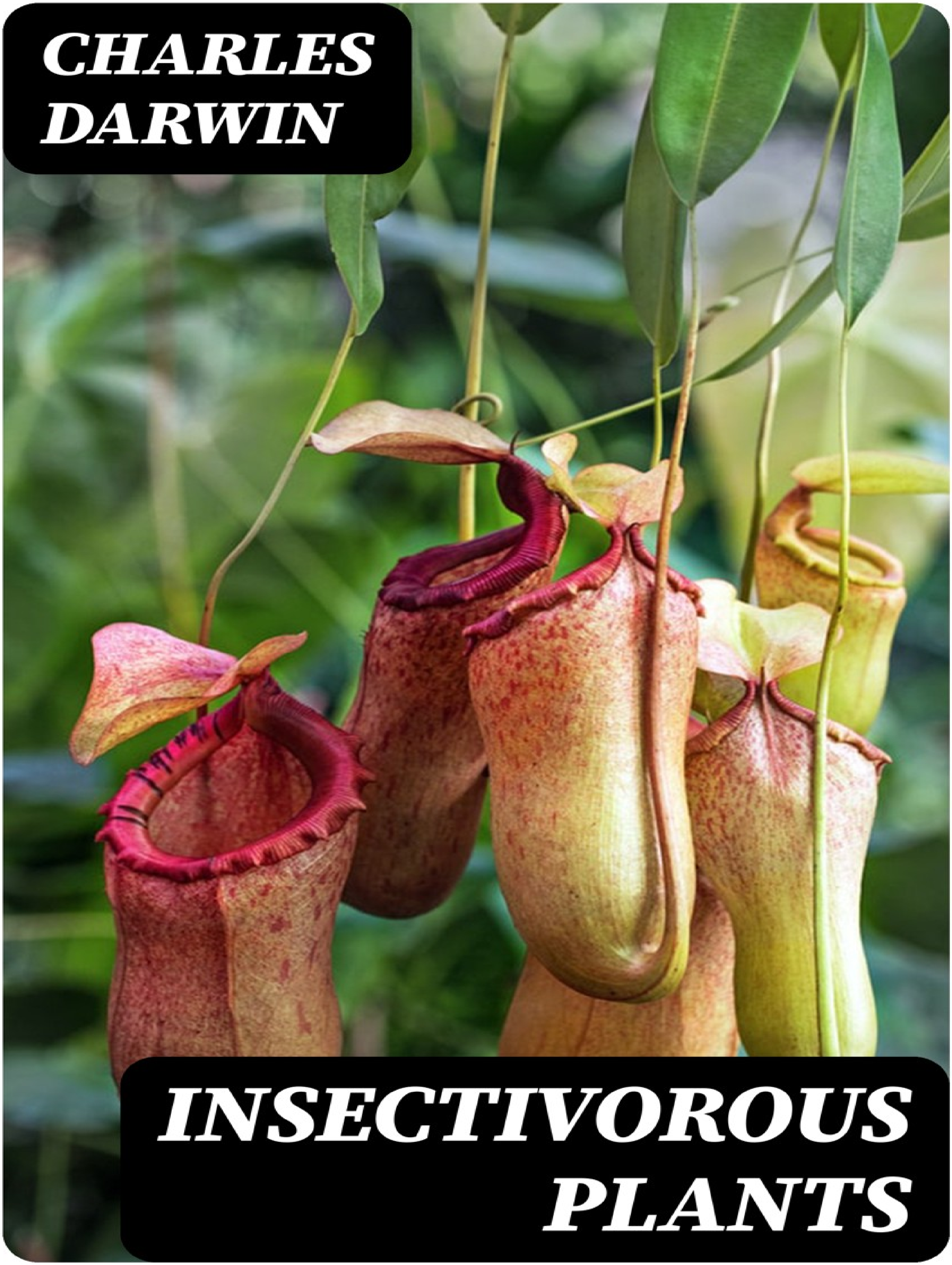
CHARLES DARWIN
INSECTIVOROUS PLANTS

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Insectivorous Plants

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CHAPTER I. DROSERA ROTUNDIFOLIA, OR THE COMMON SUN-DEW.

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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.* I

* 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, [[page 2]] 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. [page 2]

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 [page 3] 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

FIG. 1.* (Drosera rotundifolia.) Leaf viewed from above; enlarged four times.

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;

* The drawings of Drosera and Dionaea, given in this work, were made for me by my son George Darwin; those of Aldrovanda, and of the several species of Utricularia, by my son Francis. They have been excellently reproduced on wood by Mr. Cooper, 188 Strand. [page 4]

secondly, the power possessed 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,

FIG. 2. (Drosera rotundifolia.) Old leaf viewed laterally; enlarged about five times.

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 [page 5] 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.* 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

* 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 Diffrence 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. [page 6]

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

FIG. 3. (Drosera rotundifolia.) Longitudinal section of a gland; greatly magnified. From Dr. Warming.

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. [page 7] Within this layer of cells there is an inner one of differently shaped 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 [page 8] 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 Nitschke* 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 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.]

* Nitschke has elaborately described and figured these papillae, 'Bot. Zeitung,' 1861, pp. 234, 253, 254. [page 9]

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,* 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.

* 'Bot. Zeitung,' 1860, p. 246. [page 10]

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 180o; and I have seen the much reflected tentacles of a leaf which stood upright move through an angle of not less than 270o. The bending part is almost confined to a short space near the base; but a rather larger portion of the elongated exterior tentacles

FIG. 4. (Drosera rotundifolia.) Leaf (enlarged) with all the tentacles closely inflected, from immersion in a solution of phosphate of ammonia (one part to 87,500 of water.)

FIG. 5. (Drosera rotundifolia.) Leaf (enlarged) with the tentacles on one side inflected over a bit of meat placed on the disc.

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 [page 11] 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

FIG. 6. (Drosera rotundifolia.) Diagram showing one of the exterior tentacles closely inflected; the two adjoining ones in their ordinary position.)

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 [page 12] 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 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 [page 13] 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 [page 14] 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 [page

15] 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 [page 16] 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