INSECTIVOROUS PLANTS. Insectivorous or, as they are sometimes more correctly termed, carnivorous plants are, like the parasites, the climbers, or the succulents, a physiological assemblage belonging to a number of distinct natural orders. They agree in the extraordinary habit of adding to the supplies of nitrogenous material afforded them in common with other plants by the soil and atmosphere, by the capture and consumption of insects and other small animals. The curious and varied mechanical arrangements by which these supplies of animal food are obtained, the ways and degrees in which they are utilized, and the remarkable chemical, histological, and electrical phenomena which accompany these processes of prehension and utilization, can only be understood by a separate and somewhat detailed examination of the leading orders and genera. It is convenient to follow the order adopted by Mr Darwin in his work on *Insectivorous Plants* (Lond., 1875), to which our knowledge of the subject is mainly due, incorporating, however, as far as possible the leading observations of other writers on the subject. We must preface this, however, by a brief summary of the facts of taxonomy and distribution.

Taxonomy.—The best known and most important order—the *Droseraceæ*—is placed among the calycifloral exogens, and has obvious affinities with the *Saxifragaceæ*. It includes six genera—*Byblis*, *Roridula*, *Drosera*, *Drosophyllum*, *Aldrovanda*, and *Dionæa*, of which the last three are monotypic, *i.e.*, include only one species. The curious pitcher-plant, *Cephalotus follicularis*, is usually raised to the dignity of a separate natural order *Cephaloteæ*, though Bentham and Hooker (*Gen. Plant.*) place it among the *Ribesiaceæ*. The *Sarraceniaceæ* are thalamiflorals, and contain the genera *Sarracenia*, *Darlingtonia*, *Heliamphora*, while the true pitcher plants or *Nepenthaceæ*, consisting of the single large genus *Nepenthes*, are placed near the *Aristolochiaceæ* among the *Apetalæ*. Finally the genera *Pinguicula*, *Utricularia*, *Genlisea*, and *Polypompholix* belong to the gamopetalous order *Utricularia*. Thus all the four leading divisions of the exogenous plants are represented by apparently unrelated orders; certain affinities, however, are alleged between *Droseraceæ*, *Sarraceniaceæ*, and *Nepenthaceæ*.

Distribution.—While the large genus *Drosera* has an all but world-wide distribution, its congeners are restricted to well-defined and usually comparatively small areas. Thus *Drosophyllum* occurs only in Portugal and Morocco, *Byblis* in tropical Australia, and, although *Aldrovanda* is found in Queensland, in Bengal, and in Europe, a wide distribution explained by its aquatic habit, *Dionæa* is restricted to a few localities in North and South Carolina, mainly around Wilmington. *Cephalotus* occurs only near Albany in Western Australia, *Heliamphora* on the Roraima Mountains in Venezuela, *Darlingtonia* on the Sierra Nevada of California, and these three genera too are as yet monotypic; of *Sarracenia*, however, there are six or eight known species scattered over the eastern States of North America. The 36 species of *Nepenthes* are mostly natives of the hotter parts of the Indian Archipelago, but a few range into Ceylon, Bengal, Cochin China, and some even occur in tropical Australia on the one hand, and in the Seychelles and Madagascar on the other. *Pinguicula* is abundant in the north temperate zone, and ranges down the Andes as far as Patagonia; the 150 species of *Utricularia* are mostly aquatic, and some are found in all save polar regions; their unimportant congeners, *Genlisea* and *Polypompholix*, occur in tropical America and south-western Australia respectively. It is remarkable that all the insectivorous plants agree in inhabiting damp heaths, bogs, marshes, and similar situations where water is abundant,—a peculiarity perhaps due to their habit of copious secretion and consequent need of water.

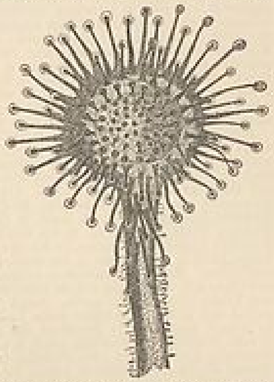


FIG. 1.—Leaf of Sundew (*Drosera rotundifolia*). ×4. (After Darwin.)

Drosera.—The Common Sundew (*D. rotundifolia*) has extremely small roots, and bears five or six radical leaves horizontally extended in a rosette around the flowerstalk. The upper surface of each leaf is covered with gland-bearing filaments or "tentacles," of which there are on an average about two hundred. Each gland is surrounded by a large dew-like drop of a viscid but transparent and glittering secretion, and the popular names (Sundew, French *Rossolis*, German *Sonnenthau*) as well as the Linnæan (from δρόσος, dew) have been thus suggested. The stalk of the tentacle has the essential structure of a leaf. A small fibro-vascular bundle, consisting mainly of spiral vessels, runs up through the stalk and is surrounded by a

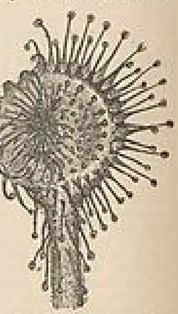


FIG. 2.—Leaf of Sundew, enlarged, with the tentacles on one side inflected over a bit of meat placed on the disk. (After Darwin.)

