placed on the disc of a leaf, as soon as the surrounding tentacles become considerably inflected, their glands pour forth an increased amount of secretion. I ascertained this by selecting leaves with equal-sized drops on the two sides, and by placing bits of meat on one side of the disc; and as soon as the tentacles on this side became much inflected, but before the glands touched the meat, the drops of secretion became larger. This was repeatedly observed, but a record was kept of only thirteen cases, in nine of which increased secretion was plainly observed; the four failures being due either to the leaves being rather torpid, or to the bits of meat being too small to cause much inflection. We must therefore conclude that the central glands, when strongly excited, transmit some influence to the glands of the circumferential tentacles, causing them to secrete more copiously.

It is a still more important fact (as we shall see more fully when we treat of the digestive power of the secretion) that when the tentacles become inflected, owing to the central glands having

been stimulated mechanically, or by contact with animal matter, the secretion not only increases in quantity, but changes its nature and becomes acid; and this occurs before the glands have touched the object on the centre of the leaf. This acid is of a different nature from that contained in the tissue of the leaves. As long as the tentacles remain closely inflected, the glands continue to secrete, and the secretion is acid; so that, if neutralised by carbonate of soda, it again becomes acid after a few hours. I have observed the same leaf with the tentacles closely inflected over rather indigestible substances, such as chemically prepared casein, pouring forth acid secretion for eight successive days, and over bits of bone for ten successive days.

The secretion seems to possess, like the gastric juice of the higher animals, some antiseptic power. During very warm weather I placed close together two equal-sized bits of raw meat, one on a leaf of the *Drosera*, and the other surrounded by wet moss. They were thus left for 48 hrs., and then examined. The bit on the moss swarmed with infusoria, and was so much decayed that the transverse striae on the muscular fibres could no longer be clearly distinguished; whilst the bit on the leaf, which was bathed by the secretion, was free from infusoria, and its striae were perfectly distinct in the central and undissolved portion. In like manner small cubes of albumen and cheese placed on wet moss became threaded with filaments of mould, and had their surfaces slightly discoloured and disintegrated; whilst those on the leaves of *Drosera* remained clean, the albumen being changed into transparent fluid.

As soon as tentacles, which have remained closely inflected during several days over an object, begin to re-expand, their glands secrete less freely, or cease to secrete, and are left dry. In this state they are covered with a film of whitish, semi-fibrous matter, which was held in solution by the secretion. The drying of the glands during the act of re-expansion is of some little service to the plant; for I have often observed that objects adhering to the leaves could then be blown away by a breath of air; the leaves being thus left unencumbered and free for future action. Nevertheless, it often happens that all the glands do not become completely dry; and in this case delicate objects, such as fragile insects, are sometimes torn by the re-expansion of the tentacles into fragments, which remain scattered all over the leaf. After the re-expansion is complete, the glands quickly begin to re-secrete, and as soon as full-sized drops are formed, the tentacles are ready to clasp a new object.

When an insect alights on the central disc, it is instantly entangled by the viscid secretion, and the surrounding tentacles after a time begin to bend, and ultimately clasp it on all sides. Insects are generally killed, according to Dr. Nitschke, in about a quarter of an hour, owing to their tracheae being closed by the secretion. If an insect adheres to only a few of the glands of the exterior tentacles, these soon become inflected and carry their prey to the tentacles next succeeding them inwards; these then bend inwards, and so onwards; until the insect is ultimately carried by a curious sort of rolling movement to the centre of the leaf. Then, after an interval, the tentacles on all sides become inflected and bathe their prey with their secretion, in the same manner as if the insect had first alighted on the central disc. It is surprising how minute an insect suffices to cause this action: for instance, I have seen one of the smallest species of gnats (*Culex*), which had just settled with its excessively delicate feet on the glands of the outermost tentacles, and these were already beginning to curve inwards, though not a single gland had as yet touched the body of the insect. Had I not interfered, this minute gnat would assuredly have been carried to the centre of the leaf and been securely clasped on all sides. We shall hereafter see what excessively small doses of certain organic fluids and saline solutions cause strongly marked inflection.

Whether insects alight on the leaves by mere chance, as a resting place, or are attracted by the odour of the secretion, I know not. I suspect from the number of insects caught by the English species of *Drosera*, and from what I have observed with some exotic species kept in my greenhouse, that the odour is attractive. In this latter case the leaves may be compared with a baited trap; in the former case with a trap laid in a run frequented by game, but without any bait.

That the glands possess the power of absorption, is shown by their almost instantaneously becoming dark-coloured when given a minute quantity of carbonate of ammonia; the change of colour being chiefly or exclusively due to the rapid aggregation of their contents. When certain other fluids are added, they become pale-coloured. Their power of absorption is, however, best shown by the widely different results which follow, from placing drops of various nitrogenous and non-nitrogenous fluids of the same density on the glands of the disc, or on a single marginal gland; and likewise by the very different lengths of time during which the tentacles remain inflected over objects, which yield or do not yield soluble nitrogenous matter. This same conclusion might indeed have been inferred from the structure and movements of the leaves, which are so admirably adapted for capturing insects.

The absorption of animal matter from captured insects explains how *Drosera* can flourish in extremely poor peaty soil, – in some cases where nothing but sphagnum moss grows, and mosses depend altogether on the atmosphere for their nourishment. Although the leaves at a hasty glance do not appear green, owing to the purple colour of the tentacles, yet the upper and lower surfaces of the blade, the pedicels of the central tentacles, and the petioles contain chlorophyll, so that, no doubt, the plant obtains and assimilates carbonic acid from the air. Nevertheless, considering the nature of the soil where it grows, the supply of nitrogen would be extremely limited, or quite deficient, unless the plant had the power of obtaining this important element from captured insects. We can thus understand how it is that the roots are so poorly developed. These usually consist of only two or three slightly divided branches, from half to one inch in length, furnished with absorbent hairs. It appears, therefore, that the roots serve only to imbibe water; though, no doubt, they would absorb nutritious matter if present in the soil; for as we shall hereafter see, they absorb a weak solution of carbonate of ammonia. A plant of *Drosera*, with the edges of its leaves curled inwards, so as to form a temporary stomach, with the glands of the closely inflected tentacles pouring forth their acid secretion, which dissolves animal matter, afterwards to be absorbed, may be said to feed like an animal. But, differently from an animal, it drinks by means of its roots; and it must drink largely, so as to retain many drops of viscid fluid round the glands, sometimes as many as 260, exposed during the whole day to a glaring sun.

CHAPTER II

THE MOVEMENTS OF THE TENTACLES FROM THE CONTACT OF SOLID BODIES

Inflection of the exterior tentacles owing to the glands of the disc being excited by repeated touches, or by objects left in contact with them – Difference in the action of bodies yielding and not yielding soluble nitrogenous matter – Inflection of the exterior tentacles directly caused by objects left in contact with their glands – Periods of commencing inflection and of subsequent re-expansion – Extreme minuteness of the particles causing inflection – Action under water – Inflection of the exterior tentacles when their glands are excited by repeated touches – Falling drops of water do not cause inflection.

I WILL give in this and the following chapters some of the many experiments made, which best illustrate the manner and rate of movement of the tentacles, when excited in various ways. The glands alone in all ordinary cases are susceptible to excitement. When excited, they do not themselves move or change form, but transmit a motor impulse to the bending part of their own and adjoining tentacles, and are thus carried towards the centre of the leaf. Strictly speaking, the glands ought to be called irritable, as the term sensitive generally implies consciousness; but no one supposes that the Sensitive-plant is conscious, and as I have found the term convenient, I shall use it without scruple. I will commence with the movements of the exterior tentacles, when indirectly excited by stimulants applied to the glands of the short tentacles on the disc. The exterior tentacles may be said in this case to be indirectly excited, because their own glands are not directly acted on. The stimulus proceeding from the glands of the disc acts on the bending part of the exterior tentacles, near their bases, and does not (as will hereafter be proved) first travel up the pedicels to the glands, to be then reflected back to the bending place. Nevertheless, some influence does travel up to the glands, causing them to secrete more copiously, and the secretion to become acid. This latter fact is, I believe, quite new in the physiology of plants; it has indeed only recently been established that in the animal kingdom an influence can be transmitted along the nerves to glands, modifying their power of secretion, independently of the state of the blood-vessels.

The Inflection of the Exterior Tentacles from the Glands of the Disc being excited by Repeated Touches, or by Objects left in Contact with them.

The central glands of a leaf were irritated with a small stiff camel-hair brush, and in 70 m. (minutes) several of the outer tentacles were inflected; in 5 hrs. (hours) all the sub-marginal tentacles were inflected; next morning after an interval of about 22 hrs. they were fully re-expanded. In all the following cases the period is reckoned from the time of first irritation. Another leaf treated in the same manner had a few tentacles inflected in 20 m.; in 4 hrs. all the submarginal and some of the extreme marginal tentacles, as well as the edge of the leaf itself, were inflected; in 17 hrs. they had recovered their proper, expanded position. I then put a dead fly in the centre of the last-mentioned leaf, and next morning it was closely clasped; five days afterwards the leaf re-expanded, and the tentacles, with their glands surrounded by secretion, were ready to act again.

Particles of meat, dead flies, bits of paper, wood, dried moss, sponge, cinders, glass, &c., were repeatedly placed on leaves, and these objects were well embraced in various periods from one hr. to as long as 24 hrs., and set free again, with the leaf fully re-expanded, in from one or two, to seven or even ten days, according to the nature of the object. On a leaf which had naturally caught two flies, and therefore had already closed and reopened either once or more probably twice, I put a fresh

fly: in 7 hrs. it was moderately, and in 21 hrs. thoroughly well, clasped, with the edges of the leaf inflected. In two days and a half the leaf had nearly re-expanded; as the exciting object was an insect, this unusually short period of inflection was, no doubt, due to the leaf having recently been in action. Allowing this same leaf to rest for only a single day, I put on another fly, and it again closed, but now very slowly; nevertheless, in less than two days it succeeded in thoroughly clasping the fly.

When a small object is placed on the glands of the disc, on one side of a leaf, as near as possible to its circumference, the tentacles on this side are first affected, those on the opposite side much later, or, as often occurred, not at all. This was repeatedly proved by trials with bits of meat; but I will here give only the case of a minute fly, naturally caught and still alive, which I found adhering by its delicate feet to the glands on the extreme left side of the central disc. The marginal tentacles on this side closed inwards and killed the fly, and after a time the edge of the leaf on this side also became inflected, and thus remained for several days, whilst neither the tentacles nor the edge on the opposite side were in the least affected.

If young and active leaves are selected, inorganic particles not larger than the head of a small pin, placed on the central glands, sometimes cause the outer tentacles to bend inwards. But this follows much more surely and quickly, if the object contains nitrogenous matter which can be dissolved by the secretion. On one occasion I observed the following unusual circumstance. Small bits of raw meat (which acts more energetically than any other substance), of paper, dried moss, and of the quill of a pen were placed on several leaves, and they were all embraced equally well in about 2 hrs. On other occasions the above-named substances, or more commonly particles of glass, coal-cinder (taken from the fire), stone, gold-leaf, dried grass, cork, blotting-paper, cotton-wool, and hair rolled up into little balls, were used, and these substances, though they were sometimes well embraced, often caused no movement whatever in the outer tentacles, or an extremely slight and slow movement. Yet these same leaves were proved to be in an active condition, as they were excited to move by substances yielding soluble nitrogenous matter, such as bits of raw or roast meat, the yolk or white of boiled eggs, fragments of insects of all orders, spiders, &c. I will give only two instances. Minute flies were placed on the discs of several leaves, and on others balls of paper, bits of moss and quill of about the same size as the flies, and the latter were well embraced in a few hours; whereas after 25 hrs. only a very few tentacles were inflected over the other objects. The bits of paper, moss, and quill were then removed from these leaves, and bits of raw meat placed on them; and now all the tentacles were soon energetically inflected.

Again, particles of coal-cinder (weighing rather more than the flies used in the last experiment) were placed on the centres of three leaves: after an interval of 19 hrs. one of the particles was tolerably well embraced; a second by a very few tentacles; and a third by none. I then removed the particles from the two latter leaves, and put on them recently killed flies. These were fairly well embraced in 7 1/2 hrs. and thoroughly after 20 1/2 hrs.; the tentacles remaining inflected for many subsequent days. On the other hand, the one leaf which had in the course of 19 hrs. embraced the bit of cinder moderately well, and to which no fly was given, after an additional 33 hrs. (i.e. in 52 hrs. from the time when the cinder was put on) was completely re-expanded and ready to act again.

From these and numerous other experiments not worth giving, it is certain that inorganic substances, or such organic substances as are not attacked by the secretion, act much less quickly and efficiently than organic substances yielding soluble matter which is absorbed. Moreover, I have met with very few exceptions to the rule, and these exceptions apparently depended on the leaf having been too recently in action, that the tentacles remain clasped for a much longer time over organic bodies of the nature just specified than over those which are not acted on by the secretion, or over inorganic objects.⁵

⁵ Owing to the extraordinary belief held by M. Ziegler ('Comptes rendus,' May 1872, p. 122), that albuminous substances, if held for a moment between the fingers, acquire the property of making the tentacles of *Drosera* contract, whereas, if not thus held, they

The Inflection of the Exterior Tentacles as directly caused by Objects left in Contact with their Glands.

I made a vast number of trials by placing, by means of a fine needle moistened with distilled water, and with the aid of a lens, particles of various substances on the viscid secretion surrounding the glands of the outer tentacles. I experimented on both the oval and long-headed glands. When a particle is thus placed on a single gland, the movement of the tentacle is particularly well seen in contrast with the stationary condition of the surrounding tentacles. (See previous fig. 6.) In four cases small particles of raw meat caused the tentacles to be greatly inflected in between 5 and 6 m. Another tentacle similarly treated, and observed with special care, distinctly, though slightly, changed its position in 10 s. (seconds); and this is the quickest movement seen by me. In 2 m. 30 s. it had moved through an angle of about 45°. The movement as seen through a lens resembled that of the hand of a large clock. In 5 m. it had moved through 90°, and when I looked again after 10 m., the particle had reached the centre of the leaf; so that the whole movement was completed in less than 17 m. 30 s. In the course of some hours this minute bit of meat, from having been brought into contact with some of the glands of the central disc, acted centrifugally on the outer tentacles, which all became closely inflected. Fragments of flies were placed on the glands of four of the outer tentacles, extended in the same plane with that of the blade, and three of these fragments were carried in 35 m. through an angle of 180° to the centre. The fragment on the fourth tentacle was very minute, and it was not carried to the centre until 3 hrs. had elapsed. In three other cases minute flies or portions of larger ones were carried to the centre in 1 hr. 30 s. In these seven cases, the fragments or small flies, which had been carried by a single tentacle to the central glands, were well embraced by the other tentacles after an interval of from 4 to 10 hrs.

I also placed in the manner just described six small balls of writing-paper (rolled up by the aid of pincers, so that they were not touched by my fingers) on the glands of six exterior tentacles on distinct leaves; three of these were carried to the centre in about 1 hr., and the other three in rather more than 4 hrs.; but after 24 hrs. only two of the six balls were well embraced by the other tentacles. It is possible that the secretion may have dissolved a trace of glue or animalised matter from the balls of paper. Four particles of coal-cinder were then placed on the glands of four exterior tentacles; one of these reached the centre in 3 hrs. 40 m.; the second in 9 hrs.; the third within 24 hrs., but had moved only part of the way in 9 hrs.; whilst the fourth moved only a very short distance in 24 hrs., and never moved any farther. Of the above three bits of cinder which were ultimately carried to the centre, one alone was well embraced by many of the other tentacles. We here see clearly that such bodies as particles of cinder or little balls of paper, after being carried by the tentacles to the central glands, act very differently from fragments of flies, in causing the movement of the surrounding tentacles.

I made, without carefully recording the times of movement, many similar trials with other substances, such as splinters of white and blue glass, particles of cork, minute bits of gold-leaf, &c.; and the proportional number of cases varied much in which the tentacles reached the centre, or moved only slightly, or not at all. One evening, particles of glass and cork, rather larger than those usually employed, were placed on about a dozen glands, and next morning, after 13 hrs., every single tentacle

have no such power, I tried some experiments with great care, but the results did not confirm this belief. Red-hot cinders were taken out of the fire, and bits of glass, cotton-thread, blotting paper and thin slices of cork were immersed in boiling water; and particles were then placed (every instrument with which they were touched having been previously immersed in boiling water) on the glands of several leaves, and they acted in exactly the same manner as other particles, which had been purposely handled for some time. Bits of a boiled egg, cut with a knife which had been washed in boiling water, also acted like any other animal substance. I breathed on some leaves for above a minute, and repeated the act two or three times, with my mouth close to [] them, but this produced no effect. I may here add, as showing that the leaves are not acted on by the odour of nitrogenous substances, that pieces of raw meat stuck on needles were fixed as close as possible, without actual contact, to several leaves, but produced no effect whatever. On the other hand, as we shall hereafter see, the vapours of certain volatile substances and fluids, such as of carbonate of ammonia, chloroform, certain essential oils, &c., cause inflection. M. Ziegler makes still more extraordinary statements with respect to the power of animal substances, which have been left close to, but not in contact with, sulphate of quinine. The action of salts of quinine will be described in a future chapter. Since the appearance of the paper above referred to, M. Ziegler has published a book on the same subject, entitled 'Atonicit et Zoicit,' 1874.)

had carried its little load to the centre; but the unusually large size of the particles will account for this result. In another case 6/7 of the particles of cinder, glass, and thread, placed on separate glands, were carried towards, or actually to, the centre; in another case 7/9, in another 7/12, and in the last case only 7/26 were thus carried inwards, the small proportion being here due, at least in part, to the leaves being rather old and inactive. Occasionally a gland, with its light load, could be seen through a strong lens to move an extremely short distance and then stop; this was especially apt to occur when excessively minute particles, much less than those of which the measurements will be immediately given, were placed on glands; so that we here have nearly the limit of any action.

I was so much surprised at the smallness of the particles which caused the tentacles to become greatly inflected that it seemed worth while carefully to ascertain how minute a particle would plainly act. Accordingly measured lengths of a narrow strip of blotting paper, of fine cotton-thread, and of a woman's hair, were carefully weighed for me by Mr. Trenham Reeks, in an excellent balance, in the laboratory in Jermyn Street. Short bits of the paper, thread, and hair were then cut off and measured by a micrometer, so that their weights could be easily calculated. The bits were placed on the viscid secretion surrounding the glands of the exterior tentacles, with the precautions already stated, and I am certain that the gland itself was never touched; nor indeed would a single touch have produced any effect. A bit of the blotting-paper, weighing 1/465 of a grain, was placed so as to rest on three glands together, and all three tentacles slowly curved inwards; each gland, therefore, supposing the weight to be distributed equally, could have been pressed on by only 1/1395 of a grain, or .0464 of a milligramme. Five nearly equal bits of cotton-thread were tried, and all acted. The shortest of these was 1/50 of an inch in length, and weighed 1/8197 of a grain. The tentacle in this case was considerably inflected in 1 hr. 30 m., and the bit of thread was carried to the centre of the leaf in 1 hr. 40 m. Again, two particles of the thinner end of a woman's hair, one of these being 18/1000 of an inch in length, and weighing 1/35714 of a grain, the other 19/1000 of an inch in length, and weighing of course a little more, were placed on two glands on opposite sides of the same leaf, and these two tentacles were inflected halfway towards the centre in 1 hr. 10 m.; all the many other tentacles round the same leaf remaining motionless. The appearance of this one leaf showed in an unequivocal manner that these minute particles sufficed to cause the tentacles to bend. Altogether, ten such particles of hair were placed on ten glands on several leaves, and seven of them caused the tentacles to move in a conspicuous manner. The smallest particle which was tried, and which acted plainly, was only 8/1000 of an inch (.203 millimetre) in length, and weighed the 1/78740 of a grain, or .000822 milligramme. In these several cases, not only was the inflection of the tentacles conspicuous, but the purple fluid within their cells became aggregated into little masses of protoplasm, in the manner to be described in the next chapter; and the aggregation was so plain that I could, by this clue alone, have readily picked out under the microscope all the tentacles which had carried their light loads towards the centre, from the hundreds of other tentacles on the same leaves which had not thus acted.

My surprise was greatly excited, not only by the minuteness of the particles which caused movement, but how they could possibly act on the glands; for it must be remembered that they were laid with the greatest care on the convex surface of the secretion. At first I thought – but, as I now know, erroneously – that particles of such low specific gravity as those of cork, thread, and paper, would never come into contact with the surfaces of the glands. The particles cannot act simply by their weight being added to that of the secretion, for small drops of water, many times heavier than the particles, were repeatedly added, and never produced any effect. Nor does the disturbance of the secretion produce any effect, for long threads were drawn out by a needle, and affixed to some adjoining object, and thus left for hours; but the tentacles remained motionless.

