IX.—THE STRUCTURE AND HABITS OF CARNIVOROUS PLANTS.

By Mr A. D. RICHARDSON.

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To sustain plants in a healthy condition, a supply of nitrogen is essential. Although that element forms nearly four-fifths of the air we breathe, plants have no power of taking it in from the atmosphere in a free or uncombined state. The source from which they derive their supply is the nitrates and salts of ammonia contained in the soil in which they grow, and the medium through which it is conveyed into the substance of the plant is the root. In some plants, however (the so-called Insectivorous or Carnivorous plants), the roots are so feebly developed that they are quite inadequate to fulfil all the functions which they perform in ordinary cases; and in these plants all or part of the leaves are modified for the purpose of capturing insects and other small animals, from the absorption of which they are able to supplement their otherwise defective nitrogenous supply.

Carnivorous plants are of two kinds,—viz., 1st, those in which there is a true digestive process; and, 2d, those in which there is merely decomposition and absorption of the liquid products. To the first group belong Drosera, Dionæa, Pinguicula, Nepenthes, and Cephalotus; and to the second, Sarracenia, Darlingtonia, and Utricularia.[1] We shall consider several members of these two groups, taking up in order, in the first, Drosera and Dionæa (*Droseraceæ*), Pinguicula (*Lentibuliariaceæ*), and Nepenthes (*Nepenthaceæ*); and in the second, Sarracenia (*Sarraceniaceæ*) and Utricularia (*Lentibuliariaceæ*).

Drosera.

This genus is distributed over the temperate parts of nearly the whole world, the plants generally inhabiting marshy or boggy ground. In Drosera rotundifolia, the plant consists of a spreading rosette of radical leaves, from the centre of which one or more flower-stalks spring. Each leaf consists of a round leaf-blade supported on a leaf-stalk, and the upper surface of the blade is beset with numerous hair-like structures, with glandular knobs, to which Mr Darwin has applied the term "tentacles." Each tentacle consists of a stalk, at the extremity of which is a glandular knob surrounded by an extremely viscid fluid secretion, which, from its glittering in the sun, has given the plant the poetical name of "Sundew." In the centre of the leaf-blade the tentacles are short and erect, but towards the margin they get longer and more inclined outwards. A fibro-vascular bundle, consisting of a spiral vessel with some simpler tissues, runs in the interior of the stalk of each tentacle, these elements being continuations of the fibro-vascular system of the leaf. The glands consist of two outer layers of small cells, which are filled with purple granular matter or fluid; and in the centre are a number of elongated cylindrical spiral cells, which seem to be connected with the spiral vessel of the stalk.

Fully more than a century ago, the discovery was made by two

[1] There are a few other genera in both groups, but most of them are not as yet in cultivation. These are, in the first group, Drosophyllum, Byblis, and Roridula; and in the second, Aldrovanda and Heliamphora.

persons, the one a German (Roth, 1779) and the other an Englishman (Whately, 1780), that the tentacles were sensitive, and that insects were imprisoned by the leaves. These observations were confirmed by another German observer (Nitschke) in 1860; by an American lady (Mrs Treat) in 1871; and the subject has been carefully worked out in this country by Mr Darwin and others. If a small object be placed on the short tentacles in the centre of the leaf, a motor impulse is conveyed to the surrounding ones, which become inflected over it, those nearest the centre becoming first bent, and then those further off, until the whole of them are closely inflected over the object. The tentacles in the centre of the leaf do not bend in this case, but remain in their original erect position. Should the object be placed on the glands away from the centre of the leaf, however, the short tentacles of the centre become bent towards the point of excitement, through a motor impulse being conveyed to them from the excited glands. When a very minute particle of meat is placed on one of the long exterior tentacles, it bends towards the centre of the leaf, while those surrounding it retain their original position. If the object be not too minute, and especially if it contains soluble nitrogenous material, immediately it comes in contact with the glands of the central tentacles a motor impulse is transmitted to the surrounding tentacles, which all bend towards the centre.

