INSECTIVOROUS PLANTS.

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.* 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. Grœnland and Trécul each published papers, with figures, on the structure of the leaves; but M. Trécul 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 Dec. 11, 1862, Mr. J. Scott read a paper before the Botanical Society of Edinburgh,

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 (*Cænonympha 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 (*Æsculus hippocastanum*), without thereby receiving, as far as we can perceive, any advantage; but it was soon evident that Drosera was

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which was published in the Gardener's 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 Différence 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 Dionæa, 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 Dionæa 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.

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

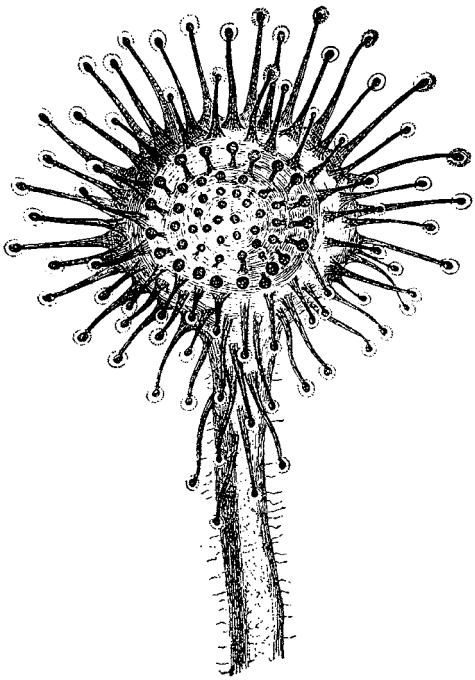

FIG. 1.*
(*Drosera rotundifolia.*)
Leaf viewed from above; enlarged four times.

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 Dionæa, 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.

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,

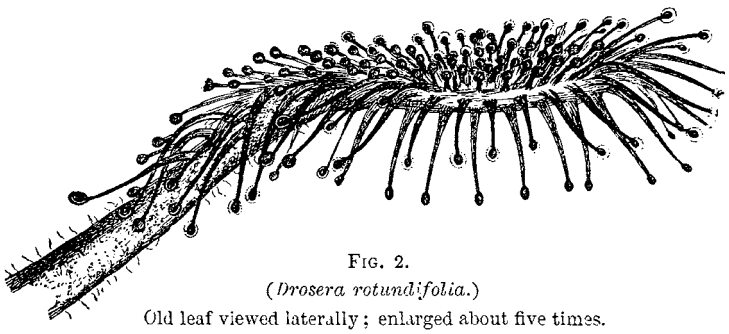

FIG. 2.
(*Drosera rotundifolia.*)
Old leaf viewed laterally; enlarged about five times.

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

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 $\frac{1}{4}$ 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 Différence entre les Trichomes,' &c., 1873), who gives references to various publications. See also Grœnland and Trécul, 'Annal. des Sc. nat. bot.' (4th series), tom. iii. 1855, pp. 297 and 303.

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 $\frac{4}{500}$ 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 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 the 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 Droseraceæ.

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 papillæ (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 papillæ 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 papillæ, are probably rudiments of formerly existing tentacles.

I may here add, in order not to recur to the papillæ, 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 papillæ 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 papillæ 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 papillæ, 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 papillæ on the backs of the leaves or on the petioles.

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

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.

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

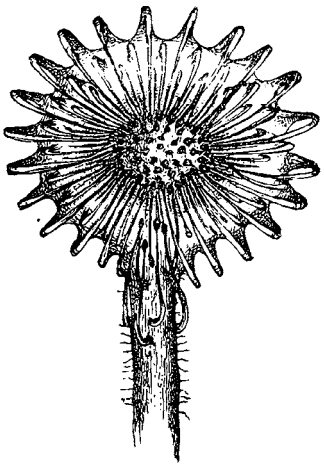

FIG. 4.

(*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).

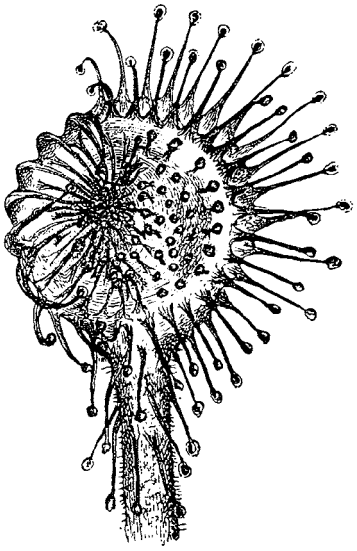

FIG. 5.

(*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