I also carefully removed the secretion from four glands with a sharply pointed piece of blotting-paper, so that they were exposed for a time naked to the air, but this caused no movement; yet these glands were in an efficient state, for after 24 hrs. had elapsed, they were tried with bits of meat, and all became quickly inflected. It then occurred to me that particles floating on the secretion would cast

shadows on the glands, which might be sensitive to the interception of the light. Although this seemed highly improbable, as minute and thin splinters of colourless glass acted powerfully, nevertheless, after it was dark, I put on, by the aid of a single tallow candle, as quickly as possible, particles of cork and glass on the glands of a dozen tentacles, as well as some of meat on other glands, and covered them up so that not a ray of light could enter; but by the next morning, after an interval of 13 hrs., all the particles were carried to the centres of the leaves.

These negative results led me to try many more experiments, by placing particles on the surface of the drops of secretion, observing, as carefully as I could, whether they penetrated it and touched the surface of the glands. The secretion, from its weight, generally forms a thicker layer on the under than on the upper sides of the glands, whatever may be the position of the tentacles. Minute bits of dry cork, thread, blotting paper, and coal cinders were tried, such as those previously employed; and I now observed that they absorbed much more of the secretion, in the course of a few minutes, than I should have thought possible; and as they had been laid on the upper surface of the secretion, where it is thinnest, they were often drawn down, after a time, into contact with at least some one point of the gland. With respect to the minute splinters of glass and particles of hair, I observed that the secretion slowly spread itself a little over their surfaces, by which means they were likewise drawn downwards or sideways, and thus one end, or some minute prominence, often came to touch, sooner or later, the gland.

In the foregoing and following cases, it is probable that the vibrations, to which the furniture in every room is continually liable, aids in bringing the particles into contact with the glands. But as it was sometimes difficult, owing to the refraction of the secretion, to feel sure whether the particles were in contact, I tried the following experiment. Unusually minute particles of glass, hair, and cork, were gently placed on the drops round several glands, and very few of the tentacles moved. Those which were not affected were left for about half an hour, and the particles were then disturbed or tilted up several times with a fine needle under the microscope, the glands not being touched. And now in the course of a few minutes almost all the hitherto motionless tentacles began to move; and this, no doubt, was caused by one end or some prominence of the particles having come into contact with the surface of the glands. But as the particles were unusually minute, the movement was small.

Lastly, some dark blue glass pounded into fine splinters was used, in order that the points of the particles might be better distinguished when immersed in the secretion; and thirteen such particles were placed in contact with the depending and therefore thicker part of the drops round so many glands. Five of the tentacles began moving after an interval of a few minutes, and in these cases I clearly saw that the particles touched the lower surface of the gland. A sixth tentacle moved after 1 hr. 45 m., and the particle was now in contact with the gland, which was not the case at first. So it was with the seventh tentacle, but its movement did not begin until 3 hrs. 45 m. had elapsed. The remaining six tentacles never moved as long as they were observed; and the particles apparently never came into contact with the surfaces of the glands.

From these experiments we learn that particles not containing soluble matter, when placed on glands, often cause the tentacles to begin bending in the course of from one to five minutes; and that in such cases the particles have been from the first in contact with the surfaces of the glands. When the tentacles do not begin moving for a much longer time, namely, from half an hour to three or four hours, the particles have been slowly brought into contact with the glands, either by the secretion being absorbed by the particles or by its gradual spreading over them, together with its consequent quicker evaporation. When the tentacles do not move at all, the particles have never come into contact with the glands, or in some cases the tentacles may not have been in an active condition. In order to excite movement, it is indispensable that the particles should actually rest on the glands; for a touch once, twice, or even thrice repeated by any hard body is not sufficient to excite movement.

Another experiment, showing that extremely minute particles act on the glands when immersed in water, may here be given. A grain of sulphate of quinine was added to an ounce of water, which

was not afterwards filtered; and on placing three leaves in ninety minims of this fluid, I was much surprised to find that all three leaves were greatly inflected in 15 m.; for I knew from previous trials that the solution does not act so quickly as this. It immediately occurred to me that the particles of the undissolved salt, which were so light as to float about, might have come into contact with the glands, and caused this rapid movement. Accordingly I added to some distilled water a pinch of a quite innocent substance, namely, precipitated carbonate of lime, which consists of an impalpable powder; I shook the mixture, and thus got a fluid like thin milk. Two leaves were immersed in it, and in 6 m. almost every tentacle was much inflected. I placed one of these leaves under the microscope, and saw innumerable atoms of lime adhering to the external surface of the secretion. Some, however, had penetrated it, and were lying on the surfaces of the glands; and no doubt it was these particles which caused the tentacles to bend. When a leaf is immersed in water, the secretion instantly swells much; and I presume that it is ruptured here and there, so that little eddies of water rush in. If so, we can understand how the atoms of chalk, which rested on the surfaces of the glands, had penetrated the secretion. Anyone who has rubbed precipitated chalk between his fingers will have perceived how excessively fine the powder is. No doubt there must be a limit, beyond which a particle would be too small to act on a gland; but what this limit is, I know not. I have often seen fibres and dust, which had fallen from the air, on the glands of plants kept in my room, and these never induced any movement; but then such particles lay on the surface of the secretion and never reached the gland itself.

Finally, it is an extraordinary fact that a little bit of soft thread, $1/50$ of an inch in length and weighing $1/8197$ of a grain, or of a human hair, $8/1000$ of an inch in length and weighing only $1/78740$ of a grain (.000822 milligramme), or particles of precipitated chalk, after resting for a short time on a gland, should induce some change in its cells, exciting them to transmit a motor impulse throughout the whole length of the pedicel, consisting of about twenty cells, to near its base, causing this part to bend, and the tentacle to sweep through an angle of above 180° . That the contents of the cells of the glands, and afterwards those of the pedicels, are affected in a plainly visible manner by the pressure of minute particles, we shall have abundant evidence when we treat of the aggregation of protoplasm. But the case is much more remarkable than as yet stated; for the particles are supported by the viscid and dense secretion; nevertheless, even smaller ones than those of which the measurements have been given, when brought by an insensibly slow movement, through the means above specified, into contact with the surface of a gland, act on it, and the tentacle bends. The pressure exerted by the particle of hair, weighing only $1/78740$ of a grain and supported by a dense fluid, must have been inconceivably slight. We may conjecture that it could hardly have equalled the millionth of a grain; and we shall hereafter see that far less than the millionth of a grain of phosphate of ammonia in solution, when absorbed by a gland, acts on it and induces movement. A bit of hair, $1/50$ of an inch in length, and therefore much larger than those used in the above experiments, was not perceived when placed on my tongue; and it is extremely doubtful whether any nerve in the human body, even if in an inflamed condition, would be in any way affected by such a particle supported in a dense fluid, and slowly brought into contact with the nerve. Yet the cells of the glands of *Drosera* are thus excited to transmit a motor impulse to a distant point, inducing movement. It appears to me that hardly any more remarkable fact than this has been observed in the vegetable kingdom.

The Inflection of the Exterior Tentacles, when their Glands are excited by Repeated Touches.

We have already seen that, if the central glands are excited by being gently brushed, they transmit a motor impulse to the exterior tentacles, causing them to bend; and we have now to consider the effects which follow from the glands of the exterior tentacles being themselves touched. On several occasions, a large number of glands were touched only once with a needle or fine brush, hard enough to bend the whole flexible tentacle; and though this must have caused a thousand-fold greater pressure than the weight of the above described particles, not a tentacle moved. On another occasion forty-five glands on eleven leaves were touched once, twice, or even thrice, with a needle or stiff bristle. This was done as quickly as possible, but with force sufficient to bend the tentacles; yet only six of

them became inflected, – three plainly, and three in a slight degree. In order to ascertain whether these tentacles which were not affected were in an efficient state, bits of meat were placed on ten of them, and they all soon became greatly incurved. On the other hand, when a large number of glands were struck four, five, or six times with the same force as before, a needle or sharp splinter of glass being used, a much larger proportion of tentacles became inflected; but the result was so uncertain as to seem capricious. For instance, I struck in the above manner three glands, which happened to be extremely sensitive, and all three were inflected almost as quickly, as if bits of meat had been placed on them. On another occasion I gave a single forcible touch to a considerable number of glands, and not one moved; but these same glands, after an interval of some hours, being touched four or five times with a needle, several of the tentacles soon became inflected.

The fact of a single touch or even of two or three touches not causing inflection must be of some service to the plant; as during stormy weather, the glands cannot fail to be occasionally touched by the tall blades of grass, or by other plants growing near; and it would be a great evil if the tentacles were thus brought into action, for the act of re-expansion takes a considerable time, and until the tentacles are re-expanded they cannot catch prey. On the other hand, extreme sensitiveness to slight pressure is of the highest service to the plant; for, as we have seen, if the delicate feet of a minute struggling insect press ever so lightly on the surfaces of two or three glands, the tentacles bearing these glands soon curl inwards and carry the insect with them to the centre, causing, after a time, all the circumferential tentacles to embrace it. Nevertheless, the movements of the plant are not perfectly adapted to its requirements; for if a bit of dry moss, peat, or other rubbish, is blown on to the disc, as often happens, the tentacles clasp it in a useless manner. They soon, however, discover their mistake and release such innutritious objects.

It is also a remarkable fact, that drops of water falling from a height, whether under the form of natural or artificial rain, do not cause the tentacles to move; yet the drops must strike the glands with considerable force, more especially after the secretion has been all washed away by heavy rain; and this often occurs, though the secretion is so viscid that it can be removed with difficulty merely by waving the leaves in water. If the falling drops of water are small, they adhere to the secretion, the weight of which must be increased in a much greater degree, as before remarked, than by the addition of minute particles of solid matter; yet the drops never cause the tentacles to become inflected. It would obviously have been a great evil to the plant (as in the case of occasional touches) if the tentacles were excited to bend by every shower of rain; but this evil has been avoided by the glands either having become through habit insensible to the blows and prolonged pressure of drops of water, or to their having been originally rendered sensitive solely to the contact of solid bodies. We shall hereafter see that the filaments on the leaves of *Dionaea* are likewise insensible to the impact of fluids, though exquisitely sensitive to momentary touches from any solid body.

When the pedicel of a tentacle is cut off by a sharp pair of scissors quite close beneath the gland, the tentacle generally becomes inflected. I tried this experiment repeatedly, as I was much surprised at the fact, for all other parts of the pedicels are insensible to any stimulus. These headless tentacles after a time re-expand; but I shall return to this subject. On the other hand, I occasionally succeeded in crushing a gland between a pair of pincers, but this caused no inflection. In this latter case the tentacles seem paralysed, as likewise follows from the action of too strong solutions of certain salts, and by too great heat, whilst weaker solutions of the same salts and a more gentle heat cause movement. We shall also see in future chapters that various other fluids, some vapours, and oxygen (after the plant has been for some time excluded from its action), all induce inflection, and this likewise results from an induced galvanic current.⁶

⁶ My son Francis, guided by the observations of Dr. Burdon Sanderson on *Dionaea*, finds that if two needles are inserted into the blade of a leaf of *Drosera*, the tentacles do not move; but that if similar needles in connection with the secondary coil of a Du Bois inductive apparatus are inserted, the tentacles curve inwards in the course of a few minutes. My son hopes soon to publish an account of his observations.

CHAPTER III

AGGREGATION OF THE PROTOPLASM WITHIN THE CELLS OF THE TENTACLES

Nature of the contents of the cells before aggregation – Various causes which excite aggregation – The process commences within the glands and travels down the tentacles – Description of the aggregated masses and of their spontaneous movements – Currents of protoplasm along the walls of the cells – Action of carbonate of ammonia – The granules in the protoplasm which flows along the walls coalesce with the central masses – Minuteness of the quantity of carbonate of ammonia causing aggregation – Action of other salts of ammonia – Of other substances, organic fluids, &c. – Of water – Of heat – Redissolution of the aggregated masses – Proximate causes of the aggregation of the protoplasm – Summary and concluding remarks – Supplementary observations on aggregation in the roots of plants.

I WILL here interrupt my account of the movements of the leaves, and describe the phenomenon of aggregation, to which subject I have already alluded. If the tentacles of a young, yet fully matured leaf, that has never been excited or become inflected, be examined, the cells forming the pedicels are seen to be filled with homogeneous, purple fluid. The walls are lined by a layer of colourless, circulating protoplasm; but this can be seen with much greater distinctness after the process of aggregation has been partly effected than before. The purple fluid which exudes from a crushed tentacle is somewhat coherent, and does not mingle with the surrounding water; it contains much flocculent or granular matter. But this matter may have been generated by the cells having been crushed; some degree of aggregation having been thus almost instantly caused.

If a tentacle is examined some hours after the gland has been excited by repeated touches, or by an inorganic or organic particle placed on it, or by the absorption of certain fluids, it presents a wholly changed appearance. The cells, instead of being filled with homogeneous purple fluid, now contain variously shaped masses of purple matter, suspended in a colourless or almost colourless fluid. The change is so conspicuous that it is visible through a weak lens, and even sometimes by the naked eye; the tentacles now have a mottled appearance, so that one thus affected can be picked out with ease from all the others. The same result follows if the glands on the disc are irritated in any manner, so that the exterior tentacles become inflected; for their contents will then be found in an aggregated condition, although their glands have not as yet touched any object. But aggregation may occur independently of inflection, as we shall presently see. By whatever cause the process may have been excited, it commences within the glands, and then travels down the tentacles. It can be observed much more distinctly in the upper cells of the pedicels than within the glands, as these are somewhat opaque. Shortly after the tentacles have re-expanded, the little masses of protoplasm are all redissolved, and the purple fluid within the cells becomes as homogeneous and transparent as it was at first. The process of redissolution travels upwards from the bases of the tentacles to the glands, and therefore in a reversed direction to that of aggregation. Tentacles in an aggregated condition were shown to Prof. Huxley, Dr. Hooker, and Dr. Burdon Sanderson, who observed the changes under the microscope, and were much struck with the whole phenomenon.

The little masses of aggregated matter are of the most diversified shapes, often spherical or oval, sometimes much elongated, or quite irregular with thread- or necklace-like or club-formed projections. They consist of thick, apparently viscid matter, which in the exterior tentacles is of a

purplish, and in the short distal tentacles of a greenish, colour. These little masses incessantly change their forms and positions, being never at rest. A single mass will often separate into two, which afterwards reunite. Their movements are rather slow, and resemble those of Amoebae or of the white corpuscles of the blood. We may, therefore, conclude that they consist of protoplasm. If their shapes are sketched at intervals of a few minutes, they are invariably seen to have undergone great changes of form; and the same cell has been observed for several hours. Eight rude, though accurate sketches of the same cell, made at intervals of between 2 m. or 3 m., are here given (fig. 7), and illustrate some of the simpler and commonest changes. The cell A, when first sketched, included two oval masses of purple protoplasm touching each other. These became separate, as shown at B, and then reunited, as at C. After the next interval a very common appearance was presented – D, namely, the formation of an extremely minute sphere at one end of an elongated mass. This rapidly increased in size, as shown in E, and was then re-absorbed, as at F, by which time another sphere had been formed at the opposite end.

The cell above figured was from a tentacle of a dark red leaf, which had caught a small moth, and was examined under water. As I at first thought that the movements of the masses might be due to the absorption of water, I placed a fly on a leaf, and when after 18 hrs. all the tentacles were well inflected, these were examined without being immersed in water. The cell here represented (fig. 8) was from this leaf, being sketched eight times in the course of 15 m. These sketches exhibit some of the more remarkable changes which the protoplasm undergoes. At first, there was at the base of the cell 1, a little mass on a short footstalk, and a larger mass near the upper end, and these seemed quite separate. Nevertheless, they may have been connected by a fine and invisible thread of protoplasm, for on two other occasions, whilst one mass was rapidly increasing, and another in the same cell rapidly decreasing, I was able by varying the light and using a high power, to detect a connecting thread of extreme tenuity, which evidently served as the channel of communication between the two. On the other hand, such connecting threads are sometimes seen to break, and their extremities then quickly become club-headed. The other sketches in fig. 8 show the forms successively assumed.

Shortly after the purple fluid within the cells has become aggregated, the little masses float about in a colourless or almost colourless fluid; and the layer of white granular protoplasm which flows along the walls can now be seen much more distinctly. The stream flows at an irregular rate, up one wall and down the opposite one, generally at a slower rate across the narrow ends of the elongated cells, and so round and round. But the current sometimes ceases. The movement is often in waves, and their crests sometimes stretch almost across the whole width of the cell, and then sink down again. Small spheres of protoplasm, apparently quite free, are often driven by the current round the cells; and filaments attached to the central masses are swayed to and fro, as if struggling to escape. Altogether, one of these cells with the ever changing central masses, and with the layer of protoplasm flowing round the walls, presents a wonderful scene of vital activity.

[Many observations were made on the contents of the cells whilst undergoing the process of aggregation, but I shall detail only a few cases under different heads. A small portion of a leaf was cut off, placed under a high power, and the glands very gently pressed under a compressor. In 15 m. I distinctly saw extremely minute spheres of protoplasm aggregating themselves in the purple fluid; these rapidly increased in size, both within the cells of the glands and of the upper ends of the pedicels. Particles of glass, cork, and cinders were also placed on the glands of many tentacles; in 1 hr. several of them were inflected, but after 1 hr. 35 m. there was no aggregation. Other tentacles with these particles were examined after 8 hrs., and now all their cells had undergone aggregation; so had the cells of the exterior tentacles which had become inflected through the irritation transmitted from the glands of the disc, on which the transported particles rested. This was likewise the case with the short tentacles round the margins of the disc, which had not as yet become inflected. This latter fact shows that the process of aggregation is independent of the inflection of the tentacles, of which indeed we have other and abundant evidence. Again, the exterior tentacles on three leaves were

carefully examined, and found to contain only homogeneous purple fluid; little bits of thread were then placed on the glands of three of them, and after 22 hrs. the purple fluid in their cells almost down to their bases was aggregated into innumerable, spherical, elongated, or filamentous masses of protoplasm. The bits of thread had been carried some time previously to the central disc, and this had caused all the other tentacles to become somewhat inflected; and their cells had likewise undergone aggregation, which however, it should be observed, had not as yet extended down to their bases, but was confined to the cells close beneath the glands.

Not only do repeated touches on the glands⁷ and the contact of minute particles cause aggregation, but if glands, without being themselves injured, are cut off from the summits of the pedicels, this induces a moderate amount of aggregation in the headless tentacles, after they have become inflected. On the other hand, if glands are suddenly crushed between pincers, as was tried in six cases, the tentacles seem paralysed by so great a shock, for they neither become inflected nor exhibit any signs of aggregation.

Carbonate of Ammonia. – Of all the causes inducing aggregation, that which, as far as I have seen, acts the quickest, and is the most powerful, is a solution of carbonate of ammonia. Whatever its strength may be, the glands are always affected first, and soon become quite opaque, so as to appear black. For instance, I placed a leaf in a few drops of a strong solution, namely, of one part to 146 of water (or 3 grs. to 1 oz.), and observed it under a high power. All the glands began to darken in 10 s. (seconds); and in 13 s. were conspicuously darker. In 1 m. extremely small spherical masses of protoplasm could be seen arising in the cells of the pedicels close beneath the glands, as well as in the cushions on which the long-headed marginal glands rest. In several cases the process travelled down the pedicels for a length twice or thrice as great as that of the glands, in about 10 m. It was interesting to observe the process momentarily arrested at each transverse partition between two cells, and then to see the transparent contents of the cell next below almost flashing into a cloudy mass. In the lower part of the pedicels, the action proceeded slower, so that it took about 20 m. before the cells halfway down the long marginal and submarginal tentacles became aggregated.