It is astonishing how minute an object will cause the tentacles to bend. Darwin found that a bit of blotting-paper weighing $\frac{1}{465}$ of a grain, placed in contact with three glands, caused them to curve slowly inwards. A bit of cotton-thread $\frac{1}{50}$ of an inch in length, and weighing $\frac{1}{8197}$ of a grain, was next placed on a tentacle, and was carried to the centre in 1 h. 40 m. Two particles of the thinner end of a human hair, one being $\frac{18}{1000}$ of an inch in length, and weighing $\frac{1}{35,714}$ of a grain, the other $\frac{19}{1000}$ of an inch in length, and weighing a little more, were placed on glands on opposite sides of the same leaf, and these two tentacles were inflected half-way towards the centre of the leaf in 1 h. 10 m., all the other tentacles round the same leaf remaining motionless. The smallest particle which was tried, and which caused the tentacle to bend, was only $\frac{8}{1000}$ of an inch in length, and weighed $\frac{1}{78,740}$ of a grain.

Darwin's surprise was greatly excited not only by the minuteness of the objects which caused inflection, but as to how they could possibly act on the glands; for he found that small drops of water many times heavier than the particles which were placed on them, although repeatedly added, produced no effect. Neither did 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. If repeatedly touched or brushed, however, although no object was left upon them, the marginal glands curved inwards. It would appear, from what Darwin has been able to make out, that an object must come in contact not only with the secretion surrounding the gland, but with the gland itself; and this is brought about by the object absorbing the secretion, and thus sinking through it to the surface of the gland. Particles which merely rest on the secretion, and do not come into actual contact with the gland, never produce any effect; and the same may be said of one or more contacts with any hard substance. Excessively small doses of certain organic fluids and saline solutions cause strongly marked inflection. Darwin found that the phosphate of ammonia was by far the most powerful in causing this. When a leaf was immersed in thirty minims of a solution of one part by weight of the salt to 21,875,000 parts of water, the absorption of the twenty-millionth of a grain by a gland was sufficient to cause the tentacle bearing it to curve to the centre of the leaf. The amount of heat which the leaves will stand without being injured is also remarkable. Darwin found that when they were immersed in water at a temperature of between 115° and 125° Fahr. they were quickly inflected, and the protoplasm became aggregated; but when afterwards placed in cold water, they slowly expanded. When exposed to a temperature of 130°, inflection did not immediately take place; but when afterwards placed in cold water, they often became inflected, and then re-expanded. When placed in cold water after exposure to a temperature of 145°, they sometimes became slightly though slowly inflected; but when placed in water at a temperature of 150° for a short time, they were killed.

The secretion surrounding the glands is extremely viscid, so that an insect alighting on the leaf is immediately entangled amongst the glands, which, on becoming excited, transmit a motor impulse to all the surrounding tentacles, which immediately bend over and soon kill it. The time during which the tentacles remain inflected depends on the age and vigour of the leaf, and Darwin mentions that they so remain for a much longer time over soluble nitrogenous substances than over those which yield no such matter. The time varies from one to seven days, and he states that he has seen the glands of the same leaf inflected three successive times over insects placed on the disc. The leaves are more quickly inflected over animal substances, and they remain so for a longer time during very warm weather than during cold weather. A living insect is more efficient in causing inflection than a dead one, as it struggles and presses against the glands of many tentacles; and an insect such as a fly, with thin integuments, is more efficient in causing prolonged inflection than a beetle with a thick coat.

When an organic or inorganic object is placed on certain glands of a leaf, the secretion from the other glands is increased in quantity, and becomes acid, and this takes place before they come in contact with the object. At the same time, a remarkable movement of the protoplasm takes place, first within the cells of the glands and then within those of the pedicels. This movement Darwin calls "aggregation." When this takes place the cells present a different appearance. Instead of being filled with a homogeneous purple fluid, they now contain variously shaped masses of purple matter suspended in a colourless or almost colourless fluid. The secretion appears to possess, like the gastric juice of the higher animals, some antiseptic power. During warm weather Darwin placed two equal-sized bits of raw meat, one on a leaf and the other on wet moss. After forty-eight hours, that on the moss swarmed with infusoria, while that on the leaf was quite free from them. Small cubes of albumen placed in similar circumstances showed that those placed on the moss became threaded with mould, while those on the leaves remained clear, and were changed into a transparent jelly.