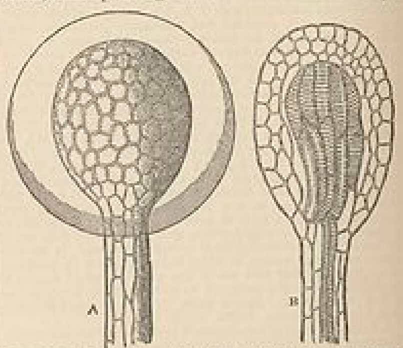


FIG. 3.—Glands of Sundew magnified. (After Dodel-Port.) A, external aspect with drop of secretion; B, internal structure.

layer of elongated parenchyma cells lined by a thin layer of colourless circulating protoplasm, and filled with a homogeneous fluid, tinted purple by a modification of chlorophyll (erythrophyll, Sorby). The epidermis bears small multicellular prominences. The glandular head of the tentacle contains a central mass of spirally thickened cells in immediate contact with the upper end of the fibro-vascular bundle. Around these (but separated from them by a layer of much elongated cells, Warming) there is a layer of cells filled with purple fluid, and outside these lies a similar series of cells, whose contents differ slightly in tinge, and in behaviour when treated with reagents.

Insects seem to be attracted by the leaves of *Drosera*, but whether by their colour, their glittering secretion, their odour, or by all three, remains as yet unsettled. A fly alighting on the disk, or even only touching one or two of the exterior tentacles, is immediately entangled by the viscid secretion; the tentacles to which it is adhering begin to bend, and thus pass on their prey to the tentacles next succeeding them inwards, and the insect is thus carried by a curious rolling movement to the centre of the leaf. The tentacles on all sides become similarly inflected; the blade or the leaf may even become almost cup-shaped; and the insect, bathed in the abundant secretion which soon closes up its tracheæ, is drowned in about a quarter of an hour. The leaves clasp also, but for a much shorter time, over inorganic bodies.

The bending of the tentacle takes place near its base, and may be excited (1) by repeated touches, although not by gusts of wind or drops of rain, thus saving the plant from much useless movement; (2) by contact with any solid, even though insoluble and of far greater minuteness than could be appreciated by our sense of touch,—a morsel of human hair weighing only $\frac{1}{78740}$ of a grain, and this largely supported too by the viscid secretion, sufficing to induce movement; (3) by the absorption of a trace of certain fluids, mostly nitrogenous. During the inflexion of the tentacle, and even before it touches the stimulating object, the secretion of the gland increases in quantity, and, instead of remaining neutral, becomes acid.

The stalk of a tentacle whose gland has been stimulated by repeated shocks, continuous pressure, or the absorption of any nitrogenous fluid, particularly a solution of ammonic carbonate, shows a mottled appearance; and, when examined under the microscope the formerly homogeneous fluid contents of its constituent cells are seen to have separated into purple masses of constantly varying number, shape, and size, suspended in a colourless fluid, and the layer of colourless circulating protoplasm which lines the cells thus becomes much more distinctly visible. This process, which is termed by Darwin "aggregation of the protoplasm," commences in the glands and gradually travels down the tentacles, being temporarily arrested at each cell-wall. The process of redissolution of the protoplasm commences at the base of the tentacles and proceeds upwards. Aggregation is a vital process: the cells must

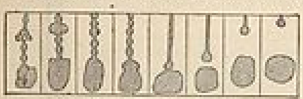


FIG. 4.—Diagram of the same cell of a tentacle of *D. rotundifolia*, showing the various forms successively assumed by the aggregated masses of protoplasm. (After Darwin.)

be alive, uninjured, and oxygenated; if they are crushed or treated with carbonic acid the phenomenon does not take place. It is not necessarily related to inflexion, for one may be induced without the other; it is totally unlike the "plasmolysis," or shrinking away of the protoplasm from the cell-wall, which takes place on treating a portion of vegetable tissue with any dense fluid, and which is simply due to exosmose; and it does not depend upon increased secretion. Darwin has also observed aggregation in the sensitive hairs of *Dionæa*, and in the roots of various plants; it seems indeed to be of wide distribution and profound importance in the physiology of the vegetable cell.

Effects of Heat.—Sachs asserts that plants are killed by immersion for ten minutes in water at 45° to 46° C., and that their protoplasm coagulates at 50° or 60°. Darwin, however, found that the immersion of leaves of *Drosera* for ten minutes in water at 50°, instead of killing the leaves, excited the tentacles into quick movement, that a temperature of 54°·4 paralysed the leaves without killing them, and that some even survived a temperature of 62° C. Some of the lowest plants have frequently been described as living in hot springs, but that so highly organized a native of temperate and even almost arctic regions should withstand so high a temperature is very remarkable.

Action of Ammonia Salts.—All the salts of ammonia produce inflexion, the carbonate strongly, the nitrate even more so, and the phosphate most of all. The immersion of a leaf in a solution of the last-mentioned salt, so weak that each gland could only absorb about $\frac{1}{20000000}$ of a grain, is sufficient to produce complete inflexion of the tentacles. Though the particles of solid matter which stimulate the olfactory nerves, and so produce the sensation of odour in animals, must be infinitely smaller than this, as Mr Darwin remarks, the fact remains truly wonderful that the absorption of so minute a quantity by a gland should induce some change in it, which leads to the transmission of a motor impulse down the entire length of the tentacle, causing the whole mass to bend, often through an angle of more than 180°, and this too in the absence of any specialized nervous system.

