Insectivorous plants

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1877

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ETC.

WITH ILLUSTRATIONS.

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1875.

CHAPTER XVII.

UTRICULARIA.

Utricularia neglecta—Structure of the bladder—The uses of the several parts — Number of imprisoned animals — Manner of capture — The bladders cannot digest animal matter, but absorb the products of its decay — Experiments on the absorption of certain fluids by the quadrifid processes — Absorption by the glands — Summary of the observation on absorption — Development of the bladders — *Utricularia vulgaris* — *Utricularia minor* — *Utricularia clandestina.*

I WAS led to investigate the habits and structure of the species of this genus partly from their belonging to the same natural family as Pinguicula, but more especially by Mr. Holland's statement, that "water insects are often found imprisoned in the bladders," which he suspects "are destined for the plant to feed on." * The plants which I first received as *Utricularia vulgaris* from the New Forest in Hampshire and from Cornwall, and which I have chiefly worked on, have been determined by Dr. Hooker to be a very rare British species, the *Utricularia neglecta* of Lehm.† I subsequently received the true *Utricularia vulgaris* from Yorkshire. Since drawing up the following description from my own observations and those of my son, Francis Darwin, an important memoir by Prof. Cohn

* The 'Quart. Mag. of the High Wycombe Nat. Hist. Soc.' July 1868, p. 5. Delpino ('Ult. Osservaz. sulla Dicogamia,' &c. 1868-1869, p. 16) also quotes Crouan as having found (1858) crustaceans within the bladders of *Utricularia vulgaris.*

† I am much indebted to the Rev. H. M. Wilkinson, of Bistern, for having sent me several fine lots of this species from the New Forest. Mr. Ralfs was also so kind as to send me living plants of the same species from near Penzance in Cornwall.

on *Utricularia vulgaris* has appeared;* and it has been no small satisfaction to me to find that my account agrees almost completely with that of this distinguished observer. I will publish my description as it stood before reading that by Prof. Cohn, adding occasionally some statements on his authority.

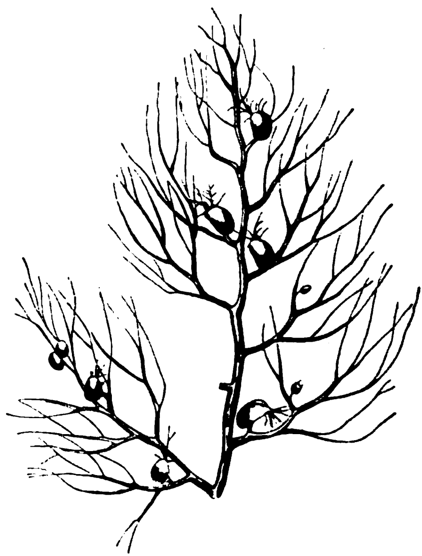

FIG. 17.
(*Utricularia neglecta.*)
Branch with the divided leaves bearing bladders; about twice enlarged.

Utricularia neglecta.—The general appearance of a branch (about twice enlarged), with the pinnatifid leaves bearing bladders, is represented in the above sketch (fig. 17). The leaves continually bifurcate, so that a full-grown one terminates in from twenty to thirty

* 'Beiträge zur Biologie der Pflanzen,' drittes Heft, 1875.

points. Each point is tipped by a short, straight bristle; and slight notches on the sides of the leaves bear similar bristles. On both surfaces there are many small papillæ, crowned with two hemispherical cells in close contact. The plants float near the surface of the water, and are quite destitute of roots, even during the earliest period of growth.* They commonly inhabit, as more than one observer has remarked to me, remarkably foul ditches.

The bladders offer the chief point of interest. There are often two or three on the same divided leaf, generally near the base; though I have seen a single one growing from the stem. They are supported on short footstalks. When fully grown, they are nearly $\frac{1}{10}$ of an inch (2·54 mm.) in length. They are translucent, of a green colour, and the walls are formed of two layers of cells. The exterior cells are polygonal and rather large; but at many of the points where the angles meet, there are smaller rounded cells. These latter support short conical projections, surmounted by two hemispherical cells in such close apposition that they appear united; but they often separate a little when immersed in certain fluids. The papillæ thus formed are exactly like those on the surfaces of the leaves. Those on the same bladder vary much in size; and there are a few, especially on very young bladders, which have an elliptical instead of a circular outline. The two terminal cells are transparent, but must hold much matter in solution, judging from the quantity coagulated by prolonged immersion in alcohol or ether.

* I infer that this is the case from a drawing of a seedling given by Dr. Warming in his paper, "Bidrag til Kundskaben om Lentibulariaceæ," from the 'Videnskabelige Meddelelser,' Copenhagen, 1874, Nos. 3–7, pp. 33–58.

The bladders are filled with water. They generally, but by no means always, contain bubbles of air. According to the quantity of the contained water and air, they vary much in thickness, but are always somewhat compressed. At an early stage of growth, the flat or ventral surface faces the axis or stem; but the footstalks must have some power of movement; for in plants kept in my greenhouse the ventral surface was generally turned either straight or obliquely downwards. The Rev. H. M. Wilkinson examined

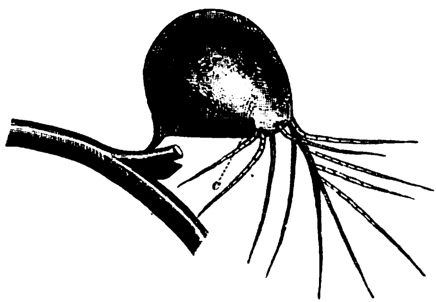

Fig. 18.
(*Utricularia neglecta.*)
Bladder; much enlarged. c, collar indistinctly seen through the walls.

plants for me in a state of nature, and found this commonly to be the case, but the younger bladders often had their valves turned upwards.