Although the leaves appear at a glance to be of a reddish colour, they nevertheless contain chlorophyll in their petioles, both surfaces of the blade, and the pedicels of the tentacles, so that they are able to decompose the carbonic acid of the air; but owing to their feeble root-development, the plants would not be able to obtain a sufficient supply of nitrogen if they had not the power of obtaining that important element from captured insects. Many plants entrap insects without apparently deriving any benefit—*e. g.*, the sticky buds of Horse-chestnut and the leaves of Saxifraga tridactylites; but Francis Darwin has proved beyond doubt that Drosera derives benefit from the insects which it captures. He grew two lots of plants under similar conditions: one lot he fed with nitrogenous substances, while from the other all such material was carefully excluded. The number of seeds produced by the fed plants was as 240 to 100 of the unfed ones; while the weight was as 380 to 100. The number and weight of the flower-stalks and seed-capsules were also in favour of the fed plants.

DIONÆA.

Dionæa muscipula is confined to the eastern part of North Carolina, where it inhabits damp situations. From the rapidity with which it closes its leaves, it has received the name of "Venus's Fly-trap." The leaf-blade is bilobed, and the petiole is foliaceous. The lobes of the blade stand at rather less than a right angle to each other, and the edges are set round with bristle-like projections, which interlace like the teeth of a rat-trap when the leaf closes. The upper surface of each lobe, towards the midrib, is thickly covered with minute red glands, which give it a rosy appearance, and the lobe also bears three erect sensitive filaments arranged in a triangular manner. The filaments are further provided with a joint or hinge near the base, so that when the leaf closes they fold down, and thus escape injury.

In 1768 an English naturalist named Ellis sent a drawing of this plant to Linnæus, along with a description of it, in which he suggested that Nature might have a view to furnishing the plant with nourishment in forming the upper joint of its leaf like a machine for catching food. He went on to state that minute red glands discharged a sweet liquor, which acted as a lure to insects, which, the moment they touched them with their feet, caused the leaf to close instantly and squeeze them to death; and that if the insects were strong, three erect spines fixed amongst the glands effectively put an end to their struggles. The movement described by Ellis is substantially correct, but he made an error in stating that the glands were sensitive, and that the erect spines played an important part in putting an insect to death. His description, however, failed to convince Linnæus that there was anything more in it than a case of extreme sensitiveness. That the sensitiveness resided in the hairs was discovered first by an English botanical draughtsman named Edwards, and subsequently by Dr Curtis, who published an account of it in the 'Boston Journal of Natural History' in 1834; and in the same account Dr Curtis states that the secretion is not a lure, but a true digestive fluid poured out after capture. The hairs are sensitive over their whole surface, so that an insect alighting on the leaf is almost certain to cause it to close. When touched, a motor impulse is conveyed from the excited hair through the cellular tissue of the leaf-blade to the midrib, the result being that the lobes instantly close. This closing, however, is not at first perfect, the teeth only slightly interlacing, so that if the insect be small it is allowed to escape; but if the insect is large, the glands are induced to secrete and absorb the animal matter, which, according to Darwin, has the effect of causing the lobes to press closely against the body of the insect. The pressure is often so great that the outline of the body of the insect can be seen on the outside of the leaf. These hairs are extremely sensitive to a momentary touch. Darwin found that a piece of human hair 2½ inches long, held dangling over one of them so as to touch it, produced no movement, but a rather thick cotton thread of the same length caused the lobes to close. It would appear, however, that although these hairs are more sensitive to a momentary touch, they are far less sensitive to prolonged pressure than the tentacles of Drosera. A piece of human hair ten times the length of that which caused the tentacles of Drosera to bend, when cautiously placed on one of the hairs produced no movement, although in the case of Drosera they were supported by the dense secretion.