We may infer that the carbonate of ammonia is absorbed by the glands, not only from its action being so rapid, but from its effect being somewhat different from that of other salts. As the glands, when excited, secrete an acid belonging to the acetic series, the carbonate is probably at once converted into a salt of this series; and we shall presently see that the acetate of ammonia causes aggregation almost or quite as energetically as does the carbonate. If a few drops of a solution of one part of the carbonate to 437 of water (or 1 gr. to 1 oz.) be added to the purple fluid which exudes from crushed tentacles, or to paper stained by being rubbed with them, the fluid and the paper are changed into a pale dirty green. Nevertheless, some purple colour could still be detected after 1 hr. 30 m. within the glands of a leaf left in a solution of twice the above strength (viz. 2 grs. to 1 oz.); and after 24 hrs. the cells of the pedicels close beneath the glands still contained spheres of protoplasm of a fine purple tint. These facts show that the ammonia had not entered as a carbonate, for otherwise the colour would have been discharged. I have, however, sometimes observed, especially with the long-headed tentacles on the margins of very pale leaves immersed in a solution, that the glands as well as the upper cells of the pedicels were discoloured; and in these cases I presume that the unchanged carbonate had been absorbed. The appearance above described, of the aggregating process being arrested for a short time at each transverse partition, impresses the mind with the idea of matter passing downwards from cell to cell. But as the cells one beneath the other undergo aggregation when inorganic and insoluble particles are placed on the glands, the process must be, at least in these cases, one of molecular change, transmitted from the glands, independently of the absorption of any matter.

⁷ Judging from an account of M. Heckel's observations, which I have only just seen quoted in the 'Gardeners' Chronicle' (Oct. 10, 1874), he appears to have observed a similar phenomenon in the stamens of *Berberis*, after they have been excited by a touch and have moved; for he says, "the contents of each individual cell are collected together in the centre of the cavity."

So it may possibly be in the case of the carbonate of ammonia. As, however, the aggregation caused by this salt travels down the tentacles at a quicker rate than when insoluble particles are placed on the glands, it is probable that ammonia in some form is absorbed not only by the glands, but passes down the tentacles.

Having examined a leaf in water, and found the contents of the cells homogeneous, I placed it in a few drops of a solution of one part of the carbonate to 437 of water, and attended to the cells immediately beneath the glands, but did not use a very high power. No aggregation was visible in 3 m.; but after 15 m. small spheres of protoplasm were formed, more especially beneath the long-headed marginal glands; the process, however, in this case took place with unusual slowness. In 25 m. conspicuous spherical masses were present in the cells of the pedicels for a length about equal to that of the glands; and in 3 hrs. to that of a third or half of the whole tentacle.

If tentacles with cells containing only very pale pink fluid, and apparently but little protoplasm, are placed in a few drops of a weak solution of one part of the carbonate to 4375 of water (1 gr. to 10 oz.), and the highly transparent cells beneath the glands are carefully observed under a high power, these may be seen first to become slightly cloudy from the formation of numberless, only just perceptible, granules, which rapidly grow larger either from coalescence or from attracting more protoplasm from the surrounding fluid. On one occasion I chose a singularly pale leaf, and gave it, whilst under the microscope, a single drop of a stronger solution of one part to 437 of water; in this case the contents of the cells did not become cloudy, but after 10 m. minute irregular granules of protoplasm could be detected, which soon increased into irregular masses and globules of a greenish or very pale purple tint; but these never formed perfect spheres, though incessantly changing their shapes and positions.

With moderately red leaves the first effect of a solution of the carbonate generally is the formation of two or three, or of several, extremely minute purple spheres which rapidly increase in size. To give an idea of the rate at which such spheres increase in size, I may mention that a rather pale purple leaf placed under a slip of glass was given a drop of a solution of one part to 292 of water, and in 13 m. a few minute spheres of protoplasm were formed; one of these, after 2 hrs. 30 m., was about two-thirds of the diameter of the cell. After 4 hrs. 25 m. it nearly equalled the cell in diameter; and a second sphere about half as large as the first, together with a few other minute ones, were formed. After 6 hrs. the fluid in which these spheres floated was almost colourless. After 8 hrs. 35 m. (always reckoning from the time when the solution was first added) four new minute spheres had appeared. Next morning, after 22 hrs., there were, besides the two large spheres, seven smaller ones, floating in absolutely colourless fluid, in which some flocculent greenish matter was suspended.

At the commencement of the process of aggregation, more especially in dark red leaves, the contents of the cells often present a different appearance, as if the layer of protoplasm (primordial utricle) which lines the cells had separated itself and shrunk from the walls; an irregularly shaped purple bag being thus formed. Other fluids, besides a solution of the carbonate, for instance an infusion of raw meat, produce this same effect. But the appearance of the primordial utricle shrinking from the walls is certainly false;⁸ for before giving the solution, I saw on several occasions that the walls were lined with colourless flowing protoplasm, and after the bag-like masses were formed, the protoplasm was still flowing along the walls in a conspicuous manner, even more so than before. It appeared indeed as if the stream of protoplasm was strengthened by the action of the carbonate, but it was impossible to ascertain whether this was really the case. The bag-like masses, when once formed, soon begin to glide slowly round the cells, sometimes sending out projections which separate into little spheres; other spheres appear in the fluid surrounding the bags, and these travel much more quickly. That the small spheres are separate is often shown by sometimes one and then another travelling in

⁸ With other plants I have often seen what appears to be a true shrinking of the primordial utricle from the walls of the cells, caused by a solution of carbonate of ammonia, as likewise follows from mechanical injuries.

advance, and sometimes they revolve round each other. I have occasionally seen spheres of this kind proceeding up and down the same side of a cell, instead of round it. The bag-like masses after a time generally divide into two rounded or oval masses, and these undergo the changes shown in figs. 7 and 8. At other times spheres appear within the bags; and these coalesce and separate in an endless cycle of change.

After leaves have been left for several hours in a solution of the carbonate, and complete aggregation has been effected, the stream of protoplasm on the walls of the cells ceases to be visible; I observed this fact repeatedly, but will give only one instance. A pale purple leaf was placed in a few drops of a solution of one part to 292 of water, and in 2 hrs. some fine purple spheres were formed in the upper cells of the pedicels, the stream of protoplasm round their walls being still quite distinct; but after an additional 4 hrs., during which time many more spheres were formed, the stream was no longer distinguishable on the most careful examination; and this no doubt was due to the contained granules having become united with the spheres, so that nothing was left by which the movement of the limpid protoplasm could be perceived. But minute free spheres still travelled up and down the cells, showing that there was still a current. So it was next morning, after 22 hrs., by which time some new minute spheres had been formed; these oscillated from side to side and changed their positions, proving that the current had not ceased, though no stream of protoplasm was visible. On another occasion, however, a stream was seen flowing round the cell-walls of a vigorous, dark-coloured leaf, after it had been left for 24 hrs. in a rather stronger solution, namely, of one part of the carbonate to 218 of water. This leaf, therefore, was not much or at all injured by an immersion for this length of time in the above solution of two grains to the ounce; and on being afterwards left for 24 hrs. in water, the aggregated masses in many of the cells were re-dissolved, in the same manner as occurs with leaves in a state of nature when they re-expand after having caught insects.

In a leaf which had been left for 22 hrs. in a solution of one part of the carbonate to 292 of water, some spheres of protoplasm (formed by the self-division of a bag-like mass) were gently pressed beneath a covering glass, and then examined under a high power. They were now distinctly divided by well-defined radiating fissures, or were broken up into separate fragments with sharp edges; and they were solid to the centre. In the larger broken spheres the central part was more opaque, darker-coloured, and less brittle than the exterior; the latter alone being in some cases penetrated by the fissures. In many of the spheres the line of separation between the outer and inner parts was tolerably well defined. The outer parts were of exactly the same very pale purple tint, as that of the last formed smaller spheres; and these latter did not include any darker central core.

From these several facts we may conclude that when vigorous dark-coloured leaves are subjected to the action of carbonate of ammonia, the fluid within the cells of the tentacles often aggregates exteriorly into coherent viscid matter, forming a kind of bag. Small spheres sometimes appear within this bag, and the whole generally soon divides into two or more spheres, which repeatedly coalesce and redivide. After a longer or shorter time the granules in the colourless layer of protoplasm, which flows round the walls, are drawn to and unite with the larger spheres, or form small independent spheres; these latter being of a much paler colour, and more brittle than the first aggregated masses. After the granules of protoplasm have been thus attracted, the layer of flowing protoplasm can no longer be distinguished, though a current of limpid fluid still flows round the walls.

If a leaf is immersed in a very strong, almost concentrated, solution of carbonate of ammonia, the glands are instantly blackened, and they secrete copiously; but no movement of the tentacles ensues. Two leaves thus treated became after 1 hr. flaccid, and seemed killed; all the cells in their tentacles contained spheres of protoplasm, but these were small and discoloured. Two other leaves were placed in a solution not quite so strong, and there was well-marked aggregation in 30 m. After 24 hrs. the spherical or more commonly oblong masses of protoplasm became opaque and granular, instead of being as usual translucent; and in the lower cells there were only innumerable minute

spherical granules. It was evident that the strength of the solution had interfered with the completion of the process, as we shall see likewise follows from too great heat.

All the foregoing observations relate to the exterior tentacles, which are of a purple colour; but the green pedicels of the short central tentacles are acted on by the carbonate, and by an infusion of raw meat, in exactly the same manner, with the sole difference that the aggregated masses are of a greenish colour; so that the process is in no way dependent on the colour of the fluid within the cells.

Finally, the most remarkable fact with respect to this salt is the extraordinary small amount which suffices to cause aggregation. Full details will be given in the seventh chapter, and here it will be enough to say that with a sensitive leaf the absorption by a gland of $1/134400$ of a grain (.000482 mgr.) is enough to cause in the course of one hour well-marked aggregation in the cells immediately beneath the gland.

The Effects of certain other Salts and Fluids. – Two leaves were placed in a solution of one part of acetate of ammonia to about 146 of water, and were acted on quite as energetically, but perhaps not quite so quickly, as by the carbonate. After 10 m. the glands were black, and in the cells beneath them there were traces of aggregation, which after 15 m. was well marked, extending down the tentacles for a length equal to that of the glands. After 2 hrs. the contents of almost all the cells in all the tentacles were broken up into masses of protoplasm. A leaf was immersed in a solution of one part of oxalate of ammonia to 146 of water; and after 24 m. some, but not a conspicuous, change could be seen within the cells beneath the glands. After 47 m. plenty of spherical masses of protoplasm were formed, and these extended down the tentacles for about the length of the glands. This salt, therefore, does not act so quickly as the carbonate. With respect to the citrate of ammonia, a leaf was placed in a little solution of the above strength, and there was not even a trace of aggregation in the cells beneath the glands, until 56 m. had elapsed; but it was well marked after 2 hrs. 20 m. On another occasion a leaf was placed in a stronger solution, of one part of the citrate to 109 of water (4 grs. to 1 oz.), and at the same time another leaf in a solution of the carbonate of the same strength. The glands of the latter were blackened in less than 2 m., and after 1 hr. 45 m. the aggregated masses, which were spherical and very dark-coloured, extended down all the tentacles, for between half and two-thirds of their lengths; whereas in the leaf immersed in the citrate the glands, after 30 m., were of a dark red, and the aggregated masses in the cells beneath them pink and elongated. After 1 hr. 45 m. these masses extended down for only about one-fifth or one-fourth of the length of the tentacles.

Two leaves were placed, each in ten minims of a solution of one part of nitrate of ammonia to 5250 of water (1 gr. to 12 oz.), so that each leaf received $1/576$ of a grain (.1124 mgr.). This quantity caused all the tentacles to be inflected, but after 24 hrs. there was only a trace of aggregation. One of these same leaves was then placed in a weak solution of the carbonate, and after 1 hr. 45 m. the tentacles for half their lengths showed an astonishing degree of aggregation. Two other leaves were then placed in a much stronger solution of one part of the nitrate to 146 of water (3 grs. to 1 oz.); in one of these there was no marked change after 3 hrs.; but in the other there was a trace of aggregation after 52 m., and this was plainly marked after 1 hr. 22 m., but even after 2 hrs. 12 m. there was certainly not more aggregation than would have followed from an immersion of from 5 m. to 10 m. in an equally strong solution of the carbonate.

Lastly, a leaf was placed in thirty minims of a solution of one part of phosphate of ammonia to 43,750 of water (1 gr. to 100 oz.), so that it received $1/1600$ of a grain (.04079 mgr.); this soon caused the tentacles to be strongly inflected; and after 24 hrs. the contents of the cells were aggregated into oval and irregularly globular masses, with a conspicuous current of protoplasm flowing round the walls. But after so long an interval aggregation would have ensued, whatever had caused inflection.

Only a few other salts, besides those of ammonia, were tried in relation to the process of aggregation. A leaf was placed in a solution of one part of chloride of sodium to 218 of water, and after 1 hr. the contents of the cells were aggregated into small, irregularly globular, brownish masses; these after 2 hrs. were almost disintegrated and pulpy. It was evident that the protoplasm had been

injuriously affected; and soon afterwards some of the cells appeared quite empty. These effects differ altogether from those produced by the several salts of ammonia, as well as by various organic fluids, and by inorganic particles placed on the glands. A solution of the same strength of carbonate of soda and carbonate of potash acted in nearly the same manner as the chloride; and here again, after 2 hrs. 30 m., the outer cells of some of the glands had emptied themselves of their brown pulpy contents. We shall see in the eighth chapter that solutions of several salts of soda of half the above strength cause inflection, but do not injure the leaves. Weak solutions of sulphate of quinine, of nicotine, camphor, poison of the cobra, &c., soon induce well-marked aggregation; whereas certain other substances (for instance, a solution of curare) have no such tendency.

Many acids, though much diluted, are poisonous; and though, as will be shown in the eighth chapter, they cause the tentacles to bend, they do not excite true aggregation. Thus leaves were placed in a solution of one part of benzoic acid to 437 of water; and in 15 m. the purple fluid within the cells had shrunk a little from the walls, yet when carefully examined after 1 hr. 20 m., there was no true aggregation; and after 24 hrs. the leaf was evidently dead. Other leaves in iodic acid, diluted to the same degree, showed after 2 hrs. 15 m. the same shrunken appearance of the purple fluid within the cells; and these, after 6 hrs. 15 m., were seen under a high power to be filled with excessively minute spheres of dull reddish protoplasm, which by the next morning, after 24 hrs., had almost disappeared, the leaf being evidently dead. Nor was there any true aggregation in leaves immersed in propionic acid of the same strength; but in this case the protoplasm was collected in irregular masses towards the bases of the lower cells of the tentacles.

A filtered infusion of raw meat induces strong aggregation, but not very quickly. In one leaf thus immersed there was a little aggregation after 1 hr. 20 m., and in another after 1 hr. 50 m. With other leaves a considerably longer time was required: for instance, one immersed for 5 hrs. showed no aggregation, but was plainly acted on in 5 m.; when placed in a few drops of a solution of one part of carbonate of ammonia to 146 of water. Some leaves were left in the infusion for 24 hrs., and these became aggregated to a wonderful degree, so that the inflected tentacles presented to the naked eye a plainly mottled appearance. The little masses of purple protoplasm were generally oval or beaded, and not nearly so often spherical as in the case of leaves subjected to carbonate of ammonia. They underwent incessant changes of form; and the current of colourless protoplasm round the walls was conspicuously plain after an immersion of 25 hrs. Raw meat is too powerful a stimulant, and even small bits generally injure, and sometimes kill, the leaves to which they are given: the aggregated masses of protoplasm become dingy or almost colourless, and present an unusual granular appearance, as is likewise the case with leaves which have been immersed in a very strong solution of carbonate of ammonia. A leaf placed in milk had the contents of its cells somewhat aggregated in 1 hr. Two other leaves, one immersed in human saliva for 2 hrs. 30 m., and another in unboiled white of egg for 1 hr. 30 m., were not acted on in this manner; though they undoubtedly would have been so, had more time been allowed. These same two leaves, on being afterwards placed in a solution of carbonate of ammonia (3 grs. to 1 oz.), had their cells aggregated, the one in 10 m. and the other in 5 m.

Several leaves were left for 4 hrs. 30 m. in a solution of one part of white sugar to 146 of water, and no aggregation ensued; on being placed in a solution of this same strength of carbonate of ammonia, they were acted on in 5 m.; as was likewise a leaf which had been left for 1 hr. 45 m. in a moderately thick solution of gum arabic. Several other leaves were immersed for some hours in denser solutions of sugar, gum, and starch, and they had the contents of their cells greatly aggregated. This effect may be attributed to exosmose; for the leaves in the syrup became quite flaccid, and those in the gum and starch somewhat flaccid, with their tentacles twisted about in the most irregular manner, the longer ones like corkscrews. We shall hereafter see that solutions of these substances, when placed on the discs of leaves, do not incite inflection. Particles of soft sugar were added to the secretion round several glands and were soon dissolved, causing a great increase of the secretion,

no doubt by exosmose; and after 24 hrs. the cells showed a certain amount of aggregation, though the tentacles were not inflected. Glycerine causes in a few minutes well-pronounced aggregation, commencing as usual within the glands and then travelling down the tentacles; and this I presume may be attributed to the strong attraction of this substance for water. Immersion for several hours in water causes some degree of aggregation. Twenty leaves were first carefully examined, and re-examined after having been left immersed in distilled water for various periods, with the following results. It is rare to find even a trace of aggregation until 4 or 5 and generally not until several more hours have elapsed. When however a leaf becomes quickly inflected in water, as sometimes happens, especially during very warm weather, aggregation may occur in little over 1 hr. In all cases leaves left in water for more than 24 hrs. have their glands blackened, which shows that their contents are aggregated; and in the specimens which were carefully examined, there was fairly well-marked aggregation in the upper cells of the pedicels. These trials were made with cut off-leaves, and it occurred to me that this circumstance might influence the result, as the footstalks would not perhaps absorb water quickly enough to supply the glands as they continued to secrete. But this view was proved erroneous, for a plant with uninjured roots, bearing four leaves, was submerged in distilled water for 47 hrs., and the glands were blackened, though the tentacles were very little inflected. In one of these leaves there was only a slight degree of aggregation in the tentacles; in the second rather more, the purple contents of the cells being a little separated from the walls; in the third and fourth, which were pale leaves, the aggregation in the upper parts of the pedicels was well marked. In these leaves the little masses of protoplasm, many of which were oval, slowly changed their forms and positions; so that a submergence for 47 hrs. had not killed the protoplasm. In a previous trial with a submerged plant, the tentacles were not in the least inflected.

Heat induces aggregation. A leaf, with the cells of the tentacles containing only homogeneous fluid, was waved about for 1 m. in water at 130o Fahr. (54o.4 Cent.) and was then examined under the microscope as quickly as possible, that is in 2 m. or 3 m.; and by this time the contents of the cells had undergone some degree of aggregation. A second leaf was waved for 2 m. in water at 125o (51o.6 Cent.) and quickly examined as before; the tentacles were well inflected; the purple fluid in all the cells had shrunk a little from the walls, and contained many oval and elongated masses of protoplasm, with a few minute spheres. A third leaf was left in water at 125o, until it cooled, and when examined after 1 hr. 45 m., the inflected tentacles showed some aggregation, which became after 3 hrs. more strongly marked, but did not subsequently increase. Lastly, a leaf was waved for 1 m. in water at 120o (48o.8 Cent.) and then left for 1 hr. 26 m. in cold water; the tentacles were but little inflected, and there was only here and there a trace of aggregation. In all these and other trials with warm water the protoplasm showed much less tendency to aggregate into spherical masses than when excited by carbonate of ammonia.

Redissolution of the Aggregated Masses of Protoplasm. – As soon as tentacles which have clasped an insect or any inorganic object, or have been in any way excited, have fully re-expanded, the aggregated masses of protoplasm are redissolved and disappear; the cells being now refilled with homogeneous purple fluid as they were before the tentacles were inflected. The process of redissolution in all cases commences at the bases of the tentacles, and proceeds up them towards the glands. In old leaves, however, especially in those which have been several times in action, the protoplasm in the uppermost cells of the pedicels remains in a permanently more or less aggregated condition. In order to observe the process of redissolution, the following observations were made: a leaf was left for 24 hrs. in a little solution of one part of carbonate of ammonia to 218 of water, and the protoplasm was as usual aggregated into numberless purple spheres, which were incessantly changing their forms. The leaf was then washed and placed in distilled water, and after 3 hrs. 15 m. some few of the spheres began to show by their less clearly defined edges signs of redissolution. After 9 hrs. many of them had become elongated, and the surrounding fluid in the cells was slightly more coloured, showing plainly that redissolution had commenced. After 24 hrs., though many cells

still contained spheres, here and there one could be seen filled with purple fluid, without a vestige of aggregated protoplasm; the whole having been redissolved. A leaf with aggregated masses, caused by its having been waved for 2 m. in water at the temperature of 125° Fahr., was left in cold water, and after 11 hrs. the protoplasm showed traces of incipient redissolution. When again examined three days after its immersion in the warm water, there was a conspicuous difference, though the protoplasm was still somewhat aggregated. Another leaf, with the contents of all the cells strongly aggregated from the action of a weak solution of phosphate of ammonia, was left for between three and four days in a mixture (known to be innocuous) of one drachm of alcohol to eight drachms of water, and when re-examined every trace of aggregation had disappeared, the cells being now filled with homogeneous fluid.