Action of various Salts and Acids.—In the case of salts the nature of the base seems to be of much more importance than that of the acid, a conclusion already arrived at by animal physiologists. Thus nine salts of sodium caused inflexion, and were not poisonous; seven of the corresponding salts of potassium did not cause inflexion, and some were poisonous. This is interesting in connexion with the fact that large doses of sodium salts may be introduced into the circulation of mammals with impunity, whereas small doses of potassium salts speedily cause death. Of twenty-four acids tried, nineteen caused inflexion, and the majority, even including most of the organic acids, were poisonous, which is the more remarkable since juice of many plants seems much more strongly acid than the solutions which were employed. The poisonous action, however, is not improbably connected with the negative osmose which is known to be induced by dilute acids.

Action of Alkaloid Poisons, of other Substances, and of Vapours.—Acetate and sulphate of quinine, citrate of strychnine, nicotine, digitaline, act more or less strongly on the glands and kill them; on the other hand, nitrate of quinine, atropine, veratrine, colchicine, theine, are quite harmless. Curare is not poisonous, and cobra poison, which kills animals by paralysing their nerve centres, causes "strong and rapid inflexion of the tentacles, and soon discharges all colour from the glands," stimulating also the movements of their protoplasm. Since alkaloids which act strongly on the nervous system of animals are without effect on *Drosera*, it seems probable that the sensibility of its glands, and their power of transmitting a stimulus to other parts of the leaf, are not due to elements analogous to nerve. Camphor in solution acts as a stimulant; the vapours however, of camphor, chloroform, alcohol, ether, and carbonic acid have a narcotic or anæsthetic action, and kill the plants after a time.

Effects of Organic Fluids.—Digestive Power of Secretion.—Darwin treated sixty-one leaves of *Drosera* with non-nitrogenous solutions (gum-arabic, sugar, starch, dilute alcohol, olive-oil, tea). The tentacles were not in a single case inflected. He then applied to sixty-four other leaves various nitrogenous fluids (milk, urine, albumen, infusion of meat, mucus, saliva, isinglass), and sixty-three had the tentacles and often the blades well inflected. Finally, taking twenty-three of the leaves which had served for the first experiment and treating them with bits of meat or drops of nitrogenous fluids, all save a few, apparently injured by exosmose caused by the density of the former solution of gum, sugar, &c., were distinctly inflected.

We are thus led to inquire whether the leaves have only the power of absorbing matter already in solution or whether they can render nitrogenous matter soluble, that is, whether they have the power of true digestion. The digestion of albuminous bodies by animals is effected by means of a ferment, pepsin, acting in presence of weak hydrochloric acid,—neither the acid nor the ferment having the power of digesting in the absence of the other, though almost any other acid may be substituted for hydrochloric. When the stomach is mechanically excited, acid is secreted, but not pepsin; this requires for its production the absorption of a minute quantity of already soluble animal matter (peptogene of Schiff). These propositions all hold good of *Drosera*. Frankland analysed the secretion obtained by stimulating four hundred and forty-five leaves with particles of glass, and came to the conclusion that its acidity was due to some acid of the acetic series, apparently either propionic or a mixture of acetic and butyric acids. Analysis of larger quantities enabled Will to show that the secretion contained formic as well as probably butyric and propionic acid, and Rees and Will prepared a glycerin extract which when acidulated rapidly digested fibrin.

Lawson Tait also separated a substance possessing the property of a digestive ferment.

Darwin fed numerous plants with roast meat and minute cubes of boiled white of egg, and placed other cubes in wet moss as a check. Solution soon took place in the former cases; and, just as in animal digestion, the edges of the cubes of egg were first rounded off, and the striation of muscle was replaced by dark points, while the bits of egg left in moss putrefied. On neutralization of the acid by alkali, digestion stops; on reacidification, it goes on again. Neither the watery nor the glycerin extract of leaves stimulated by fragments of glass was able to digest, showing that the ferment is not secreted until the glands have absorbed a trace of animal matter. The leaves digested fibrin, connective tissue, cartilage, bone, enamel, and dentine, gelatin, chondrine, casein of milk, &c., but could not digest epidermic productions (nails, hairs, feathers), fibro-elastic tissue, mucin, pepsin, urea, chitin, chlorophyll, cellulose, gun-cotton, oil, fat, and starch, thus completing the analogy with the gastric digestion of animals. Pollen-grains had their protoplasmic contents dissolved, and seeds were usually killed.

Irritability and Movements.—Cutting and pricking the leaf does not induce movement; the petiole is quite insensible, nor do the pedicels of the glands bend when rubbed or stimulated by contact with food. Only the glands remain, and these at once respond to stimuli, yet their irritability seems to extend for a very slight distance below them, since when the glands are cut off their pedicels often become inflected. When a tentacle receives an impulse either from its own gland or from the central tentacles, it bends towards the middle of the leaf, the short tentacles on which do not bend at all; in all other cases all the tentacles, even those of the centre, bend towards the point whence the stimulus comes. Thus all the tentacles of a leaf may be made to converge into two symmetrical groups by placing a fragment of phosphate of ammonia in the middle of each half of the blade. Contrary to the opinion of Ziegler, vivisection shows that the motor impulse is not transmitted through the fibro-vascular bundles, but through the cellular tissue. An impulse thus travels more rapidly along than across the leaf, since, from the elongated shape and the position of the cells, fewer cell-walls have to be crossed in a given distance. Thus, when the central glands are excited, they send centrifugally some influence to the exterior glands, where aggregation of the protoplasm is set up, which may be watched descending their tentacles, and the whole process is not without analogy to a reflex action. The motor impulse seems to be allied to the aggregating process, and it has been attempted to explain the bending which takes place at the base of the tentacles by assuming either (1) a rapid passage of fluid out of the cells in that region, which would thus contract, at least if we suppose them to be previously in a state of high tension and to possess great elasticity, (2) a contraction of the protoplasm of these cells, (3) the contraction of the cell-walls as well as the protoplasm, or (4) a shrinkage of the fluid contents of the cells, owing to a change in their molecular state with the subsequent closing in of the walls.