The general appearance of a bladder viewed laterally, with the appendages on the near side alone represented, is shown in the accompanying figure (fig. 18). The lower side, where the footstalk arises, is nearly straight, and I have called it the ventral surface. The other or dorsal surface is convex, and terminates in two long prolongations, formed of several rows of cells, containing chlorophyll, and bearing, chiefly on the outside, six or seven long, pointed, multicellular bristles. These prolongations of the bladder may be conveniently called the *antennæ*, for the whole bladder (see fig. 17) curiously resembles an entomostracan crustacean, the short footstalk representing the tail. In fig. 18, the near antenna alone is shown. Beneath the two antennæ the end of the bladder is slightly truncated, and here is situated the most important part of the whole structure, namely the entrance and valve. On each side of the entrance from three to rarely seven long, multicellular bristles project out-

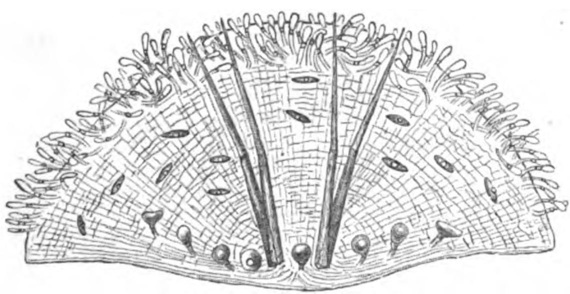

FIG. 19.
(*Utricularia neglecta.*)
Valve of bladder; greatly enlarged.

wards; but only those (four in number) on the near side are shown in the drawing. These bristles, together with those borne by the antennæ, form a sort of hollow cone surrounding the entrance.

The valve slopes into the cavity of the bladder, or upwards in fig. 18. It is attached on all sides to the bladder, excepting by its posterior margin, or the lower one in fig. 19, which is free, and forms one side of the slit-like orifice leading into the bladder. This margin is sharp, thin, and smooth, and rests on the edge of a rim or collar, which dips deeply into the bladder, as shown in the longitudinal section (fig. 20) of the collar and valve; it is also shown at *c*, in fig. 18. The edge of the valve can thus open only inwards. As both the valve and collar dip into the bladder, a hollow or depression is here formed, at the base of which lies the slit-like orifice.

The valve is colourless, highly transparent, flexible and elastic. It is convex in a transverse direction, but has been drawn (fig. 19) in a flattened state, by which its apparent breadth is increased. It is formed,

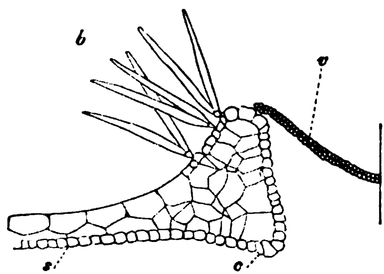

FIG. 20.
(*Utricularia neglecta.*)
Longitudinal vertical section through the ventral portion of a bladder; showing valve and collar. *v*, valve; the whole projection above *c* forms the collar; *b*, bifid processes; *s*, ventral surface of bladder.

according to Cohn, of two layers of small cells, which are continuous with the two layers of larger cells forming the walls of the bladder, of which it is evidently a prolongation. Two pairs of transparent pointed bristles, about as long as the valve itself, arise from near the free posterior margin (fig. 18), and point obliquely outwards in the direction of the antennæ. There are also on the surface of the valve numerous glands, as I will call them; for they have the power of absorption, though I doubt whether they ever secrete. They consist of three kinds, which to a certain extent graduate into one another. Those situated round the anterior margin of the valve (upper margin in fig. 19) are very numerous and crowded together; they consist of an oblong head on a long pedicel. The pedicel itself is formed of an elongated cell, surmounted by a short one. The glands towards the free posterior margin are much larger, few in number, and almost spherical, having short footstalks; the head is formed by the confluence of two cells, the lower one answering to the short upper cell of the pedicel of the oblong glands. The glands of the third kind have transversely elongated heads, and are seated on very short footstalks; so that they stand parallel and close to the surface of the valve; they may be called the two-armed glands. The cells forming all these glands contain a nucleus, and are lined by a thin layer of more or less granular protoplasm, the primordial utricle of Mohl. They are filled with fluid, which must hold much matter in solution, judging from the quantity coagulated after they have been long immersed in alcohol or ether. The depression in which the valve lies is also lined with innumerable glands; those at the sides having oblong heads and elongated pedicels, exactly like the glands on the adjoining parts of the valve.

The collar (called the peristome by Cohn) is evidently formed, like the valve, by an inward projection of the walls of the bladder. The cells composing the outer surface, or that facing the valve, have rather thick walls, are of a brownish colour, minute, very numerous, and elongated; the lower ones being divided into two by vertical partitions. The whole presents a complex and elegant appearance. The cells forming the inner surface are continuous with those over the whole inner surface of the bladder. The space between the inner and outer surface consists of coarse cellular tissue (fig. 20). The inner side is thickly covered with delicate bifid processes, hereafter to be described. The collar is thus made thick; and it is rigid, so that it retains the same outline whether the bladder contains little or much air and water. This is of great importance, as otherwise the thin and flexible valve would be liable to be distorted, and in this case would not act properly.