We have seen that leaves immersed for some hours in dense solutions of sugar, gum, and starch, have the contents of their cells greatly aggregated, and are rendered more or less flaccid, with the tentacles irregularly contorted. These leaves, after being left for four days in distilled water, became less flaccid, with their tentacles partially re-expanded, and the aggregated masses of protoplasm were partially redissolved. A leaf with its tentacles closely clasped over a fly, and with the contents of the cells strongly aggregated, was placed in a little sherry wine; after 2 hrs. several of the tentacles had re-expanded, and the others could by a mere touch be pushed back into their properly expanded positions, and now all traces of aggregation had disappeared, the cells being filled with perfectly homogeneous pink fluid. The redissolution in these cases may, I presume, be attributed to endosmose.]

On the Proximate Causes of the Process of Aggregation.

As most of the stimulants which cause the inflection of the tentacles likewise induce aggregation in the contents of their cells, this latter process might be thought to be the direct result of inflection; but this is not the case. If leaves are placed in rather strong solutions of carbonate of ammonia, for instance of three or four, and even sometimes of only two grains to the ounce of water (i.e. one part to 109, or 146, or 218, of water), the tentacles are paralysed, and do not become inflected, yet they soon exhibit strongly marked aggregation. Moreover, the short central tentacles of a leaf which has been immersed in a weak solution of any salt of ammonia, or in any nitrogenous organic fluid, do not become in the least inflected; nevertheless they exhibit all the phenomena of aggregation. On the other hand, several acids cause strongly pronounced inflection, but no aggregation.

It is an important fact that when an organic or inorganic object is placed on the glands of the disc, and the exterior tentacles are thus caused to bend inwards, not only is the secretion from the glands of the latter increased in quantity and rendered acid, but the contents of the cells of their pedicels become aggregated. The process always commences in the glands, although these have not as yet touched any object. Some force or influence must, therefore, be transmitted from the central glands to the exterior tentacles, first to near their bases causing this part to bend, and next to the glands causing them to secrete more copiously. After a short time the glands, thus indirectly excited, transmit or reflect some influence down their own pedicels, inducing aggregation in cell beneath cell to their bases.

It seems at first sight a probable view that aggregation is due to the glands being excited to secrete more copiously, so that sufficient fluid is not left in their cells, and in the cells of the pedicels, to hold the protoplasm in solution. In favour of this view is the fact that aggregation follows the inflection of the tentacles, and during the movement the glands generally, or, as I believe, always, secrete more copiously than they did before. Again, during the re-expansion of the tentacles, the glands secrete less freely, or quite cease to secrete, and the aggregated masses of protoplasm are then redissolved. Moreover, when leaves are immersed in dense vegetable solutions, or in glycerine, the fluid within the gland-cells passes outwards, and there is aggregation; and when the leaves are afterwards immersed in water, or in an innocuous fluid of less specific gravity than water, the protoplasm is redissolved, and this, no doubt, is due to endosmose.

Opposed to this view, that aggregation is caused by the outward passage of fluid from the cells, are the following facts. There seems no close relation between the degree of increased secretion and that of aggregation. Thus a particle of sugar added to the secretion round a gland causes a much greater increase of secretion, and much less aggregation, than does a particle of carbonate of ammonia given in the same manner. It does not appear probable that pure water would cause much exosmose, and yet aggregation often follows from an immersion in water of between 16 hrs. and 24 hrs., and always after from 24 hrs. to 48 hrs. Still less probable is it that water at a temperature of from 125° to 130° Fahr. (51°·6 to 54°·4 Cent.) should cause fluid to pass, not only from the glands, but from all the cells of the tentacles down to their bases, so quickly that aggregation is induced within 2 m. or 3 m. Another strong argument against this view is, that, after complete aggregation, the spheres and oval masses of protoplasm float about in an abundant supply of thin colourless fluid; so that at least the latter stages of the process cannot be due to the want of fluid to hold the protoplasm in solution. There is still stronger evidence that aggregation is independent of secretion; for the papillae, described in the first chapter, with which the leaves are studded are not glandular, and do not secrete, yet they rapidly absorb carbonate of ammonia or an infusion of raw meat, and their contents then quickly undergo aggregation, which afterwards spreads into the cells of the surrounding tissues. We shall hereafter see that the purple fluid within the sensitive filaments of *Dionaea*, which do not secrete, likewise undergoes aggregation from the action of a weak solution of carbonate of ammonia.

The process of aggregation is a vital one; by which I mean that the contents of the cells must be alive and uninjured to be thus affected, and they must be in an oxygenated condition for the transmission of the process at the proper rate. Some tentacles in a drop of water were strongly pressed beneath a slip of glass; many of the cells were ruptured, and pulpy matter of a purple colour, with granules of all sizes and shapes, exuded, but hardly any of the cells were completely emptied. I then added a minute drop of a solution of one part of carbonate of ammonia to 109 of water, and after 1 hr. examined the specimens. Here and there a few cells, both in the glands and in the pedicels, had escaped being ruptured, and their contents were well aggregated into spheres which were constantly changing their forms and positions, and a current could still be seen flowing along the walls; so that the protoplasm was alive. On the other hand, the exuded matter, which was now almost colourless instead of being purple, did not exhibit a trace of aggregation. Nor was there a trace in the many cells which were ruptured, but which had not been completely emptied of their contents. Though I looked carefully, no signs of a current could be seen within these ruptured cells. They had evidently been killed by the pressure; and the matter which they still contained did not undergo aggregation any more than that which had exuded. In these specimens, as I may add, the individuality of the life of each cell was well illustrated.

A full account will be given in the next chapter of the effects of heat on the leaves, and I need here only state that leaves immersed for a short time in water at a temperature of 120° Fahr. (48°·8 Cent.), which, as we have seen, does not immediately induce aggregation, were then placed in a few drops of a strong solution of one part of carbonate of ammonia to 109 of water, and became finely aggregated. On the other hand, leaves, after an immersion in water at 150° (65°·5 Cent.), on being placed in the same strong solution, did not undergo aggregation, the cells becoming filled with brownish, pulpy, or muddy matter. With leaves subjected to temperatures between these two extremes of 120° and 150° Fahr. (48°·8 and 65°·5 Cent.), there were gradations in the completeness of the process; the former temperature not preventing aggregation from the subsequent action of carbonate of ammonia, the latter quite stopping it. Thus, leaves immersed in water, heated to 130° (54°·4 Cent.), and then in the solution, formed perfectly defined spheres, but these were decidedly smaller than in ordinary cases. With other leaves heated to 140° (60° Cent.), the spheres were extremely small, yet well defined, but many of the cells contained, in addition, some brownish pulpy matter. In two cases of leaves heated to 145° (62°·7 Cent.), a few tentacles could be found with some of their

cells containing a few minute spheres; whilst the other cells and other whole tentacles included only the brownish, disintegrated or pulpy matter.

The fluid within the cells of the tentacles must be in an oxygenated condition, in order that the force or influence which induces aggregation should be transmitted at the proper rate from cell to cell. A plant, with its roots in water, was left for 45 m. in a vessel containing 122 oz. of carbonic acid. A leaf from this plant, and, for comparison, one from a fresh plant, were both immersed for 1 hr. in a rather strong solution of carbonate of ammonia. They were then compared, and certainly there was much less aggregation in the leaf which had been subjected to the carbonic acid than in the other. Another plant was exposed in the same vessel for 2 hrs. to carbonic acid, and one of its leaves was then placed in a solution of one part of the carbonate to 437 of water; the glands were instantly blackened, showing that they had absorbed, and that their contents were aggregated; but in the cells close beneath the glands there was no aggregation even after an interval of 3 hrs. After 4 hrs. 15 m. a few minute spheres of protoplasm were formed in these cells, but even after 5 hrs. 30 m. the aggregation did not extend down the pedicels for a length equal to that of the glands. After numberless trials with fresh leaves immersed in a solution of this strength, I have never seen the aggregating action transmitted at nearly so slow a rate. Another plant was left for 2 hrs. in carbonic acid, but was then exposed for 20 m. to the open air, during which time the leaves, being of a red colour, would have absorbed some oxygen. One of them, as well as a fresh leaf for comparison, were now immersed in the same solution as before. The former were looked at repeatedly, and after an interval of 65 m. a few spheres of protoplasm were first observed in the cells close beneath the glands, but only in two or three of the longer tentacles. After 3 hrs. the aggregation had travelled down the pedicels of a few of the tentacles for a length equal to that of the glands. On the other hand, in the fresh leaf similarly treated, aggregation was plain in many of the tentacles after 15 m.; after 65 m. it had extended down the pedicels for four, five, or more times the lengths of the glands; and after 3 hrs. the cells of all the tentacles were affected for one-third or one-half of their entire lengths. Hence there can be no doubt that the exposure of leaves to carbonic acid either stops for a time the process of aggregation, or checks the transmission of the proper influence when the glands are subsequently excited by carbonate of ammonia; and this substance acts more promptly and energetically than any other. It is known that the protoplasm of plants exhibits its spontaneous movements only as long as it is in an oxygenated condition; and so it is with the white corpuscles of the blood, only as long as they receive oxygen from the red corpuscles;⁹ but the cases above given are somewhat different, as they relate to the delay in the generation or aggregation of the masses of protoplasm by the exclusion of oxygen.

Summary and Concluding Remarks. – The process of aggregation is independent of the inflection of the tentacles and of increased secretion from the glands. It commences within the glands, whether these have been directly excited, or indirectly by a stimulus received from other glands. In both cases the process is transmitted from cell to cell down the whole length of the tentacles, being arrested for a short time at each transverse partition. With pale-coloured leaves the first change which is perceptible, but only under a high power, is the appearance of the finest granules in the fluid within the cells, making it slightly cloudy. These granules soon aggregate into small globular masses. I have seen a cloud of this kind appear in 10 s. after a drop of a solution of carbonate of ammonia had been given to a gland. With dark red leaves the first visible change often is the conversion of the outer layer of the fluid within the cells into bag-like masses. The aggregated masses, however they may have been developed, incessantly change their forms and positions. They are not filled with fluid, but are solid to their centres. Ultimately the colourless granules in the protoplasm which flows round the walls coalesce with the central spheres or masses; but there is still a current of limpid fluid flowing within

⁹ With respect to plants, Sachs, 'Trait de Bot.' 3rd edit., 1874, p. 864. On blood corpuscles, see 'Quarterly Journal of Microscopical Science,' April 1874, p. 185.'

the cells. As soon as the tentacles fully re-expand, the aggregated masses are redissolved, and the cells become filled with homogeneous purple fluid, as they were at first. The process of redissolution commences at the bases of the tentacles, thence proceeding upwards to the glands; and, therefore, in a reversed direction to that of aggregation.

Aggregation is excited by the most diversified causes, – by the glands being several times touched, – by the pressure of particles of any kind, and as these are supported by the dense secretion, they can hardly press on the glands with the weight of a millionth of a grain,¹⁰ – by the tentacles being cut off close beneath the glands, – by the glands absorbing various fluids or matter dissolved out of certain bodies, – by exosmose, – and by a certain degree of heat. On the other hand, a temperature of about 150o Fahr. (65o.5 Cent.) does not excite aggregation; nor does the sudden crushing of a gland. If a cell is ruptured, neither the exuded matter nor that which still remains within the cell undergoes aggregation when carbonate of ammonia is added. A very strong solution of this salt and rather large bits of raw meat prevent the aggregated masses being well developed. From these facts we may conclude that the protoplasmic fluid within a cell does not become aggregated unless it be in a living state, and only imperfectly if the cell has been injured. We have also seen that the fluid must be in an oxygenated state, in order that the process of aggregation should travel from cell to cell at the proper rate.

Various nitrogenous organic fluids and salts of ammonia induce aggregation, but in different degrees and at very different rates. Carbonate of ammonia is the most powerful of all known substances; the absorption of 1/134400 of a grain (.000482 mg.) by a gland suffices to cause all the cells of the same tentacle to become aggregated. The first effect of the carbonate and of certain other salts of ammonia, as well as of some other fluids, is the darkening or blackening of the glands. This follows even from long immersion in cold distilled water. It apparently depends in chief part on the strong aggregation of their cell-contents, which thus become opaque, and do not reflect light. Some other fluids render the glands of a brighter red; whilst certain acids, though much diluted, the poison of the cobra-snake, &c., make the glands perfectly white and opaque; and this seems to depend on the coagulation of their contents without any aggregation. Nevertheless, before being thus affected, they are able, at least in some cases, to excite aggregation in their own tentacles.

That the central glands, if irritated, send centrifugally some influence to the exterior glands, causing them to send back a centripetal influence inducing aggregation, is perhaps the most interesting fact given in this chapter. But the whole process of aggregation is in itself a striking phenomenon. Whenever the peripheral extremity of a nerve is touched or pressed, and a sensation is felt, it is believed that an invisible molecular change is sent from one end of the nerve to the other; but when a gland of *Drosera* is repeatedly touched or gently pressed, we can actually see a molecular change proceeding from the gland down the tentacle; though this change is probably of a very different nature from that in a nerve. Finally, as so many and such widely different causes excite aggregation, it would appear that the living matter within the gland-cells is in so unstable a condition that almost any disturbance suffices to change its molecular nature, as in the case of certain chemical compounds. And this change in the glands, whether excited directly, or indirectly by a stimulus received from other glands, is transmitted from cell to cell, causing granules of protoplasm either to be actually generated in the previously limpid fluid or to coalesce and thus to become visible.

Supplementary Observations on the Process of Aggregation in the Roots of Plants.

It will hereafter be seen that a weak solution of the carbonate of ammonia induces aggregation in the cells of the roots of *Drosera*; and this led me to make a few trials on the roots of other plants. I dug up in the latter part of October the first weed which I met with, viz. *Euphorbia peplus*, being care-

¹⁰ According to Hofmeister (as quoted by Sachs, 'Trait de Bot.' 1874, p. 958), very slight pressure on the cell-membrane arrests immediately the movements of the protoplasm, and even determines its separation from the walls. But the process of aggregation is a different phenomenon, as it relates to the contents of the cells, and only secondarily to the layer of protoplasm which flows along the walls; though no doubt the effects of pressure or of a touch on the outside must be transmitted through this layer.

ful not to injure the roots; these were washed and placed in a little solution of one part of carbonate of ammonia to 146 of water. In less than one minute I saw a cloud travelling from cell to cell up the roots, with wonderful rapidity. After from 8 m. to 9 m. the fine granules, which caused this cloudy appearance, became aggregated towards the extremities of the roots into quadrangular masses of brown matter; and some of these soon changed their forms and became spherical. Some of the cells, however, remained unaffected. I repeated the experiment with another plant of the same species, but before I could get the specimen into focus under the microscope, clouds of granules and quadrangular masses of reddish and brown matter were formed, and had run far up all the roots. A fresh root was now left for 18 hrs. in a drachm of a solution of one part of the carbonate to 437 of water, so that it received $\frac{1}{8}$ of a grain, or 2.024 mg. When examined, the cells of all the roots throughout their whole length contained aggregated masses of reddish and brown matter. Before making these experiments, several roots were closely examined, and not a trace of the cloudy appearance or of the granular masses could be seen in any of them. Roots were also immersed for 35 m. in a solution of one part of carbonate of potash to 218 of water; but this salt produced no effect.

I may here add that thin slices of the stem of the *Euphorbia* were placed in the same solution, and the cells which were green instantly became cloudy, whilst others which were before colourless were clouded with brown, owing to the formation of numerous granules of this tint. I have also seen with various kinds of leaves, left for some time in a solution of carbonate of ammonia, that the grains of chlorophyll ran together and partially coalesced; and this seems to be a form of aggregation.

Plants of duck-weed (*Lemna*) were left for between 30 m. and 45 m. in a solution of one part of this same salt to 146 of water, and three of their roots were then examined. In two of them, all the cells which had previously contained only limpid fluid now included little green spheres. After from 1 $\frac{1}{2}$ hr. to 2 hrs. similar spheres appeared in the cells on the borders of the leaves; but whether the ammonia had travelled up the roots or had been directly absorbed by the leaves, I cannot say. As one species, *Lemna arrhiza*, produces no roots, the latter alternative is perhaps the most probable. After about 2 $\frac{1}{2}$ hrs. some of the little green spheres in the roots were broken up into small granules which exhibited Brownian movements. Some duck-weed was also left for 1 hr. 30 m. in a solution of one part of carbonate of potash to 218 of water, and no decided change could be perceived in the cells of the roots; but when these same roots were placed for 25 m. in a solution of carbonate of ammonia of the same strength, little green spheres were formed.

A green marine alga was left for some time in this same solution, but was very doubtfully affected. On the other hand, a red marine alga, with finely pinnated fronds, was strongly affected. The contents of the cells aggregated themselves into broken rings, still of a red colour, which very slowly and slightly changed their shapes, and the central spaces within these rings became cloudy with red granular matter. The facts here given (whether they are new, I know not) indicate that interesting results would perhaps be gained by observing the action of various saline solutions and other fluids on the roots of plants.

CHAPTER IV

THE EFFECTS OF HEAT ON THE LEAVES

Nature of the experiments – Effects of boiling water – Warm water causes rapid inflection – Water at a higher temperature does not cause immediate inflection, but does not kill the leaves, as shown by their subsequent re-expansion and by the aggregation of the protoplasm – A still higher temperature kills the leaves and coagulates the albuminous contents of the glands.

IN my observations on *Drosera rotundifolia*, the leaves seemed to be more quickly inflected over animal substances, and to remain inflected for a longer period during very warm than during cold weather. I wished, therefore, to ascertain whether heat alone would induce inflection, and what temperature was the most efficient. Another interesting point presented itself, namely, at what degree life was extinguished; for *Drosera* offers unusual facilities in this respect, not in the loss of the power of inflection, but in that of subsequent re-expansion, and more especially in the failure of the protoplasm to become aggregated, when the leaves after being heated are immersed in a solution of carbonate of ammonia.¹¹

[My experiments were tried in the following manner. Leaves were cut off, and this does not in the least interfere with their powers; for instance, three cut off leaves, with bits of meat placed on them, were kept in a damp atmosphere, and after 23 hrs. closely embraced the meat both with their tentacles and blades; and the protoplasm within their cells was well aggregated. Three ounces of doubly distilled water was heated in a porcelain vessel, with a delicate thermometer having a long bulb obliquely suspended in it. The water was gradually raised to the required temperature by a spirit-lamp moved about under the vessel; and in all cases the leaves were continually waved for some minutes close to the bulb. They were then placed in cold water, or in a solution of carbonate of ammonia. In other cases they were left in the water, which had been raised to a certain temperature, until it cooled. Again in other cases the leaves were suddenly plunged into water of a certain temperature, and kept there for a specified time. Considering that the tentacles are extremely delicate, and that their coats are very thin, it seems scarcely possible that the fluid contents of their cells should not have been heated to within a degree or two of the temperature of the surrounding water. Any further precautions would, I think, have been superfluous, as the leaves from age or constitutional causes differ slightly in their sensitiveness to heat.

It will be convenient first briefly to describe the effects of immersion for thirty seconds in boiling water. The leaves are rendered flaccid, with their tentacles bowed backwards, which, as we shall see in a future chapter, is probably due to their outer surfaces retaining their elasticity for a longer period than their inner surfaces retain the power of contraction. The purple fluid within the cells of

¹¹ When my experiments on the effects of heat were made, I was not aware that the subject had been carefully investigated by several observers. For instance, Sachs is convinced (*Trait de Botanique*, 1874, pp. 772, 854) that the most different kinds of plants all perish if kept for 10 m. in water at 45o to 46 °Cent., or 113o to 115o Fahr.; and he concludes that the protoplasm within their cells always coagulates, if in a damp condition, at a temperature of between 50o and 60 °Cent., or 122o to 140o Fahr. Max Schultze and Khne (as quoted by Dr. Bastian in *Contemp. Review*, 1874, p. 528) "found that the protoplasm of plant-cells, with which they experimented, was always killed and [] altered by a very brief exposure to a temperature of 118 1/2o Fahr. as a maximum." As my results are deduced from special phenomena, namely, the subsequent aggregation of the protoplasm and the re-expansion of the tentacles, they seem to me worth giving. We shall find that *Drosera* resists heat somewhat better than most other plants. That there should be considerable differences in this respect is not surprising, considering that some low vegetable organisms grow in hot springs – cases of which have been collected by Prof. Wyman (*American Journal of Science*, vol. xlv. 1867). Thus, Dr. Hooker found *Confervae* in water at 168o Fahr.; Humboldt, at 185o Fahr.; and Descloizeaux, at 208o Fahr.)

the pedicels is rendered finely granular, but there is no true aggregation; nor does this follow when the leaves are subsequently placed in a solution of carbonate of ammonia. But the most remarkable change is that the glands become opaque and uniformly white; and this may be attributed to the coagulation of their albuminous contents.