When the lobes are induced to close by mechanically touching the sensitive hairs, they remain closed only a short time; but when an insect is caught, they remain closed for many days, and Darwin mentions a case where the leaf remained closed for thirty-five days over a large Tipula. On an insect or other animal substance being thus entrapped by a leaf, the peptic glands on the upper surface of the lobes pour out an acid secretion immediately the animal matter comes in contact with them. Moist nitrogenous substances, when placed on the glands of a leaf, even although the sensitive hairs are not touched, not only cause the glands to secrete, but the lobes slowly close.

Pinguicula.

The species of this genus are distributed principally over the north-temperate regions, and are mostly inhabitants of moist mountainous places. In P. vulgaris (Common Butterwort,—so called from its power of coagulating milk) the leaves are oblong, sessile, of a pale-green colour, and form a spreading rosette, from the centre of which the flower-stalks spring. Their margins are slightly incurved, and their upper surfaces are thickly beset with stalked and sessile glands: these secrete a viscid, colourless fluid, which can be drawn out into long threads. When the glands are excited by the pressure of an object, the margins curve inwards; but drops of water, or mere irritation of the surface without continuous pressure, produce no movement. Darwin found that the pressure of fragments of glass produced incurvation as soon as nitrogenous matter, but in a less degree. A motor impulse does not appear to be conveyed to the other glands when any individual one is irritated; for although the excited gland may secrete copiously, the others remain passive. Darwin found that although fragments of glass produced incurvation, they caused little or no secretion; but when a solution of carbonate of ammonia was applied, there was increase of the secretion, but no movement. It would thus appear that the secretion and movement take place independently of each other. The shortest time in which Darwin observed plainly marked incurvation was 2 h. 17 m.; and the longest time during which a leaf remained incurved was less than 48 h. In the majority of cases they had re-expanded in 24 h. The use of this incurvation is apparent, as insects are washed into the incurved margins by rain, and are thus, by the rolling in of the margins upon them, brought into contact with a greater number of glands, which are thus induced to secrete more freely. When Darwin placed large pieces of meat on the leaves, he observed that they were not embraced, but were pushed in by the incurving margins towards the centre of the leaf, in some cases as much as $\frac{1}{10}$ of an inch. The use of this pushing he conjectured was to bring large insects into contact with as many glands as possible. The incurving of the margins also serves another purpose. When many glands are induced to secrete, the secretion trickles down and is caught in the incurved margins, so that insects are more quickly and completely dissolved there than on any other part of the leaf. Insoluble substances, such as bits of glass, have little or no power of causing secretion from the glands; but non-nitrogenous fluids cause them to secrete freely. The secretion in this case, however, is not acid. Nitrogenous substances, on the other hand, cause an increased flow of the secretion, which is invariably acid, and in this state it has the power of digesting insects or other animal matter. Before absorption of animal matter, the glands are green; but after that takes place, the protoplasm contained in them becomes aggregated, and of a brown colour.

Nepenthes.

The species belonging to this genus are upwards of thirty in number, and are, with a few exceptions, natives of swamps in the hotter parts of the Asiatic archipelago. They are half-shrubby plants, and climb by the aid of their leaves, which have the power of coiling or twisting themselves round supporting objects. The leaves are metamorphosed as flattened expansions, which narrow into long tendril-like bodies, at the extremities of which the pitchers are developed. These pitchers are often highly coloured, and generally contain a fluid, into which insects, and sometimes even small quadrupeds or birds, find their way. The pitchers vary in size from an inch or two to nearly a foot in length, and one species at least has them no less than eighteen inches long.

The minute structure of the interior of the pitcher is of a very complicated nature. It presents three distinct surfaces. The first is the "attractive" surface, which occupies the inside of the lid and the mouth of the pitcher. The inside of the lid is in most species studded over with honey-secreting glands. These consist of masses of cells embedded in depressions of the cellular tissue of the lid, and each is surrounded by a ring of guard-cells. Round the mouth of the pitcher is a corrugated rim, which projects into the cavity, and which helps to keep the mouth distended, and the corrugations are often prolonged as sharp downward-directed teeth. Hooker observed that the rim secreted honey; and it has been discovered recently by Professor Dickson that a circlet of glands is present in it. These glands alternate with the corrugations of the rim, and open into the pitcher a little above its lower edge. They are of enormous length (in some cases $\frac{1}{12}$ of an inch) compared with the other glands found in the pitcher, but are comparatively narrow. They are embedded in the tissue of the rim, and open into the pitcher cavity by short canals. Next comes the "conductive" surface, which occupies a variable portion of the upper part of the interior of the pitcher. This surface is composed of smooth glassy cells, which afford no foothold to insects, and it is generally studded over with minute reniform or crescentic ledges. The remainder of the interior of the pitcher is occupied by the "secretive" surface. This is thickly covered with glands resembling those of the lid, but the depressions in which they are lodged have their concavities directed downwards, resembling much in appearance inverted waistcoat-pockets. Hooker mentions that in N. Rafflesiana 3000 of these glands occur in a square inch. A fluid is formed at the bottom of the pitcher which is secreted by these glands, and is present before the lid of the pitcher opens.