Altogether the entrance into the bladder, formed by the transparent valve, with its four obliquely projecting bristles, its numerous diversely shaped glands, surrounded by the collar, bearing glands on the inside and bristles on the outside, together with the bristles borne by the antennæ, presents an extraordinarily complex appearance when viewed under the microscope.

We will now consider the internal structure of the bladder. The whole inner surface, with the exception of the valve, is seen under a moderately high power to be covered with a serried mass of processes (fig. 21). Each of these consists of four divergent arms; whence their name of quadrifid processes. They arise from small angular cells, at the junctions of the angles of the larger cells which form the interior of the bladder. The middle part of the upper surface of these small cells projects a little, and then contracts into a very short and narrow footstalk which bears the four arms (fig. 22). Of these, two are long, but often of not quite equal length, and project obliquely inwards and towards the posterior end of the bladder. The two others are much shorter, and project at a smaller angle, that is, are more nearly horizontal, and are directed towards the anterior end of the bladder. These arms are only moderately sharp; they are composed of extremely thin transparent membrane, so that they can be bent or doubled in any direction without being broken. They are lined with a delicate layer of protoplasm, as is likewise the short conical projection from which they arise. Each arm generally (but not invariably) contains a minute, faintly brown particle, either rounded or more commonly elongated, which exhibits incessant Brownian movements. These par-

FIG. 21.
(*Utricularia neglecta.*)
Small portion of inside of bladder, much enlarged, showing quadrifid processes.

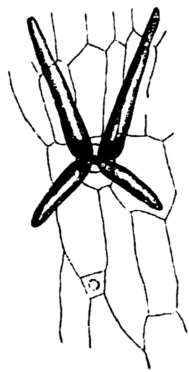

FIG. 22.
(*Utricularia neglecta.*)
One of the quadrifid processes greatly enlarged.

ticles slowly change their positions, and travel from one end to the other of the arms, but are commonly found near their bases. They are present in the quadrifids of young bladders, when only about a third of their full size. They do not resemble ordinary nuclei, but I believe that they are nuclei in a modified condition, for when absent, I could occasionally just distinguish in their places a delicate halo of matter, including a darker spot. Moreover, the quadrifids of *Utricularia montana* contain rather larger and much more regularly spherical, but otherwise similar, particles, which closely resemble the nuclei in the cells forming the walls of the bladders. In the present case there were sometimes two, three, or even more, nearly similar particles within a single arm; but, as we shall hereafter see, the presence of more than one seemed always to be connected with the absorption of decayed matter.

The inner side of the collar (see the previous fig. 20) is covered with several crowded rows of processes, differing in no important respect from the quadrifids, except in bearing only two arms instead of four; they are, however, rather narrower and more delicate. I shall call them the bifids. They project into the bladder, and are directed towards its posterior end. The quadrifid and bifid processes no doubt are homologous with the papillæ on the outside of the bladder and of the leaves; and we shall see that they are developed from closely similar papillæ.

The Uses of the several Parts.—After the above long but necessary description of the parts, we will turn to their uses. The bladders have been supposed by some authors to serve as floats; but branches which bore no bladders, and others from which they had been removed, floated perfectly, owing to the air in the intercellular spaces. Bladders containing dead and captured animals usually include bubbles of air, but these cannot have been generated solely by the process of decay, as I have often seen air in young, clean, and empty bladders; and some old bladders with much decaying matter had no bubbles.

The real use of the bladders is to capture small aquatic animals, and this they do on a large scale. In the first lot of plants, which I received from the New Forest early in July, a large proportion of the fully grown bladders contained prey; in a second lot, received in the beginning of August, most of the bladders were empty, but plants had been selected which had grown in unusually pure water. In the first lot, my son examined seventeen bladders, including prey of some kind, and eight of these contained entomostracan crustaceans, three larvæ of insects, one being still alive, and six remnants of animals so much decayed that their nature could not be distinguished. I picked out five bladders which seemed very full, and found in them four, five, eight, and ten crustaceans, and in the fifth a single much elongated larva. In five other bladders, selected from containing remains, but not appearing very full, there were one, two, four, two, and five crustaceans. A plant of *Utricularia vulgaris*, which had been kept in almost pure water, was placed by Cohn one evening into water swarming with crustaceans, and by the next morning most of the bladders contained these animals entrapped and swimming round and round their prisons. They remained alive for several days; but at last perished, asphyxiated, as I suppose, by the oxygen in the water having been all consumed. Freshwater worms were also found by Cohn in some bladders. In all cases the bladders with decayed remains swarmed with living Algæ of many kinds, Infusoria, and other low organisms, which evidently lived as intruders.

Animals enter the bladders by bending inwards the posterior free edge of the valve, which from being highly elastic shuts again instantly. As the edge is extremely thin, and fits closely against the edge of the collar, both projecting into the bladder (see section, fig. 20), it would evidently be very difficult for any animal to get out when once imprisoned, and apparently they never do escape. To show how closely the edge fits, I may mention that my son found a Daphnia which had inserted one of its antennæ into the slit, and it was thus held fast during a whole day. On three or four occasions I have seen long narrow larvæ, both dead and alive, wedged between the corner of the valve and collar, with half their bodies within the bladder and half out.