My first and preliminary experiment consisted in putting seven leaves in the same vessel of water, and warming it slowly up to the temperature of 110° Fahr. (43° Cent.); a leaf being taken out as soon as the temperature rose to 80° (26° Cent.), another at 85°, another at 90°, and so on. Each leaf, when taken out, was placed in water at the temperature of my room, and the tentacles of all soon became slightly, though irregularly, inflected. They were now removed from the cold water and kept in damp air, with bits of meat placed on their discs. The leaf which had been exposed to the temperature of 110° became in 15 m. greatly inflected; and in 2 hrs. every single tentacle closely embraced the meat. So it was, but after rather longer intervals, with the six other leaves. It appears, therefore, that the warm bath had increased their sensitiveness when excited by meat.

I next observed the degree of inflection which leaves underwent within stated periods, whilst still immersed in warm water, kept as nearly as possible at the same temperature; but I will here and elsewhere give only a few of the many trials made. A leaf was left for 10 m. in water at 100° (37° Cent.), but no inflection occurred. A second leaf, however, treated in the same manner, had a few of its exterior tentacles very slightly inflected in 6 m., and several irregularly but not closely inflected in 10 m. A third leaf, kept in water at 105° to 106° (40° to 41° Cent.), was very moderately inflected in 6 m. A fourth leaf, in water at 110° (43° Cent.), was somewhat inflected in 4 m., and considerably so in from 6 to 7 m.

Three leaves were placed in water which was heated rather quickly, and by the time the temperature rose to 115°-116° (46° to 46° Cent.), all three were inflected. I then removed the lamp, and in a few minutes every single tentacle was closely inflected. The protoplasm within the cells was not killed, for it was seen to be in distinct movement; and the leaves, having been left in cold water for 20 hrs., re-expanded. Another leaf was immersed in water at 100° (37° Cent.), which was raised to 120° (48° Cent.); and all the tentacles, except the extreme marginal ones, soon became closely inflected. The leaf was now placed in cold water, and in 7 hrs. 30 m. it had partly, and in 10 hrs. fully, re-expanded. On the following morning it was immersed in a weak solution of carbonate of ammonia, and the glands quickly became black, with strongly marked aggregation in the tentacles, showing that the protoplasm was alive, and that the glands had not lost their power of absorption. Another leaf was placed in water at 110° (43° Cent.) which was raised to 120° (48° Cent.); and every tentacle, excepting one, was quickly and closely inflected. This leaf was now immersed in a few drops of a strong solution of carbonate of ammonia (one part to 109 of water); in 10 m. all the glands became intensely black, and in 2 hrs. the protoplasm in the cells of the pedicels was well aggregated. Another leaf was suddenly plunged, and as usual waved about, in water at 120°, and the tentacles became inflected in from 2 m. to 3 m., but only so as to stand at right angles to the disc. The leaf was now placed in the same solution (viz. one part of carbonate of ammonia to 109 of water, or 4 grs. to 1 oz., which I will for the future designate as the strong solution), and when I looked at it again after the interval of an hour, the glands were blackened, and there was well-marked aggregation. After an additional interval of 4 hrs. the tentacles had become much more inflected. It deserves notice that a solution as strong as this never causes inflection in ordinary cases. Lastly a leaf was suddenly placed in water at 125° (51° Cent.), and was left in it until the water cooled; the tentacles were rendered of a bright red and soon became inflected. The contents of the cells underwent some degree of aggregation, which in the course of three hours increased; but the masses of protoplasm did not become spherical, as almost always occurs with leaves immersed in a solution of carbonate of ammonia.]

We learn from these cases that a temperature of from 120° to 125° (48° to 51° Cent.) excites the tentacles into quick movement, but does not kill the leaves, as shown either by their

subsequent re-expansion or by the aggregation of the protoplasm. We shall now see that a temperature of 130o (54o.4 Cent.) is too high to cause immediate inflection, yet does not kill the leaves.

[Experiment 1. – A leaf was plunged, and as in all cases waved about for a few minutes, in water at 130o (54o.4 Cent.), but there was no trace of inflection; it was then placed in cold water, and after an interval of 15 m. very slow movement was distinctly seen in a small mass of protoplasm in one of the cells of a tentacle.¹² After a few hours all the tentacles and the blade became inflected.

Experiment 2. – Another leaf was plunged into water at 130o to 131o, and as before there was no inflection. After being kept in cold water for an hour, it was placed in the strong solution of ammonia, and in the course of 55 m. the tentacles were considerably inflected. The glands, which before had been rendered of a brighter red, were now blackened. The protoplasm in the cells of the tentacles was distinctly aggregated; but the spheres were much smaller than those generated in unheated leaves when subjected to carbonate of ammonia. After an additional 2 hrs. all the tentacles, excepting six or seven, were closely inflected.

Experiment 3. – A similar experiment to the last, with exactly the same results.

Experiment 4. – A fine leaf was placed in water at 100o (37o.7 Cent.), which was then raised to 145o (62o.7 Cent.). Soon after immersion, there was, as might have been expected, strong inflection. The leaf was now removed and left in cold water; but from having been exposed to so high a temperature, it never re-expanded.

Experiment 5. – Leaf immersed at 130o (54o.4 Cent.), and the water raised to 145o (62o.7 Cent.), there was no immediate inflection; it was then placed in cold water, and after 1 hr. 20 m. some of the tentacles on one side became inflected. This leaf was now placed in the strong solution, and in 40 m. all the submarginal tentacles were well inflected, and the glands blackened. After an additional interval of 2 hrs. 45 m. all the tentacles, except eight or ten, were closely inflected, with their cells exhibiting a slight degree of aggregation; but the spheres of protoplasm were very small, and the cells of the exterior tentacles contained some pulpy or disintegrated brownish matter.

Experiments 6 and 7. – Two leaves were plunged in water at 135o (57o.2 Cent.) which was raised to 145o (62o.7 Cent.); neither became inflected. One of these, however, after having been left for 31 m. in cold water, exhibited some slight inflection, which increased after an additional interval of 1 hr. 45 m., until all the tentacles, except sixteen or seventeen, were more or less inflected; but the leaf was so much injured that it never re-expanded. The other leaf, after having been left for half an hour in cold water, was put into the strong solution, but no inflection ensued; the glands, however, were blackened, and in some cells there was a little aggregation, the spheres of protoplasm being extremely small; in other cells, especially in the exterior tentacles, there was much greenish-brown pulpy matter.

Experiment 8. – A leaf was plunged and waved about for a few minutes in water at 140o (60 °Cent.), and was then left for half an hour in cold water, but there was no inflection. It was now placed in the strong solution, and after 2 hrs. 30 m. the inner submarginal tentacles were well inflected, with their glands blackened, and some imperfect aggregation in the cells of the pedicels. Three or four of the glands were spotted with the white porcelain-like structure, like that produced by boiling water. I have seen this result in no other instance after an immersion of only a few minutes in water at so low a temperature as 140o, and in only one leaf out of four, after a similar immersion at a temperature of 145o Fahr. On the other hand, with two leaves, one placed in water at 145o (62o.7 Cent.), and the other in water at 140o (60 °Cent.), both being left therein until the water cooled, the glands of both became white and porcelain-like. So that the duration of the immersion is an important element in the result.

¹² Sachs states ('*Trait de Botanique*,' 1874, p. 855) that the movements of the protoplasm in the hairs of a *Cucurbita* ceased after they were exposed for 1 m. in water to a temperature of 47o to 48 °Cent., or 117o to 119o Fahr.

Experiment 9. – A leaf was placed in water at 140° (60 °Cent.), which was raised to 150°(65o.5 Cent.); there was no inflection; on the contrary, the outer tentacles were somewhat bowed backwards. The glands became like porcelain, but some of them were a little mottled with purple. The bases of the glands were often more affected than their summits. This leaf having been left in the strong solution did not undergo any inflection or aggregation.

Experiment 10. – A leaf was plunged in water at 150° to 150 1/2° (65o.5 Cent.); it became somewhat flaccid, with the outer tentacles slightly reflexed, and the inner ones a little bent inwards, but only towards their tips; and this latter fact shows that the movement was not one of true inflection, as the basal part alone normally bends. The tentacles were as usual rendered of a very bright red, with the glands almost white like porcelain, yet tinged with pink. The leaf having been placed in the strong solution, the cell-contents of the tentacles became of a muddy-brown, with no trace of aggregation.

Experiment 11. – A leaf was immersed in water at 145° (62o.7 Cent.), which was raised to 156° (68o.8 Cent.). The tentacles became bright red and somewhat reflexed, with almost all the glands like porcelain; those on the disc being still pinkish, those near the margin quite white. The leaf being placed as usual first in cold water and then in the strong solution, the cells in the tentacles became of a muddy greenish brown, with the protoplasm not aggregated. Nevertheless, four of the glands escaped being rendered like porcelain, and the pedicels of these glands were spirally curled, like a French horn, towards their upper ends; but this can by no means be considered as a case of true inflection. The protoplasm within the cells of the twisted portions was aggregated into distinct though excessively minute purple spheres. This case shows clearly that the protoplasm, after having been exposed to a high temperature for a few minutes, is capable of aggregation when afterwards subjected to the action of carbonate of ammonia, unless the heat has been sufficient to cause coagulation.]

Concluding Remarks. – As the hair-like tentacles are extremely thin and have delicate walls, and as the leaves were waved about for some minutes close to the bulb of the thermometer, it seems scarcely possible that they should not have been raised very nearly to the temperature which the instrument indicated. From the eleven last observations we see that a temperature of 130° (54o.4 Cent.) never causes the immediate inflection of the tentacles, though a temperature from 120° to 125° (48o.8 to 51o.6 Cent.) quickly produces this effect. But the leaves are paralysed only for a time by a temperature of 130°, as afterwards, whether left in simple water or in a solution of carbonate of ammonia, they become inflected and their protoplasm undergoes aggregation. This great difference in the effects of a higher and lower temperature may be compared with that from immersion in strong and weak solutions of the salts of ammonia; for the former do not excite movement, whereas the latter act energetically. A temporary suspension of the power of movement due to heat is called by Sachs¹³ heat-rigidity; and this in the case of the sensitive-plant (*Mimosa*) is induced by its exposure for a few minutes to humid air, raised to 120°-122° Fahr., or 49° to 50 °Cent. It deserves notice that the leaves of *Drosera*, after being immersed in water at 130° Fahr., are excited into movement by a solution of the carbonate so strong that it would paralyse ordinary leaves and cause no inflection.

The exposure of the leaves for a few minutes even to a temperature of 145° Fahr. (62o.7 Cent.) does not always kill them; as when afterwards left in cold water, or in a strong solution of carbonate of ammonia, they generally, though not always, become inflected; and the protoplasm within their cells undergoes aggregation, though the spheres thus formed are extremely small, with many of the cells partly filled with brownish muddy matter. In two instances, when leaves were immersed in water, at a lower temperature than 130° (54o.4 Cent.), which was then raised to 145° (62o.7 Cent.), they became during the earlier period of immersion inflected, but on being afterwards left in cold water were incapable of re-expansion. Exposure for a few minutes to a temperature of 145° sometimes causes some few of the more sensitive glands to be speckled with the porcelain-like appearance; and on one occasion this occurred at a temperature of 140° (60 °Cent.). On another occasion, when a leaf

¹³ 'Traité de Bot.' 1874, p. 1034.

was placed in water at this temperature of only 140o, and left therein till the water cooled, every gland became like porcelain. Exposure for a few minutes to a temperature of 150o (65o.5 Cent.) generally produces this effect, yet many glands retain a pinkish colour, and many present a speckled appearance. This high temperature never causes true inflection; on the contrary, the tentacles commonly become reflexed, though to a less degree than when immersed in boiling water; and this apparently is due to their passive power of elasticity. After exposure to a temperature of 150o Fahr., the protoplasm, if subsequently subjected to carbonate of ammonia, instead of undergoing aggregation, is converted into disintegrated or pulpy discoloured matter. In short, the leaves are generally killed by this degree of heat; but owing to differences of age or constitution, they vary somewhat in this respect. In one anomalous case, four out of the many glands on a leaf, which had been immersed in water raised to 156o (68o.8 Cent.), escaped being rendered porcellanous;¹⁴ and the protoplasm in the cells close beneath these glands underwent some slight, though imperfect, degree of aggregation.

Finally, it is a remarkable fact that the leaves of *Drosera rotundifolia*, which flourishes on bleak upland moors throughout Great Britain, and exists (Hooker) within the Arctic Circle, should be able to withstand for even a short time immersion in water heated to a temperature of 145o.

It may be worth adding that immersion in cold water does not cause any inflection: I suddenly placed four leaves, taken from plants which had been kept for several days at a high temperature, generally about 75o Fahr. (23o.8 Cent.), in water at 45o (7o.2 Cent.), but they were hardly at all affected; not so much as some other leaves from the same plants, which were at the same time immersed in water at 75o; for these became in a slight degree inflected.

¹⁴ As the opacity and porcelain-like appearance of the glands is probably due to the coagulation of the albumen, I may add, on the authority of Dr. Burdon Sanderson, that albumen coagulates at about 155o, but, in presence of acids, the temperature of coagulation is lower. The leaves of *Drosera* contain an acid, and perhaps a difference in the amount contained may account for the slight differences in the results above recorded. It appears that cold-blooded animals are, as might have been expected, far more sensitive to an increase of temperature than is *Drosera*. Thus, as I hear from Dr. Burdon Sanderson, a frog begins to be distressed in water at a temperature of only 85o Fahr. At 95o the muscles become rigid, and the animal dies in a stiffened condition.

CHAPTER V

THE EFFECTS OF NON-NITROGENOUS AND NITROGENOUS ORGANIC FLUIDS ON THE LEAVES

Non-nitrogenous fluids – Solutions of gum arabic – Sugar – Starch – Diluted alcohol – Olive oil – Infusion and decoction of tea – Nitrogenous fluids – Milk – Urine – Liquid albumen – Infusion of raw meat – Impure mucus – Saliva – Solution of isinglass – Difference in the action of these two sets of fluids – Decoction of green peas – Decoction and infusion of cabbage – Decoction of grass leaves.

WHEN, in 1860, I first observed *Drosera*, and was led to believe that the leaves absorbed nutritious matter from the insects which they captured, it seemed to me a good plan to make some preliminary trials with a few common fluids, containing and not containing nitrogenous matter; and the results are worth giving.

In all the following cases a drop was allowed to fall from the same pointed instrument on the centre of the leaf; and by repeated trials one of these drops was ascertained to be on an average very nearly half a minim, or 1/960 of a fluid ounce, or .0295 ml. But these measurements obviously do not pretend to any strict accuracy; moreover, the drops of the viscid fluids were plainly larger than those of water. Only one leaf on the same plant was tried, and the plants were collected from two distant localities. The experiments were made during August and September. In judging of the effects, one caution is necessary: if a drop of any adhesive fluid is placed on an old or feeble leaf, the glands of which have ceased to secrete copiously, the drop sometimes dries up, especially if the plant is kept in a room, and some of the central and submarginal tentacles are thus drawn together, giving to them the false appearance of having become inflected. This sometimes occurs with water, as it is rendered adhesive by mingling with the viscid secretion. Hence the only safe criterion, and to this alone I have trusted, is the bending inwards of the exterior tentacles, which have not been touched by the fluid, or at most only at their bases. In this case the movement is wholly due to the central glands having been stimulated by the fluid, and transmitting a motor impulse to the exterior tentacles. The blade of the leaf likewise often curves inwards, in the same manner as when an insect or bit of meat is placed on the disc. This latter movement is never caused, as far as I have seen, by the mere drying up of an adhesive fluid and the consequent drawing together of the tentacles.

First for the non-nitrogenous fluids. As a preliminary trial, drops of distilled water were placed on between thirty and forty leaves, and no effect whatever was produced; nevertheless, in some other and rare cases, a few tentacles became for a short time inflected; but this may have been caused by the glands having been accidentally touched in getting the leaves into a proper position. That water should produce no effect might have been anticipated, as otherwise the leaves would have been excited into movement by every shower of rain.

[Gum arabic. – Solutions of four degrees of strength were made; one of six grains to the ounce of water (one part to 73); a second rather stronger, yet very thin; a third moderately thick, and a fourth so thick that it would only just drop from a pointed instrument. These were tried on fourteen leaves; the drops being left on the discs from 24 hrs. to 44 hrs.; generally about 30 hrs. Inflection was never thus caused. It is necessary to try pure gum arabic, for a friend tried a solution bought ready prepared, and this caused the tentacles to bend; but he afterwards ascertained that it contained much animal matter, probably glue.

Sugar. – Drops of a solution of white sugar of three strengths (the weakest containing one part of sugar to 73 of water) were left on fourteen leaves from 32 hrs. to 48 hrs.; but no effect was produced.

Starch. – A mixture about as thick as cream was dropped on six leaves and left on them for 30 hrs., no effect being produced. I am surprised at this fact, as I believe that the starch of commerce generally contains a trace of gluten, and this nitrogenous substance causes inflection, as we shall see in the next chapter.

Alcohol, Diluted. – One part of alcohol was added to seven of water, and the usual drops were placed on the discs of three leaves. No inflection ensued in the course of 48 hrs. To ascertain whether these leaves had been at all injured, bits of meat were placed on them, and after 24 hrs. they were closely inflected. I also put drops of sherry-wine on three other leaves; no inflection was caused, though two of them seemed somewhat injured. We shall hereafter see that cut off leaves immersed in diluted alcohol of the above strength do not become inflected.

Olive Oil. – drops were placed on the discs of eleven leaves, and no effect was produced in from 24 hrs. to 48 hrs. Four of these leaves were then tested by bits of meat on their discs, and three of them were found after 24 hrs. with all their tentacles and blades closely inflected, whilst the fourth had only a few tentacles inflected. It will, however, be shown in a future place, that cut off leaves immersed in olive oil are powerfully affected.

Infusion and Decoction of Tea. – Drops of a strong infusion and decoction, as well as of a rather weak decoction, of tea were placed on ten leaves, none of which became inflected. I afterwards tested three of them by adding bits of meat to the drops which still remained on their discs, and when I examined them after 24 hrs. they were closely inflected. The chemical principle of tea, namely theine, was subsequently tried and produced no effect. The albuminous matter which the leaves must originally have contained, no doubt, had been rendered insoluble by their having been completely dried.]

We thus see that, excluding the experiments with water, sixty-one leaves were tried with drops of the above-named non-nitrogenous fluids; and the tentacles were not in a single case inflected.

[With respect to nitrogenous fluids, the first which came to hand were tried. The experiments were made at the same time and in exactly the same manner as the foregoing. As it was immediately evident that these fluids produced a great effect, I neglected in most cases to record how soon the tentacles became inflected. But this always occurred in less than 24 hrs.; whilst the drops of non-nitrogenous fluids which produced no effect were observed in every case during a considerably longer period.

Milk. – Drops were placed on sixteen leaves, and the tentacles of all, as well as the blades of several, soon became greatly inflected. The periods were recorded in only three cases, namely, with leaves on which unusually small drops had been placed. Their tentacles were somewhat inflected in 45 m.; and after 7 hrs. 45 m. the blades of two were so much curved inwards that they formed little cups enclosing the drops. These leaves re-expanded on the third day. On another occasion the blade of a leaf was much inflected in 5 hrs. after a drop of milk had been placed on it.

Human Urine. – Drops were placed on twelve leaves, and the tentacles of all, with a single exception, became greatly inflected. Owing, I presume, to differences in the chemical nature of the urine on different occasions, the time required for the movements of the tentacles varied much, but was always effected in under 24 hrs. In two instances I recorded that all the exterior tentacles were completely inflected in 17 hrs., but not the blade of the leaf. In another case the edges of a leaf, after 25 hrs. 30 m., became so strongly inflected that it was converted into a cup. The power of urine does not lie in the urea, which, as we shall hereafter see, is inoperative.

Albumen (fresh from a hen's egg), placed on seven leaves, caused the tentacles of six of them to be well inflected. In one case the edge of the leaf itself became much curled in after 20 hrs. The one leaf which was unaffected remained so for 26 hrs., and was then treated with a drop of milk, and this caused the tentacles to bend inwards in 12 hrs.