Absorption.—Bennett has described what he terms absorptive glands beneath the epidermis, consisting of two nearly hemispherical cells, filled with brownish protoplasm and bearing papillæ, which sometimes rise above the surface of the leaf, or the filaments of the tentacles. He finds similar organs in *Dionæa* and *Nepenthes*, but in no plants other than carnivorous, except *Callitriche*. Clark fed *Drosera* with flies soaked in chloride of lithium, and after several days found that all parts of the plant when burned showed the characteristic spectrum of lithium; and Tait, by cultivating plants with roots cut off and leaves buried in pure sand watered with an ammoniacal solution, showed that the sundew can not only absorb nutriment from its leaves, but can actually live and thrive by their aid alone, if supplied with small quantities of nitrogenous material.

Dionæa Muscipula, L.—This plant, the well-known Venus's Fly-trap, was first described in 1768 by Ellis in a remarkable letter to Linnæus, in which he gave a substantially correct account of the structure and functions of its leaves, and even suggested the probability of their carnivorism. Linnæus declared it the most wonderful of plants (*miraculum naturæ*), yet only admitted that it showed an extreme case of sensitiveness, supposing that the insects were only accidentally captured and subsequently allowed to escape. Two American botanists, Curtis and Canby, successively advanced our knowledge of the mode of capture and digestion, which has also been investigated by Mrs Treat, T. A. G. Balfour, and others, and most fully by Darwin.

The leaves are all radical, with broad foliaceous footstalks. Each leaf has two lobes, standing at rather less than a right angle to each other, their edges being produced into spike-like processes. The upper surface of each lobe is covered with minute circular sessile glands, each consisting of from 20 to 30 cells filled with purplish fluid. It bears also three fine-pointed sensitive filaments arranged

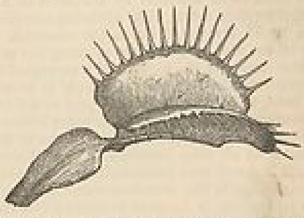


Fig. 5.—Leaf of Venus's Fly-trap (*Dionæa muscipula*), viewed laterally in its expanded state. (After Darwin.)

in a triangle. These contain no fibro-vascular bundles, but present an articulation near their bases, which enables them to bend parallel to the surface of the leaf when the lobes close. When the filaments are touched by an insect, the lobes close very sharply upon the hinge-like midrib, the spikes interlock, and the insect is imprisoned. If very minute, and so not worth digesting, it is able to escape between the interlocked spines; more usually, however, it

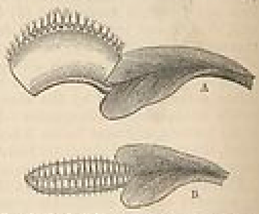


Fig. 6.—Leaf of *D. muscipula* closed over insect. A, viewed from the side; B, from above.

is retained between the lobes, which gradually but firmly compress it, until its form is distinguishable from without. The leaf thus forms itself into a temporary stomach, and the glands, hitherto dry, commence, as soon as excited by the absorption of a trace of nitrogenous matter, to pour out an acid secretion containing a ferment, which rapidly dissolves the soft parts of the insect. This is produced in such abundance that, when Darwin made a small opening at the base of one lobe of a leaf which had closed over a large crushed fly, the secretion continued to run down the footstalk during the whole time—nine days—during which the plant was kept under observation. Aggregation may be observed in the glands, and, at least on treatment with carbonate of ammonia, the aggregative process may be watched ascending the sensitive hairs.

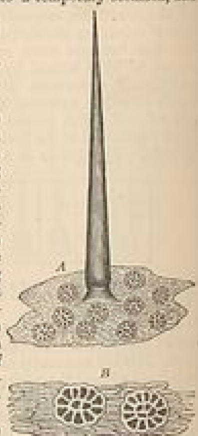


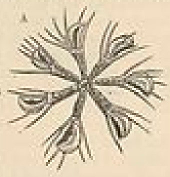
Fig. 7.—A, sensitive filament and glands of *D. muscipula*, × 50; B, glands × 600.