Insects are induced to visit the pitcher for the sake of the honey secreted by the lid and the corrugated rim, and in doing so they are apt either to fall into the pitcher or to be led on to the conductive surface, down which they glide till they reach the fluid secretion, by which they are effectually "detained." Hooker states that the fluid is invariably present, and that when emptied out of a pitcher which has not received animal matter, it collects again in small quantities, the formation going on for days, and even to some extent after the pitcher has been removed from the plant. He did not find that inorganic substances produced an increased flow of the secretion; but when animal substances were placed in the fluid, there was a marked increase. The fluid is always acid, even before the opening of the pitcher, and it seems to have the same digestive properties as Drosera, Dionæa, and Pinguicula. It would appear, however, that the digestive power of the fluid is not due entirely to the fluid first secreted by the pitcher, but that a substance resembling pepsine in its action is given off from its inner wall, chiefly after the placing of animal matter in the fluid. In support of this idea, Hooker states that very little action took place on any of the substances placed in the fluid drawn from pitchers and deposited in a glass tube, although the disintegration of the substances was three times more rapid in the fluid than in distilled water. On the other hand, substances placed in the fluid in the living pitchers were acted on in a very rapid manner. Cubes of boiled egg had their edges dissolved in 24 hours, and their surfaces gelatinised. Fragments of fibrine weighing several grains were dissolved, and totally disappeared in two or three days; while lumps of cartilage weighing 8 to 10 grains were greatly diminished, and reduced to a transparent jelly in three days.

Sarracenia.

This genus consists of eight species, all of which are natives of the eastern States of North America, where they are found growing in marshes. The leaves are funnel-shaped, and spring from the ground in tufts. The plants send up long slender stalks in the flowering season, each of which bears a solitary flower of a remarkable appearance, due to the termination of the style in an umbrella-like expansion, which caused the first English settlers to give it the name of "Side-saddle flower." There are two distinct forms of pitcher. Into one form rain enters easily; into the other, with difficulty. In the first form, of which S. purpurea may be taken as the type, the lid is either erect, or thrown back so as to direct all the rain that falls upon it into the pitcher; and in the second, of which S. variolaris may be taken as the type, the lid is thrown somewhat forward, so as to prevent the rain from entering. The pitchers generally contain water, and it was supposed by Catesby that these receptacles served as a secure retreat for insects from Frogs and other animals which feed upon them; and by Linnæus and others, that they served as water-reservoirs for birds and other animals, especially in dry weather. This idea probably originated from the fact that some birds slit open the pitchers with their beaks; but the probability is that these birds slit open the pitchers to get at the larvæ of insects which have dropped their eggs amongst the mass of decaying organic matter, where they would get suitable nourishment.