Cold Filtered Infusion of Raw Meat. – This was tried only on a single leaf, which had most of its outer tentacles and the blade inflected in 19 hrs. During subsequent years, I repeatedly used this

infusion to test leaves which had been experimented on with other substances, and it was found to act most energetically, but as no exact account of these trials was kept, they are not here introduced.

Mucus. – Thick and thin mucus from the bronchial tubes, placed on three leaves, caused inflection. A leaf with thin mucus had its marginal tentacles and blade somewhat curved inward in 5 hrs. 30 m., and greatly so in 20 hrs. The action of this fluid no doubt is due either to the saliva or to some albuminous matter¹⁵ mingled with it, and not, as we shall see in the next chapter, to mucin or the chemical principle of mucus.

Saliva. – Human saliva, when evaporated, yields from 1.14 to 1.19 per cent. of residue; and this yields 0.25 per cent. of ashes, so that the proportion of nitrogenous matter which saliva contains must be small. Nevertheless, drops placed on the discs of eight leaves acted on them all. In one case all the exterior tentacles, excepting nine, were inflected in 19 hrs. 30 m.; in another case a few became so in 2 hrs., and after 7 hrs. 30 m. all those situated near where the drop lay, as well as the blade, were acted on. Since making these trials, I have many scores of times just touched glands with the handle of my scalpel wetted with saliva, to ascertain whether a leaf was in an active condition; for this was shown in the course of a few minutes by the bending inwards of the tentacles. The edible nest of the Chinese swallow is formed of matter secreted by the salivary glands; two grains were added to one ounce of distilled water (one part to 218), which was boiled for several minutes, but did not dissolve the whole. The usual-sized drops were placed on three leaves, and these in 1 hr. 30 m. were well, and in 2 hrs. 15 m. closely, inflected.

Isinglass. – Drops of a solution about as thick as milk, and of a still thicker solution, were placed on eight leaves, and the tentacles of all became inflected. In one case the exterior tentacles were well curved in after 6 hrs. 30 m., and the blade of the leaf to a partial extent after 24 hrs. As saliva acted so efficiently, and yet contains so small a proportion of nitrogenous matter, I tried how small a quantity of isinglass would act. One part was dissolved in 218 parts of distilled water, and drops were placed on four leaves. After 5 hrs. two of these were considerably and two moderately inflected; after 22 hrs. the former were greatly and the latter much more inflected. In the course of 48 hrs. from the time when the drops were placed on the leaves, all four had almost re-expanded. They were then given little bits of meat, and these acted more powerfully than the solution. One part of isinglass was next dissolved in 437 of water; the fluid thus formed was so thin that it could not be distinguished from pure water. The usual-sized drops were placed on seven leaves, each of which thus received 1/960 of a grain (.0295 mg.). Three of them were observed for 41 hrs., but were in no way affected; the fourth and fifth had two or three of their exterior tentacles inflected after 18 hrs.; the sixth had a few more; and the seventh had in addition the edge of the leaf just perceptibly curved inwards. The tentacles of the four latter leaves began to re-expand after an additional interval of only 8 hrs. Hence the 1/960 of a grain of isinglass is sufficient to affect very slightly the more sensitive or active leaves. On one of the leaves, which had not been acted on by the weak solution, and on another, which had only two of its tentacles inflected, drops of the solution as thick as milk were placed; and next morning, after an interval of 16 hrs., both were found with all their tentacles strongly inflected.]

Altogether I experimented on sixty-four leaves with the above nitrogenous fluids, the five leaves tried only with the extremely weak solution of isinglass not being included, nor the numerous trials subsequently made, of which no exact account was kept. Of these sixty-four leaves, sixty-three had their tentacles and often their blades well inflected. The one which failed was probably too old and torpid. But to obtain so large a proportion of successful cases, care must be taken to select young and active leaves. Leaves in this condition were chosen with equal care for the sixty-one trials with non-nitrogenous fluids (water not included); and we have seen that not one of these was in the least affected. We may therefore safely conclude that in the sixty-four experiments with nitrogenous fluids

¹⁵ Mucus from the air-passages is said in Marshall, 'Outlines of Physiology,' vol. ii. 1867, p. 364, to contain some albumen. Miller's 'Elements of Physiology,' Eng. Trans. vol. i., p. 514.

the inflection of the exterior tentacles was due to the absorption of nitrogenous matter by the glands of the tentacles on the disc.

Some of the leaves which were not affected by the non-nitrogenous fluids were, as above stated, immediately afterwards tested with bits of meat, and were thus proved to be in an active condition. But in addition to these trials, twenty-three of the leaves, with drops of gum, syrup, or starch, still lying on their discs, which had produced no effect in the course of between 24 hrs. and 48 hrs., were then tested with drops of milk, urine, or albumen. Of the twenty-three leaves thus treated, seventeen had their tentacles, and in some cases their blades, well inflected; but their powers were somewhat impaired, for the rate of movement was decidedly slower than when fresh leaves were treated with these same nitrogenous fluids. This impairment, as well as the insensibility of six of the leaves, may be attributed to injury from exosmose, caused by the density of the fluids placed on their discs.

[The results of a few other experiments with nitrogenous fluids may be here conveniently given. Decoctions of some vegetables, known to be rich in nitrogen, were made, and these acted like animal fluids. Thus, a few green peas were boiled for some time in distilled water, and the moderately thick decoction thus made was allowed to settle. Drops of the superincumbent fluid were placed on four leaves, and when these were looked at after 16 hrs., the tentacles and blades of all were found strongly inflected. I infer from a remark by Gerhardt¹⁶ that legumin is present in peas "in combination with an alkali, forming an incoagulable solution," and this would mingle with boiling water. I may mention, in relation to the above and following experiments, that according to Schiff certain forms of albumen exist which are not coagulated by boiling water, but are converted into soluble peptones.

On three occasions chopped cabbage-leaves¹⁷ were boiled in distilled water for 1 hr. or for 1/4 hr.; and by decanting the decoction after it had been allowed to rest, a pale dirty green fluid was obtained. The usual-sized drops were placed on thirteen leaves. Their tentacles and blades were inflected after 4 hrs. to a quite extraordinary degree. Next day the protoplasm within the cells of the tentacles was found aggregated in the most strongly marked manner. I also touched the viscid secretion round the glands of several tentacles with minute drops of the decoction on the head of a small pin, and they became well inflected in a few minutes. The fluid proving so powerful, one part was diluted with three of water, and drops were placed on the discs of five leaves; and these next morning were so much acted on that their blades were completely doubled over. We thus see that a decoction of cabbage-leaves is nearly or quite as potent as an infusion of raw meat.

About the same quantity of chopped cabbage-leaves and of distilled water, as in the last experiment, were kept in a vessel for 20 hrs. in a hot closet, but not heated to near the boiling-point. Drops of this infusion were placed on four leaves. One of these, after 23 hrs., was much inflected; a second slightly; a third had only the submarginal tentacles inflected; and the fourth was not at all affected. The power of this infusion is therefore very much less than that of the decoction; and it is clear that the immersion of cabbage-leaves for an hour in water at the boiling temperature is much more efficient in extracting matter which excites *Drosera* than immersion during many hours in warm water. Perhaps the contents of the cells are protected (as Schiff remarks with respect to legumin) by the walls being formed of cellulose, and that until these are ruptured by boiling-water, but little of the contained albuminous matter is dissolved. We know from the strong odour of cooked cabbage-leaves that boiling water produces some chemical change in them, and that they are thus rendered far more digestible and nutritious to man. It is therefore an interesting fact that water at this temperature extracts matter from them which excites *Drosera* to an extraordinary degree.

Grasses contain far less nitrogenous matter than do peas or cabbages. The leaves and stalks of three common kinds were chopped and boiled for some time in distilled water. Drops of this

¹⁶ Watts' 'Dictionary of Chemistry,' vol. iii., p. 568. 'Leons sur la Phys. de la Digestion,' tom. i, p. 379; tom. ii. pp. 154, 166, on legumin.

¹⁷ The leaves of young plants, before the heart is formed, such as were used by me, contain 2.1 per cent. of albuminous matter, and the outer leaves of mature plants 1.6 per cent. Watts' 'Dictionary of Chemistry,' vol. i. p. 653.

decoction (after having stood for 24 hrs.) were placed on six leaves, and acted in a rather peculiar manner, of which other instances will be given in the seventh chapter on the salts of ammonia. After 2 hrs. 30 m. four of the leaves had their blades greatly inflected, but not their exterior tentacles; and so it was with all six leaves after 24 hrs. Two days afterwards the blades, as well as the few submarginal tentacles which had been inflected, all re-expanded; and much of the fluid on their discs was by this time absorbed. It appears that the decoction strongly excites the glands on the disc, causing the blade to be quickly and greatly inflected; but that the stimulus, differently from what occurs in ordinary cases, does not spread, or only in a feeble degree, to the exterior tentacles.

I may here add that one part of the extract of belladonna (procured from a druggist) was dissolved in 437 of water, and drops were placed on six leaves. Next day all six were somewhat inflected, and after 48 hrs. were completely re-expanded. It was not the included atropine which produced this effect, for I subsequently ascertained that it is quite powerless. I also procured some extract of hyoscyamus from three shops, and made infusions of the same strength as before. Of these three infusions, only one acted on some of the leaves, which were tried. Though druggists believe that all the albumen is precipitated in the preparation of these drugs, I cannot doubt that some is occasionally retained; and a trace would be sufficient to excite the more sensitive leaves of *Drosera*.

CHAPTER VI

THE DIGESTIVE POWER OF THE SECRETION OF DROSERA

The secretion rendered acid by the direct and indirect excitement of the glands – Nature of the acid – Digestible substances – Albumen, its digestion arrested by alkalies, recommences by the addition of an acid – Meat – Fibrin – Syntonin – Areolar tissue – Cartilage – Fibro-cartilage – Bone – Enamel and dentine – Phosphate of lime – Fibrous basis of bone – Gelatine – Chondrin – Milk, casein and cheese – Gluten – Legumin – Pollen – Globulin – Haematin – Indigestible substances – Epidermic productions – Fibro-elastic tissue – Mucin – Pepsin – Urea – Chitine – Cellulose – Gun-cotton – Chlorophyll – Fat and oil – Starch – Action of the secretion on living seeds – Summary and concluding remarks.

AS we have seen that nitrogenous fluids act very differently on the leaves of *Drosera* from non-nitrogenous fluids, and as the leaves remain clasped for a much longer time over various organic bodies than over inorganic bodies, such as bits of glass, cinder, wood, &c., it becomes an interesting inquiry, whether they can only absorb matter already in solution, or render it soluble, – that is, have the power of digestion. We shall immediately see that they certainly have this power, and that they act on albuminous compounds in exactly the same manner as does the gastric juice of mammals; the digested matter being afterwards absorbed. This fact, which will be clearly proved, is a wonderful one in the physiology of plants. I must here state that I have been aided throughout all my later experiments by many valuable suggestions and assistance given me with the greatest kindness by Dr. Burdon Sanderson.

It may be well to premise for the sake of any reader who knows nothing about the digestion of albuminous compounds by animals that this is effected by means of a ferment, pepsin, together with weak hydrochloric acid, though almost any acid will serve. Yet neither pepsin nor an acid by itself has any such power.¹⁸ We have seen that when the glands of the disc are excited by the contact of any object, especially of one containing nitrogenous matter, the outer tentacles and often the blade become inflected; the leaf being thus converted into a temporary cup or stomach. At the same time the discal glands secrete more copiously, and the secretion becomes acid. Moreover, they transmit some influence to the glands of the exterior tentacles, causing them to pour forth a more copious secretion, which also becomes acid or more acid than it was before.

As this result is an important one, I will give the evidence. The secretion of many glands on thirty leaves, which had not been in any way excited, was tested with litmus paper; and the secretion of twenty-two of these leaves did not in the least affect the colour, whereas that of eight caused an exceedingly feeble and sometimes doubtful tinge of red. Two other old leaves, however, which appeared to have been inflected several times, acted much more decidedly on the paper. Particles of clean glass were then placed on five of the leaves, cubes of albumen on six, and bits of raw meat on three, on none of which was the secretion at this time in the least acid. After an interval of 24 hrs., when almost all the tentacles on these fourteen leaves had become more or less inflected, I again tested the secretion, selecting glands which had not as yet reached the centre or touched any object, and it was now plainly acid. The degree of acidity of the secretion varied somewhat on the glands of the same leaf. On some leaves, a few tentacles did not, from some unknown cause, become inflected,

¹⁸ It appears, however, according to Schiff, and contrary to the opinion of some physiologists, that weak hydrochloric dissolves, though slowly, a very minute quantity of coagulated albumen. Schiff, 'Phys. de la Digestion,' tom. ii. 1867, p. 25.

as often happens; and in five instances their secretion was found not to be in the least acid; whilst the secretion of the adjoining and inflected tentacles on the same leaf was decidedly acid. With leaves excited by particles of glass placed on the central glands, the secretion which collects on the disc beneath them was much more strongly acid than that poured forth from the exterior tentacles, which were as yet only moderately inflected. When bits of albumen (and this is naturally alkaline), or bits of meat were placed on the disc, the secretion collected beneath them was likewise strongly acid. As raw meat moistened with water is slightly acid, I compared its action on litmus paper before it was placed on the leaves, and afterwards when bathed in the secretion; and there could not be the least doubt that the latter was very much more acid. I have indeed tried hundreds of times the state of the secretion on the discs of leaves which were inflected over various objects, and never failed to find it acid. We may, therefore, conclude that the secretion from unexcited leaves, though extremely viscid, is not acid or only slightly so, but that it becomes acid, or much more strongly so, after the tentacles have begun to bend over any inorganic or organic object; and still more strongly acid after the tentacles have remained for some time closely clasped over any object.

I may here remind the reader that the secretion appears to be to a certain extent antiseptic, as it checks the appearance of mould and infusoria, thus preventing for a time the discoloration and decay of such substances as the white of an egg, cheese, &c. It therefore acts like the gastric juice of the higher animals, which is known to arrest putrefaction by destroying the microzymes.

[As I was anxious to learn what acid the secretion contained, 445 leaves were washed in distilled water, given me by Prof. Frankland; but the secretion is so viscid that it is scarcely possible to scrape or wash off the whole. The conditions were also unfavourable, as it was late in the year and the leaves were small. Prof. Frankland with great kindness undertook to test the fluid thus collected. The leaves were excited by clean particles of glass placed on them 24 hrs. previously. No doubt much more acid would have been secreted had the leaves been excited by animal matter, but this would have rendered the analysis more difficult. Prof. Frankland informs me that the fluid contained no trace of hydrochloric, sulphuric, tartaric, oxalic, or formic acids. This having been ascertained, the remainder of the fluid was evaporated nearly to dryness, and acidified with sulphuric acid; it then evolved volatile acid vapour, which was condensed and digested with carbonate of silver. "The weight of the silver salt thus produced was only .37 gr., much too small a quantity for the accurate determination of the molecular weight of the acid. The number obtained, however, corresponded nearly with that of propionic acid; and I believe that this, or a mixture of acetic and butyric acids, were present in the liquid. The acid doubtless belongs to the acetic or fatty series."

Prof. Frankland, as well as his assistant, observed (and this is an important fact) that the fluid, "when acidified with sulphuric acid, emitted a powerful odour like that of pepsin." The leaves from which the secretion had been washed were also sent to Prof. Frankland; they were macerated for some hours, then acidified with sulphuric acid and distilled, but no acid passed over. Therefore the acid which fresh leaves contain, as shown by their discolouring litmus paper when crushed, must be of a different nature from that present in the secretion. Nor was any odour of pepsin emitted by them.

Although it has long been known that pepsin with acetic acid has the power of digesting albuminous compounds, it appeared advisable to ascertain whether acetic acid could be replaced, without the loss of digestive power, by the allied acids which are believed to occur in the secretion of *Drosera*, namely, propionic, butyric, or valerianic. Dr. Burdon Sanderson was so kind as to make for me the following experiments, the results of which are valuable, independently of the present inquiry. Prof. Frankland supplied the acids.

"1. The purpose of the following experiments was to determine the digestive activity of liquids containing pepsin, when acidulated with certain volatile acids belonging to the acetic series, in comparison with liquids acidulated with hydrochloric acid, in proportion similar to that in which it exists in gastric juice.

"2. It has been determined empirically that the best results are obtained in artificial digestion when a liquid containing two per thousand of hydrochloric acid gas by weight is used. This corresponds to about 6.25 cubic centimetres per litre of ordinary strong hydrochloric acid. The quantities of propionic, butyric, and valerianic acids respectively which are required to neutralise as much base as 6.25 cubic centimetres of HCl, are in grammes 4.04 of propionic acid, 4.82 of butyric acid, and 5.68 of valerianic acid. It was therefore judged expedient, in comparing the digestive powers of these acids with that of hydrochloric acid, to use them in these proportions.

"3. Five hundred cub. cent. of a liquid containing about 8 cub. cent. of a glycerine extract of the mucous membrane of the stomach of a dog killed during digestion having been prepared, 10 cub. cent. of it were evaporated and dried at 110°. This quantity yielded 0.0031 of residue.

"4. Of this liquid four quantities were taken which were severally acidulated with hydrochloric, propionic, butyric, and valerianic acids, in the proportions above indicated. Each liquid was then placed in a tube, which was allowed to float in a water bath, containing a thermometer which indicated a temperature of 38° to 40 °Cent. Into each, a quantity of unboiled fibrin was introduced, and the whole allowed to stand for four hours, the temperature being maintained during the whole time, and care being taken that each contained throughout an excess of fibrin. At the end of the period each liquid was filtered. Of the filtrate, which of course contained as much of the fibrin as had been digested during the four hours, 10 cub. cent. were measured out and evaporated, and dried at 110° as before. The residues were respectively —

"In the liquid containing hydrochloric acid 0.4079 " " propionic acid 0.0601 " " butyric acid 0.1468 " " valerianic acid 0.1254

"Hence, deducting from each of these the above-mentioned residue, left when the digestive liquid itself was evaporated, viz. 0.0031, we have,

"For propionic acid 0.0570 " butyric acid 0.1437 " valerianic acid 0.1223

as compared with 0.4048 for hydrochloric acid; these several numbers expressing the quantities of fibrin by weight digested in presence of equivalent quantities of the respective acids under identical conditions.

"The results of the experiment may be stated thus: — If 100 represent the digestive power of a liquid containing pepsin with the usual proportion of hydrochloric acid, 14.0, 35.4, and 30.2, will represent respectively the digestive powers of the three acids under investigation.

"5. In a second experiment in which the procedure was in every respect the same, excepting that all the tubes were plunged into the same water-bath, and the residues dried at 115 °C., the results were as follows: —

"Quantity of fibrin dissolved in four hours by 10 cub. cent. of the liquid: —

"Propionic acid 0.0563 Butyric acid 0.0835 Valerianic acid 0.0615

"The quantity digested by a similar liquid containing hydrochloric acid was 0.3376. Hence, taking this as 100, the following numbers represent the relative quantities digested by the other acids:

—
"Propionic acid 16.5 Butyric acid 24.7 Valerianic acid 16.1

"6. A third experiment of the same kind gave:

"Quantity of fibrin digested in four hours by 10 cub. cent. of the liquid: —

"Hydrochloric acid 0.2915 Propionic acid 0.1490 Butyric acid 0.1044
Valerianic acid 0.0520

"Comparing, as before, the three last numbers with the first taken as 100, the digestive power of propionic acid is represented by 16.8; that of butyric acid by 35.8; and that of valerianic by 17.8.

"The mean of these three sets of observations (hydrochloric acid being taken as 100) gives for

"Propionic acid 15.8 Butyric acid 32.0 Valerianic acid 21.4

"7. A further experiment was made to ascertain whether the digestive activity of butyric acid (which was selected as being apparently the most efficacious) was relatively greater at ordinary

temperatures than at the temperature of the body. It was found that whereas 10 cub. cent. of a liquid containing the ordinary proportion of hydrochloric acid digested 0.1311 gramme, a similar liquid prepared with butyric acid digested 0.0455 gramme of fibrin.

"Hence, taking the quantities digested with hydrochloric acid at the temperature of the body as 100, we have the digestive power of hydrochloric acid at the temperature of 160 to 18 °Cent. represented by 44.9; that of butyric acid at the same temperature being 15.6."