Though the filaments are exquisitely sensitive to the slightest contact with solid bodies, yet they are far less sensitive than those of *Drosera* to prolonged pressure, a singular difference in evident relation to the habits of the two plants. Like the leaves of *Drosera*, however, these of *Dionæa* are completely indifferent to wind and rain. The surface of the blade is very slightly sensitive; it may be roughly handled or scratched without causing movement, but closes when its surface or midrib is deeply pricked or cut. Irritation of the triangular area on each lobe enclosed by the sensitive filaments causes closure. The footstalk is quite insensitive. Inorganic or non-nitrogenous bodies, placed on the leaves without touching the sensitive filaments, do not excite movement, but nitrogenous bodies, if in the least degree damp, cause after several hours the lobes to close slowly. So too the leaf which has closed over a digestible body applies a gradual pressure, which serves to bring the glands on both sides into contact with the body, and may also, as Balfour suggests, aid in absorption. Thus we see that there are two kinds of movement, adapted for different purposes, one rapid, excited mechanically, the other slow, excited chemically. Leaves made to close over insoluble bodies reopen in less than twenty-four hours, and are ready, even before being fully expanded, to shut again. But if they have closed over nitrogen-yielding bodies, they remain closely shut for many days, and after re-expanding are torpid, and never act again, or only after a considerable time. Even in a state of nature, the most vigorous leaves are very rarely able to digest more than twice, or at most thrice, during their life. The secretion is a true gastric juice containing formic acid, and like gastric juice has remarkable antiseptic powers. Lindsay fed leaves with such quantities of meat as to kill them with indigestion, yet showed that the meat inside the leaf remained perfectly fresh while portions hanging outside putrefied.

While evidence is thus afforded of the absorption of the products of digestion by the complete disappearance of fibrin, albumen, &c., placed upon the leaf of *Dionæa*, Fraustadt was able, by feeding leaves with albumen dyed with aniline-red, to colour the contents and nuclei of the gland-cells.

The motor impulse, as in *Drosera*, is transmitted through the cellular tissue. Burdon Sanderson has demonstrated the existence of a normal electric current in the leaf of *Dionæa*, and the negative variation undergone by that current at the moment of closure of the leaf due to the conversion of electromotive force into mechanical work. This discovery, which is of the highest importance as showing the profound resemblance between the closure of the leaf of *Dionæa* and the contraction of a muscle, has been followed up and extended by Munk. C. de Candolle ascribes the closure of the valves to variations in the turgescence of the parenchyma of their upper surface.

A



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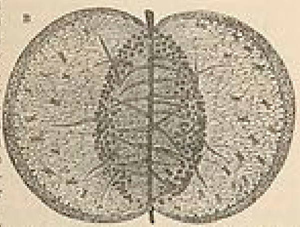

FIG. 8.—*Aldrovanda vesiculosa*.—A, whorl of leaves; B, leaf pressed open and enlarged, showing glands, sensitive filaments, and quadrifid hairs. (After Darwin.)

Aldrovanda vesiculosa.—This "minute aquatic *Dionæa*" floats freely, and is destitute of roots. Its whorled leaves have two lobes, with slightly inflected margins, which open only about as much as the valves of a living mussel-shell, and thus capture the more easily the small crustaceans and mollusks which may get between them. Part of the upper surface of each lobe next the midrib bears colourless glands (like those of *Dionæa*, but stalked), together with numerous long sensitive filaments which have both median and basal articulations; the outer thinner portion bears small quadrifid hairs. Darwin holds that the glands secrete and digest, while the quadrifids are destined to the absorption of decaying animal matter, the two regions of the leaf thus serving for very different purposes.

Drosophyllum lusitanicum.—This plant catches such vast numbers of flies in a state of nature that the Portuguese cottagers call it the fly-catcher, and hang up branches of it in their houses for this purpose. Its linear leaves are thickly covered with stalked glands which resemble in the main the tentacles of *Drosera*, save in that they are incapable of movement, and that their secretion is acid before excitement. The secretion too is less viscid, and freely leaves the gland to wet the insect, which, creeping onward, soon clogs its wings and dies. There are, moreover, many minute colourless sessile glands which only begin to secrete when stimulated by the absorption of nitrogenous matter, with which they seem to be mainly concerned.

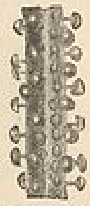

FIG. 9.—Part of leaf of *Drosophyllum lusitanicum*. × 7. Showing lower surface. (After Darwin.)

Roridula and *Byblis* resemble *Drosophyllum*, but their glands are of simpler structure than those of the latter, scarcely differing appreciably from the glandular hairs of other plants. Mr Darwin has thrown considerable light upon the question of how far the glands of plants not adapted for capturing insects share the power of absorption exhibited by those of the *Droseraceæ*. Choosing a number of plants at hazard, he found that the glands of two species of *Saxifraga*, a genus distantly allied to *Drosera*, of a *Primula*, and of *Pelargonium* have the power of rapid absorption, and exhibit movements of aggregation in their protoplasm, whereas those of *Erica*, *Mirabilis*, and *Nicotiana* appear to have no such power. Heckel has made similar observations on the floral glands of *Parnassia palustris*, and on the leaf-glands of *Geranium sparmannia*, &c. The glandular hairs of at least some plants are known to be capable of absorbing ammonia, both in solution and in vapour, and probably some obtain animal matter from the insects which are occasionally entangled in the viscid secretion.

A B

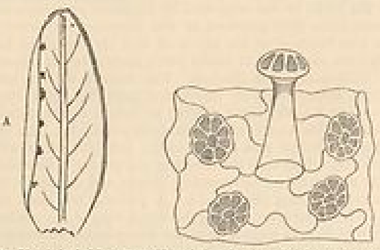

FIG. 10.—A, leaf of Butterwort (*Pinguicula vulgaris*), with left margin inflected over a row of small flies. (After Darwin.) B, glands from surface of leaf (× 200).