As I felt much difficulty in understanding how such minute and weak animals, as are often captured, could force their way into the bladders, I tried many experiments to ascertain how this was effected. The free margin of the valve bends so easily that no resistance is felt when a needle or thin bristle is inserted. A thin human hair, fixed to a handle, and cut off so as to project barely $\frac{1}{4}$ of an inch, entered with some difficulty; a longer piece yielded instead of entering. On three occasions minute particles of blue glass (so as to be easily distinguished) were placed on valves whilst under water; and on trying gently to move them with a needle, they disappeared so suddenly that, not seeing what had happened, I thought that I had flirted them off; but on examining the bladders, they were found safely enclosed. The same thing occurred to my son, who placed little cubes of green box-wood (about $\frac{1}{60}$ of an inch, ·423 mm.) on some valves; and thrice in the act of placing them on, or whilst gently moving them to another spot, the valve suddenly opened and they were engulfed. He then placed similar bits of wood on other valves, and moved them about for some time, but they did not enter. Again, particles of blue glass were placed by me on three valves, and extremely minute shavings of lead on two other valves; after 1 or 2 hrs. none had entered, but in from 2 to 5 hrs. all five were enclosed. One of the particles of glass was a long splinter, of which one end rested obliquely on the valve, and after a few hours it was found fixed, half within the bladder and half projecting out, with the edge of the valve fitting closely all round, except at one angle, where a small open space was left. It was so firmly fixed, like the above mentioned larvæ, that the bladder was torn from the branch and shaken, and yet the splinter did not fall out. My son also placed little cubes (about $\frac{1}{65}$ of an inch, ·391 mm.) of green box-wood, which were just heavy enough to sink in water, on three valves. These were examined after 19 hrs. 30 m., and were still lying on the valves; but after 22 hrs. 30 m. one was found enclosed. I may here mention that I found in a bladder on a naturally growing plant a grain of sand, and in another bladder three grains; these must have fallen by some accident on the valves, and then entered like the particles of glass.

The slow bending of the valve from the weight of particles of glass and even of box-wood, though largely supported by the water, is, I suppose, analogous to the slow bending of colloid substances. For instance, particles of glass were placed on various points of narrow strips of moistened gelatine, and these yielded and became bent with extreme slowness. It is much more difficult to understand how gently moving a particle from one part of a valve to another causes it suddenly to open. To ascertain whether the valves were endowed with irritability, the surfaces of several were scratched with a needle or brushed with a fine camel-hair brush, so as to imitate the crawling movement of small crustaceans, but the valve did not open. Some bladders, before being brushed, were left for a time in water at temperatures between 80° and 130° F. (26°·6—54°·4 Cent.), as, judging from a widespread analogy, this would have rendered them more sensitive to irritation, or would by itself have excited movement; but no effect was produced. We may, therefore, conclude that animals enter merely by forcing their way through the slit-like orifice; their heads serving as a wedge. But I am surprised that such small and weak creatures as are often captured (for instance, the nauplius of a crustacean, and a tardigrade) should be strong enough to act in this manner, seeing that it was difficult to push in one end of a bit of a hair ¼ of an inch in length. Nevertheless, it is certain that weak and small creatures do enter, and Mrs. Treat, of New Jersey, has been more successful than any other observer, and has often witnessed in the case of *Utricularia clandestina* the whole process.* She saw a tardigrade slowly walking round a bladder, as if reconnoitring; at last it crawled into the depression where the valve lies, and then easily entered. She also witnessed the entrapment of various minute crustaceans. Cypris "was "quite wary, but nevertheless was often caught. "Coming to the entrance of a bladder, it would some-"times pause a moment, and then dash away; at "other times it would come close up, and even ven-"ture part of the way into the entrance and back out "as if afraid. Another, more heedless, would open "the door and walk in; but it was no sooner in than "it manifested alarm, drew in its feet and antennæ, and closed its shell." Larvæ, apparently of gnats, when "feeding near the entrance, are pretty certain "to run their heads into the net, whence there is no "retreat. A large larva is sometimes three or four "hours in being swallowed, the process bringing to

* 'New York Tribune,' reprinted in the 'Gard. Chron.' 1875, p. 303.

"mind what I have witnessed when a small snake "makes a large frog its victim." But as the valve does not appear to be in the least irritable, the slow swallowing process must be the effect of the onward movement of the larva.

It is difficult to conjecture what can attract so many creatures, animal- and vegetable-feeding crustaceans, worms, tardigrades, and various larvæ, to enter the bladders. Mrs. Treat says that the larvæ just referred to are vegetable-feeders, and seem to have a special liking for the long bristles round the valve, but this taste will not account for the entrance of animal-feeding crustaceans. Perhaps small aquatic animals habitually try to enter every small crevice, like that between the valve and collar, in search of food or protection. It is not probable that the remarkable transparency of the valve is an accidental circumstance, and the spot of light thus formed may serve as a guide. The long bristles round the entrance apparently serve for the same purpose. I believe that this is the case, because the bladders of some epiphytic and marsh species of Utricularia which live embedded either in entangled vegetation or in mud, have no bristles round the entrance, and these under such conditions would be of no service as a guide. Nevertheless, with these epiphytic and marsh species, two pairs of bristles project from the surface of the valve, as in the aquatic species; and their use probably is to prevent too large animals from trying to force an entrance into the bladder, thus rupturing the orifice.