We here see that at the lower of these two temperatures, hydrochloric acid with pepsin digests, within the same time, rather less than half the quantity of fibrin compared with what it digests at the higher temperature; and the power of butyric acid is reduced in the same proportion under similar conditions and temperatures. We have also seen that butyric acid, which is much more efficacious than propionic or valerianic acids, digests with pepsin at the higher temperature less than a third of the fibrin which is digested at the same temperature by hydrochloric acid.]

I will now give in detail my experiments on the digestive power of the secretion of *Drosera*, dividing the substances tried into two series, namely those which are digested more or less completely, and those which are not digested. We shall presently see that all these substances are acted on by the gastric juice of the higher animals in the same manner. I beg leave to call attention to the experiments under the head albumen, showing that the secretion loses its power when neutralised by an alkali, and recovers it when an acid is added.

Substances which are completely or partially digested by the Secretion of *Drosera*.

Albumen. – After having tried various substances, Dr. Burdon Sanderson suggested to me the use of cubes of coagulated albumen or hard-boiled egg. I may premise that five cubes of the same size as those used in the following experiments were placed for the sake of comparison at the same time on wet moss close to the plants of *Drosera*. The weather was hot, and after four days some of the cubes were discoloured and mouldy, with their angles a little rounded; but they were not surrounded by a zone of transparent fluid as in the case of those undergoing digestion. Other cubes retained their angles and white colour. After eight days all were somewhat reduced in size, discoloured, with their angles much rounded. Nevertheless in four out of the five specimens, the central parts were still white and opaque. So that their state differed widely, as we shall see, from that of the cubes subjected to the action of the secretion.

[Experiment 1.

Rather large cubes of albumen were first tried; the tentacles were well inflected in 24 hrs.; after an additional day the angles of the cubes were dissolved and rounded;¹⁹ but the cubes were too large, so that the leaves were injured, and after seven days one died and the others were dying. Albumen which has been kept for four or five days, and which, it may be presumed, has begun to decay slightly, seems to act more quickly than freshly boiled eggs. As the latter were generally used, I often moistened them with a little saliva, to make the tentacles close more quickly.

Experiment 2. – A cube of 1/10 of an inch (i.e. with each side 1/10 of an inch, or 2.54 mm. in length) was placed on a leaf, and after 50 hrs. it was converted into a sphere about 3/40 of an inch (1.905 mm.) in diameter, surrounded by perfectly transparent fluid. After ten days the leaf re-expanded, but there was still left on the disc a minute bit of albumen now rendered transparent. More albumen had been given to this leaf than could be dissolved or digested.

Experiment 3. – Two cubes of albumen of 1/20 of an inch (1.27 mm.) were placed on two leaves. After 46 hrs. every atom of one was dissolved, and most of the liquefied matter was absorbed, the fluid which remained being in this, as in all other cases, very acid and viscid. The other cube was acted on at a rather slower rate.

¹⁹ In all my numerous experiments on the digestion of cubes of albumen, the angles and edges were invariably first rounded. Now, Schiff states ('Leons phys. de la Digestion,' vol. ii. 1867, page 149) that this is characteristic of the digestion of albumen by the gastric juice of animals. On the other hand, he remarks "les dissolutions, en chimie, ont lieu sur toute la surface des corps en contact avec l'agent dissolvant."

Experiment 4. – Two cubes of albumen of the same size as the last were placed on two leaves, and were converted in 50 hrs. into two large drops of transparent fluid; but when these were removed from beneath the inflected tentacles, and viewed by reflected light under the microscope, fine streaks of white opaque matter could be seen in the one, and traces of similar streaks in the other. The drops were replaced on the leaves, which re-expanded after 10 days; and now nothing was left except a very little transparent acid fluid.

Experiment 5. – This experiment was slightly varied, so that the albumen might be more quickly exposed to the action of the secretion. Two cubes, each of about 1/40 of an inch (.635 mm.), were placed on the same leaf, and two similar cubes on another leaf. These were examined after 21 hrs. 30 m., and all four were found rounded. After 46 hrs. the two cubes on the one leaf were completely liquefied, the fluid being perfectly transparent; on the other leaf some opaque white streaks could still be seen in the midst of the fluid. After 72 hrs. these streaks disappeared, but there was still a little viscid fluid left on the disc; whereas it was almost all absorbed on the first leaf. Both leaves were now beginning to re-expand.]

The best and almost sole test of the presence of some ferment analogous to pepsin in the secretion appeared to be to neutralise the acid of the secretion with an alkali, and to observe whether the process of digestion ceased; and then to add a little acid and observe whether the process recommenced. This was done, and, as we shall see, with success, but it was necessary first to try two control experiments; namely, whether the addition of minute drops of water of the same size as those of the dissolved alkalis to be used would stop the process of digestion; and, secondly, whether minute drops of weak hydrochloric acid, of the same strength and size as those to be used, would injure the leaves. The two following experiments were therefore tried: —

Experiment 6. – Small cubes of albumen were put on three leaves, and minute drops of distilled water on the head of a pin were added two or three times daily. These did not in the least delay the process; for, after 48 hrs., the cubes were completely dissolved on all three leaves. On the third day the leaves began to re-expand, and on the fourth day all the fluid was absorbed.

Experiment 7. – Small cubes of albumen were put on two leaves, and minute drops of hydrochloric acid, of the strength of one part to 437 of water, were added two or three times. This did not in the least delay, but seemed rather to hasten, the process of digestion; for every trace of the albumen disappeared in 24 hrs. 30 m. After three days the leaves partially re-expanded, and by this time almost all the viscid fluid on their discs was absorbed. It is almost superfluous to state that cubes of albumen of the same size as those above used, left for seven days in a little hydrochloric acid of the above strength, retained all their angles as perfect as ever.

Experiment 8. – Cubes of albumen (of 1/20 of an inch, or 2.54 mm.) were placed on five leaves, and minute drops of a solution of one part of carbonate of soda to 437 of water were added at intervals to three of them, and drops of carbonate of potash of the same strength to the other two. The drops were given on the head of a rather large pin, and I ascertained that each was equal to about 1/10 of a minim (.0059 ml.), so that each contained only 1/4800 of a grain (.0135 mg.) of the alkali. This was not sufficient, for after 46 hrs. all five cubes were dissolved.

Experiment 9. – The last experiment was repeated on four leaves, with this difference, that drops of the same solution of carbonate of soda were added rather oftener, as often as the secretion became acid, so that it was much more effectually neutralised. And now after 24 hrs. the angles of three of the cubes were not in the least rounded, those of the fourth being so in a very slight degree. Drops of extremely weak hydrochloric acid (viz. one part to 847 of water) were then added, just enough to neutralise the alkali which was still present; and now digestion immediately recommenced, so that after 23 hrs. 30 m. three of the cubes were completely dissolved, whilst the fourth was converted into a minute sphere, surrounded by transparent fluid; and this sphere next day disappeared.

Experiment 10. – Stronger solutions of carbonate of soda and of potash were next used, viz. one part to 109 of water; and as the same-sized drops were given as before, each drop contained

1/1200 of a grain (.0539 mg.) of either salt. Two cubes of albumen (each about 1/40 of an inch, or .635 mm.) were placed on the same leaf, and two on another. Each leaf received, as soon as the secretion became slightly acid (and this occurred four times within 24 hrs.), drops either of the soda or potash, and the acid was thus effectually neutralised. The experiment now succeeded perfectly, for after 22 hrs. the angles of the cubes were as sharp as they were at first, and we know from experiment 5 that such small cubes would have been completely rounded within this time by the secretion in its natural state. Some of the fluid was now removed with blotting-paper from the discs of the leaves, and minute drops of hydrochloric acid of the strength of the one part to 200 of water was added. Acid of this greater strength was used as the solutions of the alkalies were stronger. The process of digestion now commenced, so that within 48 hrs. from the time when the acid was given the four cubes were not only completely dissolved, but much of the liquefied albumen was absorbed.

Experiment 11. – Two cubes of albumen (1/40 of an inch, or .635 mm.) were placed on two leaves, and were treated with alkalies as in the last experiment, and with the same result; for after 22 hrs. they had their angles perfectly sharp, showing that the digestive process had been completely arrested. I then wished to ascertain what would be the effect of using stronger hydrochloric acid; so I added minute drops of the strength of 1 per cent. This proved rather too strong, for after 48 hrs. from the time when the acid was added one cube was still almost perfect, and the other only very slightly rounded, and both were stained slightly pink. This latter fact shows that the leaves were injured,²⁰ for during the normal process of digestion the albumen is not thus coloured, and we can thus understand why the cubes were not dissolved.]

From these experiments we clearly see that the secretion has the power of dissolving albumen, and we further see that if an alkali is added, the process of digestion is stopped, but immediately recommences as soon as the alkali is neutralised by weak hydrochloric acid. Even if I had tried no other experiments than these, they would have almost sufficed to prove that the glands of *Drosera* secrete some ferment analogous to pepsin, which in presence of an acid gives to the secretion its power of dissolving albuminous compounds.

Splinters of clean glass were scattered on a large number of leaves, and these became moderately inflected. They were cut off and divided into three lots; two of them, after being left for some time in a little distilled water, were strained, and some discoloured, viscid, slightly acid fluid was thus obtained. The third lot was well soaked in a few drops of glycerine, which is well known to dissolve pepsin. Cubes of albumen (1/20 of an inch) were now placed in the three fluids in watch-glasses, some of which were kept for several days at about 90° Fahr. (32° Cent.), and others at the temperature of my room; but none of the cubes were dissolved, the angles remaining as sharp as ever. This fact probably indicates that the ferment is not secreted until the glands are excited by the absorption of a minute quantity of already soluble animal matter, – a conclusion which is supported by what we shall hereafter see with respect to *Dionaea*. Dr. Hooker likewise found that, although the fluid within the pitchers of *Nepenthes* possesses extraordinary power of digestion, yet when removed from the pitchers before they have been excited and placed in a vessel, it has no such power, although it is already acid; and we can account for this fact only on the supposition that the proper ferment is not secreted until some exciting matter is absorbed.

On three other occasions eight leaves were strongly excited with albumen moistened with saliva; they were then cut off, and allowed to soak for several hours or for a whole day in a few drops of glycerine. Some of this extract was added to a little hydrochloric acid of various strengths (generally one to 400 of water), and minute cubes of albumen were placed in the mixture.²¹ In two of these trials the cubes were not in the least acted on; but in the third the experiment was successful. For in

²⁰ Sachs remarks ('*Trait de Bot.*' 1874, p. 774), that cells which are killed by freezing, by too great heat, or by chemical agents, allow all their colouring matter to escape into the surrounding water.

²¹ As a control experiment bits of albumen were placed in the same glycerine with hydrochloric acid of the same strength; and the albumen, as might have been expected, was not in the least affected after two days.

a vessel containing two cubes, both were reduced in size in 3 hrs.; and after 24 hrs. mere streaks of undissolved albumen were left. In a second vessel, containing two minute ragged bits of albumen, both were likewise reduced in size in 3 hrs., and after 24 hrs. completely disappeared. I then added a little weak hydrochloric acid to both vessels, and placed fresh cubes of albumen in them; but these were not acted on. This latter fact is intelligible according to the high authority of Schiff,²² who has demonstrated, as he believes, in opposition to the view held by some physiologists, that a certain small amount of pepsin is destroyed during the act of digestion. So that if my solution contained, as is probable, an extremely small amount of the ferment, this would have been consumed by the dissolution of the cubes of albumen first given; none being left when the hydrochloric acid was added. The destruction of the ferment during the process of digestion, or its absorption after the albumen had been converted into a peptone, will also account for only one out of the three latter sets of experiments having been successful.

Digestion of Roast Meat. – Cubes of about 1/20 of an inch (1.27 mm.) of moderately roasted meat were placed on five leaves which became in 12 hrs. closely inflected. After 48 hrs. I gently opened one leaf, and the meat now consisted of a minute central sphere, partially digested and surrounded by a thick envelope of transparent viscid fluid. The whole, without being much disturbed, was removed and placed under the microscope. In the central part the transverse striae on the muscular fibres were quite distinct; and it was interesting to observe how gradually they disappeared, when the same fibre was traced into the surrounding fluid. They disappeared by the striae being replaced by transverse lines formed of excessively minute dark points, which towards the exterior could be seen only under a very high power; and ultimately these points were lost. When I made these observations, I had not read Schiff's account²³ of the digestion of meat by gastric juice, and I did not understand the meaning of the dark points. But this is explained in the following statement, and we further see how closely similar is the process of digestion by gastric juice and by the secretion of *Drosera*.

["On a dit le suc gastrique faisait perdre la fibre musculaire ses stries transversales. Ainsi nonce, cette proposition pourrait donner lieu une quivoque, car ce qui se perd, ce n'est que l'aspect exterieur de la striature et non les lments anatomiques qui la composent. On sait que les stries qui donnent un aspect si caractristique la fibre musculaire, sont le rsultat de la juxtaposition et du parallisme des corpuscules lmentaires, placs, distances gales, dans l'intrieur des fibrilles contigus. Or, ds que le tissu connectif qui relie entre elles les fibrilles lmentaires vient se gonfler et se dissoudre, et que les fibrilles elles-mmes se dissocient, ce parallisme est dtruit et avec lui l'aspect, le phnomne optique des stries. Si, aprs la dsagrgation des fibres, on examine au microscope les fibrilles lmentaires, on distingue encore trs-nettement leur intrieur les corpuscules, et on continue les voir, de plus en plus ples, jusqu'au moment o les fibrilles elles-mmes se liqufient et disparaissent dans le suc gastrique. Ce qui constitue la striature, proprement parler, n'est donc pas dtruit, avant la liqufaction de la fibre charnue elle-mme."]

In the viscid fluid surrounding the central sphere of undigested meat there were globules of fat and little bits of fibro-elastic tissue; neither of which were in the least digested. There were also little free parallelograms of yellowish, highly translucent matter. Schiff, in speaking of the digestion of meat by gastric juice, alludes to such parallelograms, and says: —

["Le gonflement par lequel commence la digestion de la viande, rsulte de l'action du suc gastrique acide sur le tissu connectif qui se dissout d'abord, et qui, par sa liqufaction, dsagrges les fibrilles. Celles-ci se dissolvent ensuite en grande partie, mais, avant de passer l'tat liquide, elles tendent se briser en petits fragments transversaux. Les 'sarcous elements' de Bowman, qui ne sont

²² 'Leons phys. de la Digestion,' 1867, tom. ii. pp. 114-126.

²³ 'Leons phys. de la Digestion,' tom. ii. p. 145.

autre chose que les produits de cette division transversale des fibrilles limentaires, peuvent tre prpars et isols l'aide du suc gastrique, pourvu qu'on n'attend pas jusqu' la liqufaction complte du muscle."]

After an interval of 72 hrs., from the time when the five cubes were placed on the leaves, I opened the four remaining ones. On two nothing could be seen but little masses of transparent viscid fluid; but when these were examined under a high power, fat-globules, bits of fibro-elastic tissue, and some few parallelograms of sarcous matter, could be distinguished, but not a vestige of transverse striae. On the other two leaves there were minute spheres of only partially digested meat in the centre of much transparent fluid.

Fibrin. – Bits of fibrin were left in water during four days, whilst the following experiments were tried, but they were not in the least acted on. The fibrin which I first used was not pure, and included dark particles: it had either not been well prepared or had subsequently undergone some change. Thin portions, about 1/10 of an inch square, were placed on several leaves, and though the fibrin was soon liquefied, the whole was never dissolved. Smaller particles were then placed on four leaves, and minute drops of hydrochloric acid (one part to 437 of water) were added; this seemed to hasten the process of digestion, for on one leaf all was liquified and absorbed after 20 hrs.; but on the three other leaves some undissolved residue was left after 48 hrs. It is remarkable that in all the above and following experiments, as well as when much larger bits of fibrin were used, the leaves were very little excited; and it was sometimes necessary to add a little saliva to induce complete inflection. The leaves, moreover, began to re-expand after only 48 hrs., whereas they would have remained inflected for a much longer time had insects, meat, cartilage, albumen, &c., been placed on them.

I then tried some pure white fibrin, sent me by Dr. Burdon Sanderson.

[Experiment 1. – Two particles, barely 1/20 of an inch (1.27 mm.) square, were placed on opposite sides of the same leaf. One of these did not excite the surrounding tentacles, and the gland on which it rested soon dried. The other particle caused a few of the short adjoining tentacles to be inflected, the more distant ones not being affected. After 24 hrs. both were almost, and after 72 hrs. completely, dissolved.

Experiment 2. – The same experiment with the same result, only one of the two bits of fibrin exciting the short surrounding tentacles. This bit was so slowly acted on that after a day I pushed it on to some fresh glands. In three days from the time when it was first placed on the leaf it was completely dissolved.

Experiment 3. – Bits of fibrin of about the same size as before were placed on the discs of two leaves; these caused very little inflection in 23 hrs., but after 48 hrs. both were well clasped by the surrounding short tentacles, and after an additional 24 hrs. were completely dissolved. On the disc of one of these leaves much clear acid fluid was left.

Experiment 4. – Similar bits of fibrin were placed on the discs of two leaves; as after 2 hrs. the glands seemed rather dry, they were freely moistened with saliva; this soon caused strong inflection both of the tentacles and blades, with copious secretion from the glands. In 18 hrs. the fibrin was completely liquefied, but undigested atoms still floated in the liquid; these, however, disappeared in under two additional days.]

From these experiments it is clear that the secretion completely dissolves pure fibrin. The rate of dissolution is rather slow; but this depends merely on this substance not exciting the leaves sufficiently, so that only the immediately adjoining tentacles are inflected, and the supply of secretion is small.

Syntonin. – This substance, extracted from muscle, was kindly prepared for me by Dr. Moore. Very differently from fibrin, it acts quickly and energetically. Small portions placed on the discs of three leaves caused their tentacles and blades to be strongly inflected within 8 hrs.; but no further observations were made. It is probably due to the presence of this substance that raw meat is too powerful a stimulant, often injuring or even killing the leaves.

Areolar Tissue. – Small portions of this tissue from a sheep were placed on the discs of three leaves; these became moderately well inflected in 24 hrs., but began to re-expand after 48 hrs., and

were fully re-expanded in 72 hrs., always reckoning from the time when the bits were first given. This substance, therefore, like fibrin, excites the leaves for only a short time. The residue left on the leaves, after they were fully re-expanded, was examined under a high power and found much altered, but, owing to the presence of a quantity of elastic tissue, which is never acted on, could hardly be said to be in a liquefied condition.

Some areolar tissue free from elastic tissue was next procured from the visceral cavity of a toad, and moderately sized, as well as very small, bits were placed on five leaves. After 24 hrs. two of the bits were completely liquefied; two others were rendered transparent, but not quite liquefied; whilst the fifth was but little affected. Several glands on the three latter leaves were now moistened with a little saliva, which soon caused much inflection and secretion, with the result that in the course of 12 additional hrs. one leaf alone showed a remnant of undigested tissue. On the discs of the four other leaves (to one of which a rather large bit had been given) nothing was left except some transparent viscid fluid. I may add that some of this tissue included points of black pigment, and these were not at all affected. As a control experiment, small portions of this tissue were left in water and on wet moss for the same length of time, and remained white and opaque. From these facts it is clear that areolar tissue is easily and quickly digested by the secretion; but that it does not greatly excite the leaves.

Cartilage. – Three cubes ($\frac{1}{20}$ of an inch or 1.27 mm.) of white, translucent, extremely tough cartilage were cut from the end of a slightly roasted leg-bone of a sheep. These were placed on three leaves, borne by poor, small plants in my greenhouse during November; and it seemed in the highest degree improbable that so hard a substance would be digested under such unfavourable circumstances. Nevertheless, after 48 hrs., the cubes were largely dissolved and converted into minute spheres, surrounded by transparent, very acid fluid. Two of these spheres were completely softened to their centres; whilst the third still contained a very small irregularly shaped core of solid cartilage. Their surfaces were seen under the microscope to be curiously marked by prominent ridges, showing that the cartilage had been unequally corroded by the secretion. I need hardly say that cubes of the same cartilage, kept in water for the same length of time, were not in the least affected.

During a more favourable season, moderately sized bits of the skinned ear of a cat, which includes cartilage, areolar and elastic tissue, were placed on three leaves. Some of the glands were touched with saliva, which caused prompt inflection. Two of the leaves began to re-expand after three days, and the third on the fifth day. The fluid residue left on their discs was now examined, and consisted in one case of perfectly transparent, viscid matter; in the other two cases, it contained some elastic tissue and apparently remnants of half digested areolar tissue.