Pinguicula or *Butterwort*.—The large thick radical leaves of this genus have a very viscous surface and a pale colour, and bear two sets of glands, the larger borne on usually unicellular pedicels, the smaller almost sessile. When a fly is captured, the viscous secretion becomes strongly acid, the naturally incurved margins of the leaf are excited to curve still farther inwards, and in short all the phenomena of secretion, aggregation, digestion, absorption, &c., may be observed which have been described in *Drosera*.

Utricularia.—The aquatic species of this plant are found floating in foul and stagnant water. Their much divided filamentous leaves bear bladders (fig. 11, A), averaging about $\frac{1}{10}$ of an inch in length, each of which bears six or seven long bristles around the mouth, which is fitted with a thin transparent valve, that opens inwards and is covered with peculiar glands. The interior of the bladder is lined by quadrifid hairs (fig. 11, B), like those described in *Aldrovanda*. Aquatic crustaceans, worms, insect larvæ, and other small animals easily enter by pushing inwards the posterior free edge of the valve, which is highly elastic.

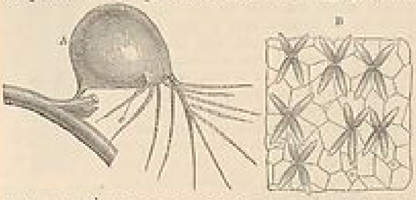

Fig. 11.—A, bladder of *Utricularia neglecta* (after Darwin), showing at *c* collar indistinctly seen through walls. B, quadrifid hairs from interior of bladder of *U. vulgaris* (× 300).

This instantly shuts against an interior thickened collar or projection around the mouth, and so renders escape impossible. The means by which the plant attracts its victims are unknown, but their success is very remarkable. Few bladders fail altogether, and many are found quite filled with crustaceans, as many as ten having been counted by Darwin within a single bladder. These bladders, however, have no secretion, and are quite unable to digest; they merely absorb the products of decomposition by means of their quadrifid hairs.

The terrestrial species (*e.g.*, *U. montana*), as also those of *Polypompholix*, bear numerous minute bladders of essentially similar structure along their creeping subterranean rhizomes, and these usually contain the decomposed remains of small terrestrial articulate animals. *Genlisea* has curious long-necked pitchers, lined with long downward directed hairs, which at once aid an animal in its entrance and prevent its retreat.

Sarracenia.—Long supposed to be reservoirs of water for the birds, as was suggested by Linnæus, or refuges for insects from their pursuers, as was supposed by Catesby, the true function of the leaves of this curious plant has only been elucidated of recent years, mainly by the labours of Mellichamp and Hooker. The mouths of the long radical trumpet-shaped leaves are protected by a large spreading lid, the inner surface of which is abundantly smeared with nectar, and often gaily coloured. Into one form of pitcher rain enters easily, into the other with difficulty. This with the mouth of the pitcher is furnished with numerous honey-secreting glands, and furnishes the attractive surface (fig. 12, A). A pathway too leads upwards from the ground along the broad wing of the pitcher, and is at least in some species also honey-baited; along this creeping insects are lured to their destruction. Below it is the conducting surface (B) of glassy epidermic cells, with short downward-directed points, which like those of *Genlisea* facilitate the descent, but impede the ascent of an insect. Then come the glandular surface (C), which is formed of smooth polished epidermis with numerous glands, that secrete the fluid contents of the pitcher, and finally the detentive surface (D), of which the cells are produced into long and strong bristles which point downwards and meet in the centre of the diminishing cavity so as to render escape impossible. The secretion wets an insect very rapidly, and appears to have remarkable anæsthetic effects. It seems to be completely destitute of digestive power, indeed rather to accelerate decomposition. The pitchers accumulate vast quantities of insects in the course

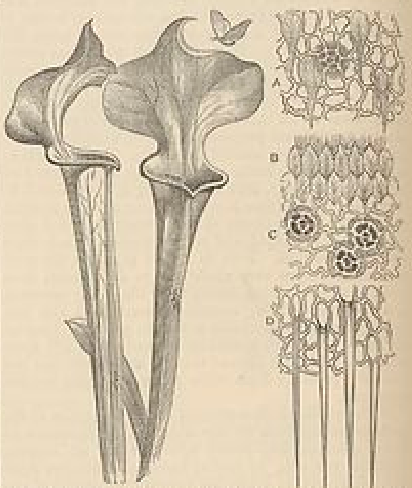

Fig. 12.—Leaves of *Sarracenia purpurea*. A, attractive surface of lid; B, conducting, C, glandular, and D, detentive surface; magnified. A and D are taken from *S. flava*.

of a season, and must thus abundantly manure the surrounding soil when they die. Moreover, the feast is largely shared by unbidden guests (commensals). Not to speak of insects which feed upon the pitcher itself, some drop their eggs into the putrescent mass, where their larvæ find abundant nourishment, while birds often slit open the pitchers with their beaks and devour the maggots in their turn.

Darlingtonia.—Of the two forms of pitcher in this genus the larger and ordinary form, that of the adult plant, is somewhat twisted, and instead of a lid has a large inflated hood overarching the small mouth. A large bilobed nectariferous and brightly coloured expansion hangs down from this, and attracts insects, particularly moths. As in *Sarracenia*, the plant seems merely to absorb the products of their putrefaction.