As under favourable circumstances most of the bladders succeed in securing prey, in one case as many as ten crustaceans;—as the valve is so well fitted to allow animals to enter and to prevent their escape;— and as the inside of the bladder presents so singular a structure, clothed with innumerable quadrifid and bifid processes, it is impossible to doubt that the plant has been specially adapted for securing prey. From the analogy of Pinguicula, belonging to the same family, I naturally expected that the bladders would have digested their prey; but this is not the case, and there are no glands fitted for secreting the proper fluid. Nevertheless, in order to test their power of digestion, minute fragments of roast meat, three small cubes of albumen, and three of cartilage, were pushed through the orifice into the bladders of vigorous plants. They were left from one day to three days and a half within, and the bladders were then cut open; but none of the above substances exhibited the least signs of digestion or dissolution; the angles of the cubes being as sharp as ever. These observations were made subsequently to those on Drosera, Dionæa, Drosophyllum, and Pinguicula; so that I was familiar with the appearance of these substances when undergoing the early and final stages of digestion. We may therefore conclude that Utricularia cannot digest the animals which it habitually captures.

In most of the bladders the captured animals are so much decayed that they form a pale brown, pulpy mass, with their chitinous coats so tender that they fall to pieces with the greatest ease. The black pigment of the eye-spots is preserved better than anything else. Limbs, jaws, &c. are often found quite detached; and this I suppose is the result of the vain struggles of the later captured animals. I have sometimes felt surprised at the small proportion of imprisoned animals in a fresh state compared with those utterly decayed. Mrs. Treat states with respect of the larvæ above referred to, that "usually in less "than two days after a large one was captured the fluid "contents of the bladders began to assume a cloudy "or muddy appearance, and often became so dense "that the outline of the animal was lost to view." This statement raises the suspicion that the bladders secrete some ferment hastening the process of decay. There is no inherent improbability in this supposition, considering that meat soaked for ten minutes in water mingled with the milky juice of the papaw becomes quite tender and soon passes, as Browne remarks in his 'Natural History of Jamaica,' into a state of putridity.

Whether or not the decay of the imprisoned animals is in any way hastened, it is certain that matter is absorbed from them by the quadrifid and bifid processes. The extremely delicate nature of the membrane of which these processes are formed, and the large surface which they expose, owing to their number crowded over the whole interior of the bladder, are circumstances all favouring the process of absorption. Many perfectly clean bladders which had never caught any prey were opened, and nothing could be distinguished with a No. 8 object-glass of Hartnack within the delicate, structureless protoplasmic lining of the arms, excepting in each a single yellowish particle or modified nucleus. Sometimes two or even three such particles were present; but in this case traces of decaying matter could generally be detected. On the other hand, in bladders containing either one large or several small decayed animals, the processes presented a widely different appearance. Six such bladders were carefully examined; one contained an elongated, coiled-up larva; another a single large entomostracan crustacean, and the others from two to five smaller ones, all in a decayed state. In these six bladders, a large number of the quadrifid processes contained transparent, often yellowish, more or less confluent, spherical or irregularly shaped, masses of matter. Some of the processes, however, contained only fine granular matter, the particles of which were so small that they could not be defined clearly with No. 8 of Hartnack. The delicate layer of protoplasm lining their walls was in some cases a little shrunk. On three occasions the above small masses of matter were observed and sketched at short intervals of time; and they certainly changed their positions relatively to each other and to the walls of the arms. Separate masses sometimes became confluent, and then again divided. A single little mass would send out a projection, which after a time separated itself. Hence there could be no doubt that these masses consisted of protoplasm. Bearing in mind that many clean bladders were examined with equal care, and that these presented no such appearance, we may confidently believe that the protoplasm in the above cases had been generated by the absorption of nitrogenous matter from the decaying animals. In two or three other bladders, which at first appeared quite clean, on careful search a few processes were found, with their outsides clogged with a little brown matter, showing that some minute animal had been captured and had decayed, and the arms here included a very few more or less spherical and aggregated masses; the processes in other parts of the bladders being empty and transparent. On the other hand, it must be stated that in three bladders containing dead crustaceans, the processes were likewise empty. This fact may be accounted for by the animals not having been sufficiently decayed, or by time enough not having been allowed for the generation of protoplasm, or by its subsequent absorption and transference to other parts of the plant. It will hereafter be seen that in three or four other species of Utricularia the quadrifid processes in contact with decaying animals likewise contained aggregated masses of protoplasm.

On the Absorption of certain Fluids by the Quadrifid and Bifid Processes.—These experiments were tried to ascertain whether certain fluids, which seemed adapted for the purpose, would produce the same effects on the processes as the absorption of decayed animal matter. Such experiments are, however, troublesome; for it is not sufficient merely to place a branch in the fluid, as the valve shuts so closely that the fluid apparently does not enter soon, if at all. Even when bristles were pushed into the orifices, they were in several cases wrapped so closely round by the thin flexible edge of the valve that the fluid was apparently excluded; so that the experiments tried in this manner are doubtful and not worth giving. The best plan would have been to puncture the bladders, but I did not think of this till too late, excepting in a few cases. In all such trials, however, it cannot be ascertained positively that the bladder, though translucent, does not contain some minute animal in the last stage of decay. Therefore most of my experiments were made by cutting bladders longitudinally into two; the quadrifids were examined with No. 8 of Hartnack, then irrigated, whilst under the covering glass, with a few drops of the fluid under trial, kept in a damp chamber, and re-examined after stated intervals of time with the same power as before.