Fibro-cartilage (from between the vertebrae of the tail of a sheep). Moderately sized and small bits (the latter about $\frac{1}{20}$ of an inch) were placed on nine leaves. Some of these were well and some very little inflected. In the latter case the bits were dragged over the discs, so that they were well bedaubed with the secretion, and many glands thus irritated. All the leaves re-expanded after only two days; so that they were but little excited by this substance. The bits were not liquefied, but were certainly in an altered condition, being swollen, much more transparent, and so tender as to disintegrate very easily. My son Francis prepared some artificial gastric juice, which was proved efficient by quickly dissolving fibrin, and suspended portions of the fibro-cartilage in it. These swelled and became hyaline, exactly like those exposed to the secretion of *Drosera*, but were not dissolved. This result surprised me much, as two physiologists were of opinion that fibro-cartilage would be easily digested by gastric juice. I therefore asked Dr. Klein to examine the specimens; and he reports that the two which had been subjected to artificial gastric juice were "in that state of digestion in which we find connective tissue when treated with an acid, viz. swollen, more or less hyaline, the fibrillar bundles having become homogeneous and lost their fibrillar structure." In the specimens which had been left on the leaves of *Drosera*, until they re-expanded, "parts were altered, though only slightly so, in the same manner as those subjected to the gastric juice as they had become more

transparent, almost hyaline, with the fibrillation of the bundles indistinct." Fibro-cartilage is therefore acted on in nearly the same manner by gastric juice and by the secretion of *Drosera*.

Bone. – Small smooth bits of the dried hyoidal bone of a fowl moistened with saliva were placed on two leaves, and a similarly moistened splinter of an extremely hard, broiled mutton-chop bone on a third leaf. These leaves soon became strongly inflected, and remained so for an unusual length of time; namely, one leaf for ten and the other two for nine days. The bits of bone were surrounded all the time by acid secretion. When examined under a weak power, they were found quite softened, so that they were readily penetrated by a blunt needle, torn into fibres, or compressed. Dr. Klein was so kind as to make sections of both bones and examine them. He informs me that both presented the normal appearance of decalcified bone, with traces of the earthy salts occasionally left. The corpuscles with their processes were very distinct in most parts; but in some parts, especially near the periphery of the hyoidal bone, none could be seen. Other parts again appeared amorphous, with even the longitudinal striation of bone not distinguishable. This amorphous structure, as Dr. Klein thinks, may be the result either of the incipient digestion of the fibrous basis or of all the animal matter having been removed, the corpuscles being thus rendered invisible. A hard, brittle, yellowish substance occupied the position of the medulla in the fragments of the hyoidal bone.

As the angles and little projections of the fibrous basis were not in the least rounded or corroded, two of the bits were placed on fresh leaves. These by the next morning were closely inflected, and remained so, – the one for six and the other for seven days, – therefore for not so long a time as on the first occasion, but for a much longer time than ever occurs with leaves inflected over inorganic or even over many organic bodies. The secretion during the whole time coloured litmus paper of a bright red; but this may have been due to the presence of the acid super-phosphate of lime. When the leaves re-expanded, the angles and projections of the fibrous basis were as sharp as ever. I therefore concluded, falsely as we shall presently see, that the secretion cannot touch the fibrous basis of bone. The more probable explanation is that the acid was all consumed in decomposing the phosphate of lime which still remained; so that none was left in a free state to act in conjunction with the ferment on the fibrous basis.

Enamel and Dentine. – As the secretion decalcified ordinary bone, I determined to try whether it would act on enamel and dentine, but did not expect that it would succeed with so hard a substance as enamel. Dr. Klein gave me some thin transverse slices of the canine tooth of a dog; small angular fragments of which were placed on four leaves; and these were examined each succeeding day at the same hour. The results are, I think, worth giving in detail.]

[Experiment 1. – May 1st, fragment placed on leaf; 3rd, tentacles but little inflected, so a little saliva was added; 6th, as the tentacles were not strongly inflected, the fragment was transferred to another leaf, which acted at first slowly, but by the 9th closely embraced it. On the 11th this second leaf began to re-expand; the fragment was manifestly softened, and Dr. Klein reports, "a great deal of enamel and the greater part of the dentine decalcified."

Experiment 2. – May 1st, fragment placed on leaf; 2nd, tentacles fairly well inflected, with much secretion on the disc, and remained so until the 7th, when the leaf re-expanded. The fragment was now transferred to a fresh leaf, which next day (8th) was inflected in the strongest manner, and thus remained until the 11th, when it re-expanded. Dr. Klein reports, "a great deal of enamel and the greater part of the dentine decalcified."

Experiment 3. – May 1st, fragment moistened with saliva and placed on a leaf, which remained well inflected until 5th, when it re-expanded. The enamel was not at all, and the dentine only slightly, softened. The fragment was now transferred to a fresh leaf, which next morning (6th) was strongly inflected, and remained so until the 11th. The enamel and dentine both now somewhat softened; and Dr. Klein reports, "less than half the enamel, but the greater part of the dentine decalcified."

Experiment 4. – May 1st, a minute and thin bit of dentine, moistened with saliva, was placed on a leaf, which was soon inflected, and re-expanded on the 5th. The dentine had become as flexible

as thin paper. It was then transferred to a fresh leaf, which next morning (6th) was strongly inflected, and reopened on the 10th. The decalcified dentine was now so tender that it was torn into shreds merely by the force of the re-expanding tentacles.]

From these experiments it appears that enamel is attacked by the secretion with more difficulty than dentine, as might have been expected from its extreme hardness; and both with more difficulty than ordinary bone. After the process of dissolution has once commenced, it is carried on with greater ease; this may be inferred from the leaves, to which the fragments were transferred, becoming in all four cases strongly inflected in the course of a single day; whereas the first set of leaves acted much less quickly and energetically. The angles or projections of the fibrous basis of the enamel and dentine (except, perhaps, in No. 4, which could not be well observed) were not in the least rounded; and Dr. Klein remarks that their microscopical structure was not altered. But this could not have been expected, as the decalcification was not complete in the three specimens which were carefully examined.

Fibrous Basis of Bone. – I at first concluded, as already stated, that the secretion could not digest this substance. I therefore asked Dr. Burdon Sanderson to try bone, enamel, and dentine, in artificial gastric juice, and he found that they were after a considerable time completely dissolved. Dr. Klein examined some of the small lamellae, into which part of the skull of a cat became broken up after about a week's immersion in the fluid, and he found that towards the edges the "matrix appeared rarefied, thus producing the appearance as if the canaliculi of the bone-corpuscles had become larger. Otherwise the corpuscles and their canaliculi were very distinct." So that with bone subjected to artificial gastric juice complete decalcification precedes the dissolution of the fibrous basis. Dr. Burdon Sanderson suggested to me that the failure of *Drosera* to digest the fibrous basis of bone, enamel, and dentine, might be due to the acid being consumed in the decomposition of the earthy salts, so that there was none left for the work of digestion. Accordingly, my son thoroughly decalcified the bone of a sheep with weak hydrochloric acid; and seven minute fragments of the fibrous basis were placed on so many leaves, four of the fragments being first damped with saliva to aid prompt inflection. All seven leaves became inflected, but only very moderately, in the course of a day. They quickly began to re-expand; five of them on the second day, and the other two on the third day. On all seven leaves the fibrous tissue was converted into perfectly transparent, viscid, more or less liquefied little masses. In the middle, however, of one, my son saw under a high power a few corpuscles, with traces of fibrillation in the surrounding transparent matter. From these facts it is clear that the leaves are very little excited by the fibrous basis of bone, but that the secretion easily and quickly liquefies it, if thoroughly decalcified. The glands which had remained in contact for two or three days with the viscid masses were not discoloured, and apparently had absorbed little of the liquefied tissue, or had been little affected by it.

Phosphate of Lime. – As we have seen that the tentacles of the first set of leaves remained clasped for nine or ten days over minute fragments of bone, and the tentacles of the second set for six or seven days over the same fragments, I was led to suppose that it was the phosphate of lime, and not any included animal matter, which caused such long continued inflection. It is at least certain from what has just been shown that this cannot have been due to the presence of the fibrous basis. With enamel and dentine (the former of which contains only 4 per cent. of organic matter) the tentacles of two successive sets of leaves remained inflected altogether for eleven days. In order to test my belief in the potency of phosphate of lime, I procured some from Prof. Frankland absolutely free of animal matter and of any acid. A small quantity moistened with water was placed on the discs of two leaves. One of these was only slightly affected; the other remained closely inflected for ten days, when a few of the tentacles began to re-expand, the rest being much injured or killed. I repeated the experiment, but moistened the phosphate with saliva to insure prompt inflection; one leaf remained inflected for six days (the little saliva used would not have acted for nearly so long a time) and then died; the other leaf tried to re-expand on the sixth day, but after nine days failed to do so, and likewise died.

Although the quantity of phosphate given to the above four leaves was extremely small, much was left in every case undissolved. A larger quantity wetted with water was next placed on the discs of three leaves; and these became most strongly inflected in the course of 24 hrs. They never re-expanded; on the fourth day they looked sickly, and on the sixth were almost dead. Large drops of not very viscid fluid hung from their edges during the six days. This fluid was tested each day with litmus paper, but never coloured it; and this circumstance I do not understand, as the superphosphate of lime is acid. I suppose that some superphosphate must have been formed by the acid of the secretion acting on the phosphate, but that it was all absorbed and injured the leaves; the large drops which hung from their edges being an abnormal and dropsical secretion. Anyhow, it is manifest that the phosphate of lime is a most powerful stimulant. Even small doses are more or less poisonous, probably on the same principle that raw meat and other nutritious substances, given in excess, kill the leaves. Hence the conclusion, that the long continued inflection of the tentacles over fragments of bone, enamel, and dentine, is caused by the presence of phosphate of lime, and not of any included animal matter, is no doubt correct.

Gelatine. – I used pure gelatine in thin sheets given me by Prof. Hoffmann. For comparison, squares of the same size as those placed on the leaves were left close by on wet moss. These soon swelled, but retained their angles for three days; after five days they formed rounded, softened masses, but even on the eighth day a trace of gelatine could still be detected. Other squares were immersed in water, and these, though much swollen, retained their angles for six days. Squares of 1/10 of an inch (2.54 mm.), just moistened with water, were placed on two leaves; and after two or three days nothing was left on them but some acid viscid fluid, which in this and other cases never showed any tendency to regelatinise; so that the secretion must act on the gelatine differently to what water does, and apparently in the same manner as gastric juice.²⁴ Four squares of the same size as before were then soaked for three days in water, and placed on large leaves; the gelatine was liquefied and rendered acid in two days, but did not excite much inflection. The leaves began to re-expand after four or five days, much viscid fluid being left on their discs, as if but little had been absorbed. One of these leaves, as soon as it re-expanded, caught a small fly, and after 24 hrs. was closely inflected, showing how much more potent than gelatine is the animal matter absorbed from an insect. Some larger pieces of gelatine, soaked for five days in water, were next placed on three leaves, but these did not become much inflected until the third day; nor was the gelatine completely liquefied until the fourth day. On this day one leaf began to re-expand; the second on the fifth; and third on the sixth. These several facts prove that gelatine is far from acting energetically on *Drosera*.

In the last chapter it was shown that a solution of isinglass of commerce, as thick as milk or cream, induces strong inflection. I therefore wished to compare its action with that of pure gelatine. Solutions of one part of both substances to 218 of water were made; and half-minim drops (.0296 ml.) were placed on the discs of eight leaves, so that each received 1/480 of a grain, or .135 mg. The four with the isinglass were much more strongly inflected than the other four. I conclude therefore that isinglass contains some, though perhaps very little, soluble albuminous matter. As soon as these eight leaves re-expanded, they were given bits of roast meat, and in some hours all became greatly inflected; again showing how much more meat excites *Drosera* than does gelatine or isinglass. This is an interesting fact, as it is well known that gelatine by itself has little power of nourishing animals.²⁵

Chondrin. – This was sent me by Dr. Moore in a gelatinous state. Some was slowly dried, and a small chip was placed on a leaf, and a much larger chip on a second leaf. The first was liquefied in a day; the larger piece was much swollen and softened, but was not completely liquefied until the third day. The undried jelly was next tried, and as a control experiment small cubes were left in water

²⁴ Dr. Lauder Brunton, 'Handbook for the Phys. Laboratory,' 1873, pp. 477, 487; Schiff, 'Leons phys. de la Digestion,' 1867, p. 249.

²⁵ Dr. Lauder Brunton gives in the 'Medical Record,' January 1873, p. 36, an account of Voit's view of the indirect part which gelatine plays in nutrition.

for four days and retained their angles. Cubes of the same size were placed on two leaves, and larger cubes on two other leaves. The tentacles and laminae of the latter were closely inflected after 22 hrs., but those of the two leaves with the smaller cubes only to a moderate degree. The jelly on all four was by this time liquefied, and rendered very acid. The glands were blackened from the aggregation of their protoplasmic contents. In 46 hrs. from the time when the jelly was given, the leaves had almost re-expanded, and completely so after 70 hrs.; and now only a little slightly adhesive fluid was left unabsorbed on their discs.

One part of chondrin jelly was dissolved in 218 parts of boiling water, and half-minim drops were given to four leaves; so that each received about 1/480 of a grain (.135 mg.) of the jelly; and, of course, much less of dry chondrin. This acted most powerfully, for after only 3 hrs. 30 m. all four leaves were strongly inflected. Three of them began to re-expand after 24 hrs., and in 48 hrs. were completely open; but the fourth had only partially re-expanded. All the liquefied chondrin was by this time absorbed. Hence a solution of chondrin seems to act far more quickly and energetically than pure gelatine or isinglass; but I am assured by good authorities that it is most difficult, or impossible, to know whether chondrin is pure, and if it contained any albuminous compound, this would have produced the above effects. Nevertheless, I have thought these facts worth giving, as there is so much doubt on the nutritious value of gelatine; and Dr. Lauder Brunton does not know of any experiments with respect to animals on the relative value of gelatine and chondrin.

Milk. – We have seen in the last chapter that milk acts most powerfully on the leaves; but whether this is due to the contained casein or albumen, I know not. Rather large drops of milk excite so much secretion (which is very acid) that it sometimes trickles down from the leaves, and this is likewise characteristic of chemically prepared casein. Minute drops of milk, placed on leaves, were coagulated in about ten minutes. Schiff denies²⁶ that the coagulation of milk by gastric juice is exclusively due to the acid which is present, but attributes it in part to the pepsin; and it seems doubtful whether with *Drosera* the coagulation can be wholly due to the acid, as the secretion does not commonly colour litmus paper until the tentacles have become well inflected; whereas the coagulation commences, as we have seen, in about ten minutes. Minute drops of skimmed milk were placed on the discs of five leaves; and a large proportion of the coagulated matter or curd was dissolved in 6 hrs. and still more completely in 8 hrs. These leaves re-expanded after two days, and the viscid fluid left on their discs was then carefully scraped off and examined. It seemed at first sight as if all the casein had not been dissolved, for a little matter was left which appeared of a whitish colour by reflected light. But this matter, when examined under a high power, and when compared with a minute drop of skimmed milk coagulated by acetic acid, was seen to consist exclusively of oil-globules, more or less aggregated together, with no trace of casein. As I was not familiar with the microscopical appearance of milk, I asked Dr. Lauder Brunton to examine the slides, and he tested the globules with ether, and found that they were dissolved. We may, therefore, conclude that the secretion quickly dissolves casein, in the state in which it exists in milk.

Chemically Prepared Casein. – This substance, which is insoluble in water, is supposed by many chemists to differ from the casein of fresh milk. I procured some, consisting of hard globules, from Messrs. Hopkins and Williams, and tried many experiments with it. Small particles and the powder, both in a dry state and moistened with water, caused the leaves on which they were placed to be inflected very slowly, generally not until two days had elapsed. Other particles, wetted with weak hydrochloric acid (one part to 437 of water) acted in a single day, as did some casein freshly prepared for me by Dr. Moore. The tentacles commonly remained inflected for from seven to nine days; and during the whole of this time the secretion was strongly acid. Even on the eleventh day some secretion left on the disc of a fully re-expanded leaf was strongly acid. The acid seems to be secreted

²⁶ 'Leons,' &c. tom. ii. page 151.

quickly, for in one case the secretion from the discal glands, on which a little powdered casein had been strewed, coloured litmus paper, before any of the exterior tentacles were inflected.

Small cubes of hard casein, moistened with water, were placed on two leaves; after three days one cube had its angles a little rounded, and after seven days both consisted of rounded softened masses, in the midst of much viscid and acid secretion; but it must not be inferred from this fact that the angles were dissolved, for cubes immersed in water were similarly acted on. After nine days these leaves began to re-expand, but in this and other cases the casein did not appear, as far as could be judged by the eye, much, if at all, reduced in bulk. According to Hoppe-Seyler and Lubavin²⁷ casein consists of an albuminous, with a non-albuminous, substance; and the absorption of a very small quantity of the former would excite the leaves, and yet not decrease the casein to a perceptible degree. Schiff asserts²⁸ – and this is an important fact for us – that "la casine purifiée des chimistes est un corps presque complètement inattaquable par le suc gastrique." So that here we have another point of accordance between the secretion of *Drosera* and gastric juice, as both act so differently on the fresh casein of milk, and on that prepared by chemists.

A few trials were made with cheese; cubes of 1/20 of an inch (1.27 mm.) were placed on four leaves, and these after one or two days became well inflected, their glands pouring forth much acid secretion. After five days they began to re-expand, but one died, and some of the glands on the other leaves were injured. Judging by the eye, the softened and subsided masses of cheese, left on the discs, were very little or not at all reduced in bulk. We may, however, infer from the time during which the tentacles remained inflected, – from the changed colour of some of the glands, – and from the injury done to others, that matter had been absorbed from the cheese.

Legumin. – I did not procure this substance in a separate state; but there can hardly be a doubt that it would be easily digested, judging from the powerful effect produced by drops of a decoction of green peas, as described in the last chapter. Thin slices of a dried pea, after being soaked in water, were placed on two leaves; these became somewhat inflected in the course of a single hour, and most strongly so in 21 hrs. They re-expanded after three or four days.

The slices were not liquefied, for the walls of the cells, composed of cellulose, are not in the least acted on by the secretion.

Pollen. – A little fresh pollen from the common pea was placed on the discs of five leaves, which soon became closely inflected, and remained so for two or three days.

The grains being then removed, and examined under the microscope, were found discoloured, with the oil-globules remarkably aggregated. Many had their contents much shrunk, and some were almost empty. In only a few cases were the pollen-tubes emitted. There could be no doubt that the secretion had penetrated the outer coats of the grains, and had partially digested their contents. So it must be with the gastric juice of the insects which feed on pollen, without masticating it.²⁹ *Drosera* in a state of nature cannot fail to profit to a certain extent by this power of digesting pollen, as innumerable grains from the carices, grasses, rumices, fir-trees, and other wind-fertilised plants, which commonly grow in the same neighbourhood, will be inevitably caught by the viscid secretion surrounding the many glands.

Gluten. – This substance is composed of two albuminoids, one soluble, the other insoluble in alcohol. Some was prepared by merely washing wheaten flour in water. A provisional trial was made with rather large pieces placed on two leaves; these, after 21 hrs., were closely inflected, and remained so for four days, when one was killed and the other had its glands extremely blackened, but was not afterwards observed.

²⁷ Dr. Lauder Brunton, 'Handbook for Phys. Lab.' p. 529.

²⁸ 'Leons' &c. tom. ii. page 153.

²⁹ Mr. A.W. Bennett found the undigested coats of the grains in the intestinal canal of pollen-eating Diptera; see 'Journal of Hort. Soc. of London,' vol. iv. 1874, p. 158. Watts' 'Dict. of Chemistry,' vol. ii. 1872, p. 873.

Smaller bits were placed on two leaves; these were only slightly inflected in two days, but afterwards became much more so. Their secretion was not so strongly acid as that of leaves excited by casein. The bits of gluten, after lying for three days on the leaves, were more transparent than other bits left for the same time in water. After seven days both leaves re-expanded, but the gluten seemed hardly at all reduced in bulk. The glands which had been in contact with it were extremely black. Still smaller bits of half putrid gluten were now tried on two leaves; these were well inflected in 24 hrs., and thoroughly in four days, the glands in contact being much blackened. After five days one leaf began to re-expand, and after eight days both were fully re-expanded, some gluten being still left on their discs. Four little chips of dried gluten, just dipped in water, were next tried, and these acted rather differently from fresh gluten. One leaf was almost fully re-expanded in three days, and the other three leaves in four days. The chips were greatly softened, almost liquefied, but not nearly all dissolved. The glands which had been in contact with them, instead of being much blackened, were of a very pale colour, and many of them were evidently killed.

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