Nepenthes.—The pitchers of this genus are borne at the ends of long tendril-like prolongations of the leaves, and are of considerable size, varying from an inch to a foot or more in depth. Again we have two varieties of pitchers, one belonging to the young state of the plant, short, broad, and provided with broad external wings, adapted for the capture of ground game, while the adult form, intended for winged game, is long, narrow, and often destitute of lateral appendages. The mouth of the pitcher is strengthened and kept open by a thickened rim, which, like the under surface of the lid, secretes honey, and is frequently produced inwards and downwards into a short funnel-shaped tube which prevents the escape of insects, or into a row of incurved hooks sometimes strong enough to retain a small bird. The younger form of pitcher has its whole interior lined by secreting glands; the other and more common form has an attractive, a conductive, and a secreting surface analogous to those of *Sarracenia*, but wholly different in histological details. The detentive surface is represented by the fluid secretion which is invariably present. This is developed before the pitcher opens, and has generally a

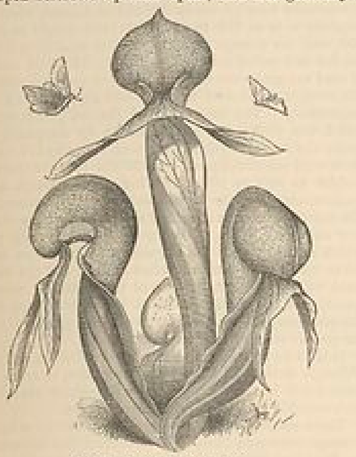

FIG. 13.—*Darlingtonia californica*.

faintly acid reaction; it contains, as shown by Voelcker, malic and citric acids, together with chloride of potassium, and carbonates of soda, magnesia, and lime. Hooker proved the digestive powers of the fluid, even on substances

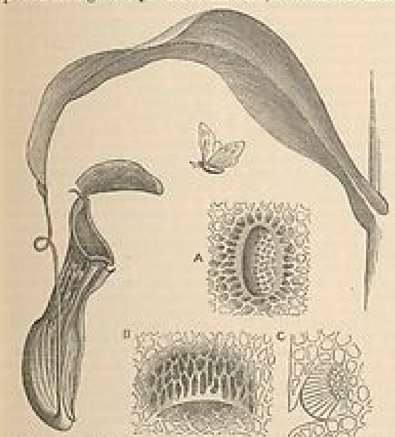

FIG. 14.—Pitcher of *Nepenthes distillatoria*. A, honey-gland from attractive surface of lid; B, digestive gland from interior of pitcher, in pocket-like depression of epidermis, opening downwards; C, transverse section of the same. A, B, and C magnified about 100 diameters.

so resisting as cartilage; Rees and Will found that fibrin was dissolved even more rapidly by the secretion of the excited pitchers than in a test experiment with pepsin from the pig's stomach; and Lawson Tait, Vines, and others have obtained the ferment in a separate state. Tait indeed finds two substances, both possessing great antiseptic powers, and both being apparently, together with acid, essential to digestion—one a greyish-white precipitate with alkalies, which he terms "droserin," and which seems the analogue of pepsin; the other, "azerin," a transparent straw-coloured substance precipitated by alcohol, he compares to ptyalin, the ferment of saliva. Droserin seems to be present in the secretion of all those insectivorous plants which possess the power of digestion, azerin perhaps in all without exception. The latter substance has the property of rapid deliquescence, so that it can only be preserved in hermetically sealed tubes, and its solution, like glycerin, quickly wets any body with which it comes in contact. A fly thrown into water never gets completely wetted, while one which falls into the secretion of any insectivorous plant is rapidly soaked and drowned by the fluid entering its tracheæ.

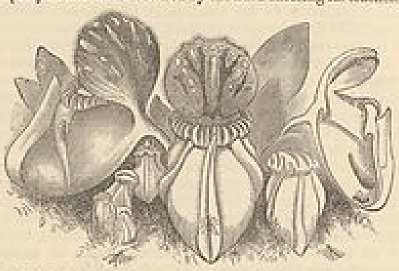

FIG. 15.—*Cephalotus follicularis*, showing ordinary leaves and pitchers, the right hand one cut open to show internal structure.

Cephalotus.—This plant bears ordinary leaves as well as pitchers. The latter somewhat resemble in general form those of *Nepenthes*, but are more complicated in histological details. Tait has proved the digestive action of their secretion.

Morphology of Pitchers.—Baillon, and indeed first of all Linnæus, have pointed out how by exaggerating the concavity of a peltate leaf like that of *Nymphæa* we obtain a pitcher of the type of *Sarracenia*. Intermediate forms are frequently shown by a variety of *Piperomia arifolia*. Hooker has given reason to believe that the pitcher of *Nepenthes* is not a transformed leaf, but a mere leaf-appendage answering to the water-secreting gland found at the end of many leaves. The apex of the leaf, instead of forming the lid as in *Sarracenia*, is represented by a filiform appendage (see fig. 16, F). Finally, Dickson has

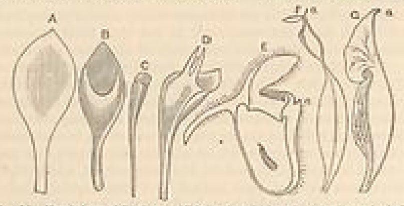

FIG. 16.—Morphology of Pitchers. (Chiefly after Dickson.) A, ordinary leaf of *Cephalotus*; B, monstrous leaf with spoon-shaped depression; C and D, other abnormal forms more deeply pouched, showing formation of pitcher; E, ordinary pitcher of *Cephalotus*; F, pitcher of *Nepenthes*; G, pitcher of *Sarracenia*; *a*, apex of leaf.

proved by comparison with monstrous forms that the pitcher of *Cephalotus* arises in a third and totally distinct way, by a calceolate pouching from the upper surface of the ordinary spathulate leaves, the lid here arising from the proximal side of the pitcher-orifice.