Four bladders were first tried as a control experiment, in the manner just described, in a solution of one part of gum arabic to 218 of water, and two bladders in a solution of one part of sugar to 437 of water; and in neither case was any change perceptible in the quadrifids or bifids after 21 hrs. Four bladders were then treated in the same manner with a solution of one part of nitrate of ammonia to 437 of water, and re-examined after 21 hrs. In two of these the quadrifids now appeared full of very finely granular matter, and their protoplasmic lining or primordial utricle was a little shrunk. In the third bladder, the quadrifids included distinctly visible granules, and the primordial utricle was a little shrunk after only 8 hrs. In the fourth bladder the primordial utricle in most of the processes was here and there thickened into little, irregular, yellowish specks; and from the gradations which could be traced in this and other cases, these specks appear to give rise to the larger free granules contained within some of the processes. Other bladders, which, as far as could be judged, had never caught any prey, were punctured and left in the same solution for 17 hrs.; and their quadrifids now contained very fine granular matter.

A bladder was bisected, examined, and irrigated with a solution of one part of carbonate of ammonia to 437 of water. After 8 hrs. 30 m. the quadrifids contained a good many granules, and the primordial utricle was somewhat shrunk; after 23 hrs. the quadrifids and bifids contained many spheres of hyaline matter, and in one arm twenty-four such spheres of moderate size were counted. Two bisected bladders, which had been previously left for 21 hrs. in the solution of gum (one part to 218 of water) without being affected, were irrigated with the solution of carbonate of ammonia; and both had their quadrifids modified in nearly the same manner as just described,—one after only 9 hrs., and the other after 24 hrs. Two bladders which appeared never to have caught any prey were punctured and placed in the solution; the quadrifids of one were examined after 17 hrs., and found slightly opaque; the quadrifids of the other, examined after 45 hrs., had their primordial utricles more or less shrunk with thickened yellowish specks, like those due to the action of nitrate of ammonia. Several uninjured bladders were left in the same solution, as well as in a weaker solution of one part to 1750 of water, or 1 gr. to 4 oz.; and after two days the quadrifids were more or less opaque, with their contents finely granular; but whether the solution had entered by the orifice, or had been absorbed from the outside, I know not.

Two bisected bladders were irrigated with a solution of one part of urea to 218 of water; but when this solution was employed, I forgot that it had been kept for some days in a warm room, and had therefore probably generated ammonia; anyhow the quadrifids were affected after 21 hrs. as if a solution of carbonate of ammonia had been used; for the primordial utricle was thickened in specks, which seemed to graduate into separate granules. Three bisected bladders were also irrigated with a fresh solution of urea of the same strength; their quadrifids after 21 hrs. were much less affected than in the former case; nevertheless, the primordial utricle in some of the arms was a little shrunk, and in others was divided into two almost symmetrical sacks.

Three bisected bladders, after being examined, were irrigated with a putrid and very offensive infusion of raw meat. After 23 hrs. the quadrifids and bifids in all three specimens abounded with minute, hyaline, spherical masses; and some of their primordial utricles were a little shrunk. Three bisected bladders were also irrigated with a fresh infusion of raw meat; and to my surprise the quadrifids in one of them appeared, after 23 hrs., finely granular, with their primordial utricles somewhat shrunk and marked with thickened yellowish specks; so that they had been acted on in the same manner as by the putrid infusion or by the salts of ammonia. In the second bladder some of the quadrifids were similarly acted on, though to a very slight degree; whilst the third bladder was not at all affected.

From these experiments it is clear that the quadrifid and bifid processes have the power of absorbing carbonate and nitrate of ammonia, and matter of some kind from a putrid infusion of meat. Salts of ammonia were selected for trial, as they are known to be rapidly generated by the decay of animal matter in the presence of air and water, and would therefore be generated within the bladders containing captured prey. The effect produced on the processes by these salts and by a putrid infusion of raw meat differs from that produced by the decay of the naturally captured animals only in the aggregated masses of protoplasm being in the latter case of larger size; but it is probable that the fine granules and small hyaline spheres produced by the solutions would coalesce into larger masses, with time enough allowed.

We have seen with Drosera that the first effect of a weak solution of carbonate of ammonia on the cell-contents is the production of the finest granules, which afterwards aggregate into larger, more or less rounded, masses; and that the granules in the layer of protoplasm which flows round the walls ultimately coalesce with these masses. Changes of this nature are, however, far more rapid in Drosera than in Utricularia. Since the bladders have no power of digesting albumen, cartilage, or roast meat, I was surprised that matter was absorbed, at least in one case, from a fresh infusion of raw meat. I was also surprised, from what we shall presently see with respect to the glands round the orifice, that a fresh solution of urea produced only a moderate effect on the quadrifids.

As the quadrifids are developed from papillæ which at first closely resemble those on the outside of the bladders and on the surfaces of the leaves, I may here state that the two hemispherical cells with which these latter papillæ are crowned, and which in their natural state are perfectly transparent, likewise absorb carbonate and nitrate of ammonia; for, after an immersion of 23 hrs. in solutions of one part of both these salts to 437 of water, their primordial utricles were a little shrunk and of a pale brown tint, and sometimes finely granular. The same result followed from the immersion of a whole branch for nearly three days in a solution of one part of the carbonate to 1750 of water. The grains of chlorophyll, also, in the cells of the leaves on this branch became in many places aggregated into little green masses, which were often connected together by the finest threads.