It was Linnæus who first made the suggestion, which has since been worked out in detail by Baillon, that the pitchers of Sarracenia are analogous to the leaves of Water-lilies; and he supposed that they were originally aquatic in their habits, and had Nymphæa-like leaves, but that they afterwards took to terrestrial habits, and their leaves became hollowed out to contain the water in which they could not float. The pitcher-lid would thus represent the apex of the leaf. The internal structure of the pitchers is exceedingly beautiful, and in most species presents, like Nepenthes, three distinct surfaces. The first is the "attractive" surface, which occupies the inner part of the lid and the mouth of the pitcher. The lid is often more highly coloured than the rest of the pitcher, and, in common with the mouth, is studded over with honey-secreting glands. These glands are also found on the outside of the pitcher. The epidermis cells of the inner surface of the lid are wavy in outline, and many of them are prolonged on their free surface into sharp downward-directed hairs. Occupying the upper part of the inner surface of the pitcher proper, and extending some distance down its cavity, is the "conducting" surface. In this each epidermis cell is prolonged downwards into a short, glassy, sharp-pointed hair, which is finely striated. These hairs overlap like the tiles of a house, and they thus afford no foothold to insects. The whole of the cavity of the pitcher below the conducting surface is occupied by the "detentive" surface. In this many of the epidermis cells are prolonged into enormously elongated downward-directed hairs, which increase in length towards the bottom of the pitcher; and as the cavity diminishes in width, they meet in the centre, and thus completely prevent the escape of any insect which may have been lured into it. Secreting glands are embedded in the detentive surface of all the species with the exception of S. purpurea. In this species, however, there is a special glandular surface which occupies a portion of the wall of the pitcher between the conducting and detentive surfaces. The epidermis cells of this surface are wavy in outline, and embedded amongst them are numerous secreting glands.

Insects are induced to visit the honey secretion of the lid and mouth of the pitcher, and are thus led on to the conducting surface. This affords no foothold, and they glide down till they reach the detentive surface. When once amongst the hairs of this part of the pitcher, there is no possibility of returning, their struggles only serving to wedge them deeper and more firmly. The secretion "wets" an insect much more rapidly than water: but it apparently has no digestive properties, appearing rather to hasten decomposition. The broad wing of the pitcher is also said to be baited with honey, so as to lure insects to their destruction by presenting a pathway from the ground.

Utricularia.

The British species of this genus are all aquatic, but some exotic species are terrestrial. The aquatic plants are entirely destitute of roots, and the submerged stem and branches are clothed with leaves, which are dissected up into slender filiform segments; and on these segments numerous little bladders or ampullæ are developed. The leaves are tipped with short straight bristles. The plants float near the surface of the water, above which they send their flowers supported on slender stalks.

In U. vulgaris the bladders are supported on short footstalks, and are about $\frac{1}{10}$ of an inch in length. They are generally filled with water, but sometimes they contain air-bubbles. At the apex is a small orifice, around which are a number of hair-like prolongations called antennæ. On the inside of this orifice is a small hemispherical valve, which shuts against the rim or collar of the orifice. The valve is elastic, and can be pushed back by a small insect, which thus easily finds admission to the inside of the bladder. When once in, there is no chance of its getting out, for the valve springs back against the collar and completely closes the entrance. All over the interior of the bladder small processes called "quadrifids" are placed. These consist of very short stalks, which spring from angular cells at the junctions of the angles of the larger cells; and at their apices four arm-like processes are developed, each of which consists of a single cell. In U. vulgaris two of these arms are long and two short, but in U. montana they are all nearly of the same length. The bladders were supposed by some to act as floats; but as they seldom contain air, it is probable that the plants are floated up by the air contained in the intercellular spaces. The real use of the bladder is to capture small insects, which they do in great numbers. As already mentioned, they enter the bladder by pushing back the valve; and the free edge of this is so thin, and shuts so closely against the collar, that a Daphnia which Darwin mentions as having inserted one of its antennæ into the slit was held fast for a whole day. The insects captured are all small water-insects, such as Cyclops, &c.; and, as in

Sarracenia, they are not digested, but simply undergo decomposition. The quadrifid hairs are supposed to be the active agents in the absorption of the liquid products.

Such is a short survey of a few of these most interesting plants. While their general structure includes them in the Vegetable Kingdom, their habits, in some respects, are curiously allied to those of the members of the Animal Kingdom. It is only of recent years that these habits have been investigated and understood, principally through the laborious and painstaking experiments of Darwin, Hooker, and others, in this country. Now that attention has so largely been drawn to them, and so many workers have entered on the task of their further elucidation, even more startling facts than any yet discovered may some day be brought to light.

[In illustration of the above, a number of microscopic preparations were shown, which included the minute structure of most of the plants enumerated and described.]