Other Insectivorous Plants.—*Dischidia*, an Asiatic genus of *Asclepiadaceæ*, and *Martynia*, one of the *Pedalineæ*, have also been described as insectivorous, as well as *Caltha dionæfolia* and several Aroids. Even *Anomoclada*, a South American liverwort, and a fern (*Elaphoglossum glutinosum*) have been described by Spruce as capturing numerous insects. All these cases, however, require much further investigation. The connate leaves of *Dipsacus* frequently enclose water in which insects are drowned, and Francis Darwin has discovered protoplasmic filaments which are emitted by the cells of certain glands within these cups, and which appear to absorb the products of decomposition. A similar process has recently also been shown by Ludwig to occur in *Silphium*, an allied genus.

Conclusion.—When Mr Darwin's work appeared, numerous objections were made to accepting his conclusions, on the *a priori* ground that digestion was too purely an animal function to be conceivable of plants. Morren demolished these by showing that digestion—the conversion of insoluble and indiffusible proteids, fats, and amyloids into soluble and diffusible compounds by means of appropriate ferments—is not confined either to animals or to carnivorous plants, but is a universal property of living beings, in fact the necessary preliminary of all assimilation. Not only are all the important animal digestive ferments represented among plants, but vegetable physiologists have made us acquainted with several ferments—synaptase, erythrozyme, myrosine, &c.—which have no known analogues in the animal kingdom. It is merely the exudation, not the existence, of the ferment, then, which is remarkable in carnivorous plants, and this Darwin suggests might begin by an exosmose accompanying the absorption of animal matter by any plant possessing viscid glandular hairs, and, once set up, would be perfected by natural selection. Insectivorous plants too are not the only ones which exhibit peculiarities of nutrition. The true parasites absorb the juices of the plants which they infest, and, not to mention the fungi, many of which subsist partly or wholly on animal matter, the phanerogamous saprophytes (*Neottia*, *Monotropa*, &c.) live by absorbing the partially decomposed materials of other plants; and from the absorption of vegetable to that of animal matter the transition is easy. The reciprocal case too occurs in the animal kingdom; animals possessing chlorophyll have been shown to nourish themselves like plants, without feeding, by decomposition of carbonic acid and the formation of starch in sunlight, and thus carnivorous plants—trespassers into the animal kingdom—are paralleled by vegetating animals. Thus, then, we have only to change our standpoint, and look, not at the anomalous plant or animal, but at the essentially similar cells, and the yet more essentially similar protoplasm of which both are composed, to see that their apparent anomalies are but additional proofs of the unity of nature.

But a more serious criticism affected the completeness of Darwin's work. Though Knight in 1818 had thought plants of *Dionæa* on which he placed morsels of beef grew more luxuriantly than others not so treated, many observers have since failed to see any improvement on insectivorous plants when regularly fed, or any disadvantage when prevented from obtaining animal food altogether; while others have even asserted that animal food was hurtful, having injured or killed their plants by feeding. In the latter case the explanation was of course that the feeding was excessive, but to meet the objections of the former a very careful research was undertaken by Francis Darwin. He took six plates full of thriving plants of sundew, and divided off each by a transverse bar. Then, choosing the least flourishing side of each, he placed, on June 12, 1877, roast meat, in morsels of about $\frac{1}{50}$ of a grain on the leaves, and renewed the dose occasionally. The plants on the fed sides were soon clearly greener than those on the starved sides, and their leaves contained more chlorophyll and starch. In less than two months the number of flowerstalks was half as numerous again on the fed as on the unfed sides, while the number and diameter of the leaves and the colour of the flowerstalks all showed a great superiority. The flowerstalks were all cut at the end of August, when their numbers were as 165 to 100, their total weight as 230 to 100, and the average weight per stem as 140 to 100 for the fed and unfed sides respectively. The total numbers of seed capsules were as 194 to 100, or nearly double, and the average number of seeds in each capsule as 12 to 10 respectively. The superiority of the fed plants over the unfed was even more clearly shown by comparing their seeds, the average weights per seed being as 157 to 100, their total calculated number as 240 to 100, and their total weight as 380 to 100. The fed plants, though at the commencement of the experiment in a slight minority, at the end of the season exceeded the unfed by more than 20 per cent., while the following spring the young plants which sprang up on the fed side exceeded those on the other by 18 per cent. in number and by 150 per cent. in total weight, so that, in spite of the relatively enormous quantity of flowerstalk produced by the fed plants during the previous summer, they had still been able to lay up a far greater store of reserve material.

It is to be remarked that the beneficial effect of feeding, although distinct in the vegetative system, is much more remarkable in the reproductive, a fact which explains the unfavourable opinion of previous observers.

These results were also independently arrived at by three German observers, Rees, Kellerman, and Von Räumer, who used aphides instead of roast meat. The question of the utility of the carnivorous habit may thus be considered as no less indisputable than its existence.

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