On the Absorption of certain Fluids by the Glands on the Valve and Collar.—The glands round the orifices of bladders which are still young, or which have been long kept in moderately pure water, are colourless; and their primordial utricles are only slightly or hardly at all granular. But in the greater number of plants in a state of nature—and we must remember that they generally grow in very foul water—and with plants kept in an aquarium in foul water, most of the glands were of a pale brownish tint; their primordial utricles were more or less shrunk, sometimes ruptured, with their contents often coarsely granular or aggregated into little masses. That this state of the glands is due to their having absorbed matter from the surrounding water, I cannot doubt; for, as we shall immediately see, nearly the same results follow from their immersion for a few hours in various solutions. Nor is it probable that this absorption is useless, seeing that it is almost universal with plants growing in a state of nature, excepting when the water is remarkably pure.

The pedicels of the glands which are situated close to the slit-like orifice, both those on the valve and on the collar, are short; whereas the pedicels of the more distant glands are much elongated and project inwards. The glands are thus well placed so to be washed by any fluid coming out of the bladder through the orifice. The valve fits so closely, judging from the result of immersing uninjured bladders in various solutions, that it is doubtful whether any putrid fluid habitually passes outwards. But we must remember that a bladder generally captures several animals; and that each time a fresh animal enters, a puff of foul water must pass out and bathe the glands. Moreover, I have repeatedly found that, by gently pressing bladders which contained air, minute bubbles were driven out through the orifice; and if a bladder is laid on blotting paper and gently pressed, water oozes out.

In this latter case, as soon as the pressure is relaxed, air is drawn in, and the bladder recovers its proper form. If it is now placed under water and again gently pressed, minute bubbles issue from the orifice and nowhere else, showing that the walls of the bladder have not been ruptured. I mention this because Cohn quotes a statement by Treviranus, that air cannot be forced out of a bladder without rupturing it. We may therefore conclude that whenever air is secreted within a bladder already full of water, some water will be slowly driven out through the orifice. Hence I can hardly doubt that the numerous glands crowded round the orifice are adapted to absorb matter from the putrid water, which will occasionally escape from bladders including decayed animals.

In order to test this conclusion, I experimented with various solutions on the glands. As in the case of the quadrifids, salts of ammonia were tried, since these are generated by the final decay of animal matter under water. Unfortunately the glands cannot be carefully examined whilst attached to the bladders in their entire state. Their summits, therefore, including the valve, collar, and antennæ, were sliced off, and the condition of the glands observed; they were then irrigated, whilst beneath a covering glass, with the solutions, and after a time re-examined with the same power as before, namely No. 8 of Hartnack. The following experiments were thus made.

As a control experiment solutions of one part of white sugar and of one part of gum to 218 of water were first used, to see whether these produced any change in the glands. It was also necessary to observe whether the glands were affected by the summits of the bladders having been cut off. The summits of four were thus tried; one being examined after 2 hrs. 30 m., and the other three after 23 hrs.; but there was no marked change in the glands of any of them.

Two summits bearing quite colourless glands were irrigated with a solution of carbonate of ammonia of the same strength (viz. one part to 218 of water), and in 5 m. the primordial utricles of most of the glands were somewhat contracted; they were also thickened in specks or patches, and had assumed a pale brown tint. When looked at again after 1 hr. 30 m., most of them presented a somewhat different appearance. A third specimen was treated with a weaker solution of one part of the carbonate to 437 of water, and after 1 hr. the glands were pale brown and contained numerous granules.

Four summits were irrigated with a solution of one part of nitrate of ammonia to 437 of water. One was examined after 15 m., and the glands seemed affected; after 1 hr. 10 m. there was a greater change, and the primordial utricles in most of them were somewhat shrunk, and included many granules. In the second specimen, the primordial utricles were considerably shrunk and brownish after 2 hrs. Similar effects were observed in the two other specimens, but these were not examined until 21 hrs. had elapsed. The nuclei of many of the glands apparently had increased in size. Five bladders on a branch, which had been kept for a long time in moderately pure water, were cut off and examined, and their glands found very little modified. The remainder of this branch was placed in the solution of the nitrate, and after 21 hrs. two bladders were examined, and all their glands were brownish, with their primordial utricles somewhat shrunk and finely granular.

The summit of another bladder, the glands of which were in a beautifully clear condition, was irrigated with a few drops of a mixed solution of nitrate and phosphate of ammonia, each of one part to 437 of water. After 2 hrs. some few of the glands were brownish. After 8 hrs. almost all the oblong glands were brown and much more opaque than they were before; their primordial utricles were somewhat shrunk and contained a little aggregated granular matter. The spherical glands were still white, but their utricles were broken up into three or four small hyaline spheres, with an irregularly contracted mass in the middle of the basal part. These smaller spheres changed their forms in the course of a few hours, and some of them disappeared. By the next morning, after 23 hrs. 30 m., they had all disappeared, and the glands were brown; their utricles now formed a globular shrunken mass in the middle. The utricles of the oblong glands had shrunk very little, but their contents were somewhat aggregated. Lastly, the summit of a bladder which had been previously irrigated for 21 hrs. with a solution of one part of sugar to 218 of water without being affected, was treated with the above mixed solution; and after 8 hrs. 30 m. all the glands became brown, with their primordial utricles slightly shrunk.

Four summits were irrigated with a putrid infusion of raw meat. No change in the glands was observable for some hours, but after 24 hrs. most of them had become brownish, and more opaque and granular than they were before. In these specimens, as in those irrigated with the salts of ammonia, the nuclei seemed to have increased both in size and solidity, but they were not measured. Five summits were also irrigated with a fresh infusion of raw meat; three of these were not at all affected in 24 hrs., but the glands of the other two had perhaps become more granular. One of the specimens which was not affected was then irrigated with the mixed solution of the nitrate and phosphate of ammonia, and after only 25 m. the glands contained from four or five to a dozen granules. After six additional hours their primordial utricles were greatly shrunk.

The summit of a bladder was examined, and all the glands found colourless, with their primordial utricles not at all shrunk; yet many of the oblong glands contained granules just resolvable with No. 8 of Hartnack. It was then irrigated with a few drops of a solution of one part of urea to 218 of water. After 2 hrs. 25 m. the spherical glands were still colourless; whilst the oblong and two-armed ones were of a brownish tint, and their primordial utricles much shrunk, some containing distinctly visible granules. After 9 hrs. some of the spherical glands were brownish, and the oblong glands were still more changed, but they contained fewer separate granules; their nuclei, on the other hand, appeared larger, as if they had absorbed the granules. After 23 hrs. all the glands were brown, their primordial utricles greatly shrunk, and in many cases ruptured.

A bladder was now experimented on, which was already somewhat affected by the surrounding water; for the spherical glands, though colourless, had their primordial utricles slightly shrunk; and the oblong glands were brownish, with their utricles much, but irregularly, shrunk. The summit was treated with the solution of urea, but was little affected by it in 9 hrs.; nevertheless, after 23 hrs. the spherical glands were brown, with their utricles more shrunk; several of the other glands were still browner, with their utricles contracted into irregular little masses.

Two other summits, with their glands colourless and their utricles not shrunk, were treated with the same solution of urea. After 5 hrs. many of the glands presented a shade of brown, with their utricles slightly shrunk. After 20 hrs. 40 m. some few of them were quite brown, and contained irregularly aggregated masses; others were still colourless, though their utricles were shrunk; but the greater number were not much affected. This was a good instance of how unequally the glands on the same bladder are sometimes affected, as likewise often occurs with plants growing in foul water. Two other summits were treated with a solution which had been kept during several days in a warm room, and their glands were not at all affected when examined after 21 hrs.

A weaker solution of one part of urea to 437 of water was next tried on six summits, all carefully examined before being irrigated. The first was re-examined after 8 hrs. 30 m., and the glands, including the spherical ones, were brown; many of the oblong glands having their primordial utricles much shrunk and including granules. The second summit, before being irrigated, had been somewhat affected by the surrounding water, for the spherical glands were not quite uniform in appearance; and a few of the oblong ones were brown, with their utricles shrunk. Of the oblong glands, those which were before colourless, became brown in 3 hrs. 12 m. after irrigation, with their utricles slightly shrunk. The spherical glands did not become brown, but their contents seemed changed in appearance, and after 23 hrs. still more changed and granular. Most of the oblong glands were now dark brown, but their utricles were not greatly shrunk. The four other specimens were examined after 3 hrs. 30 m., after 4 hrs., and 9 hrs.; a brief account of their condition will be sufficient. The spherical glands were not brown, but some of them were finely granular. Many of the oblong glands were brown; and these, as well as others which still remained colourless, had their utricles more or less shrunk, some of them including small aggregated masses of matter.

Summary of the Observations on Absorption.—From the facts now given there can be no doubt that the variously shaped glands on the valve and round the collar have the power of absorbing matter from weak solutions of certain salts of ammonia and urea, and from a putrid infusion of raw meat. Prof. Cohn believes that they secrete slimy matter; but I was not able to perceive any trace of such action, excepting that, after immersion in alcohol, extremely fine lines could sometimes be seen radiating from their surfaces. The glands are variously affected by absorption; they often become of a brown colour; sometimes they contain very fine granules, or moderately sized grains, or irregularly aggregated little masses; sometimes the nuclei appear to have increased in size; the primordial utricles are generally more or less shrunk and sometimes ruptured. Exactly the same changes may be observed in the glands of plants growing and flourishing in foul water. The spherical glands are generally affected rather differently from the oblong and two-armed ones. The former do not so commonly become brown, and are acted on more slowly. We may therefore infer that they differ somewhat in their natural functions.

It is remarkable how unequally the glands on the bladders on the same branch, and even the glands of the same kind on the same bladder, are affected by the foul water in which the plants have grown, and by the solutions which were employed. In the former case I presume that this is due either to little currents bringing matter to some glands and not to others, or to unknown differences in their constitution. When the glands on the same bladder are differently affected by a solution, we may suspect that some of them had previously absorbed a small amount of matter from the water. However this may be, we have seen that the glands on the same leaf of Drosera are sometimes very unequally affected, more especially when exposed to certain vapours.

If glands which have already become brown, with their primordial utricles shrunk, are irrigated with one of the effective solutions, they are not acted on, or only slightly and slowly. If, however, a gland contains merely a few coarse granules, this does not prevent a solution from acting. I have never seen any appearance making it probable that glands which have been strongly affected by absorbing matter of any kind are capable of recovering their pristine, colourless, and homogeneous condition, and of regaining the power of absorbing.

From the nature of the solutions which were tried, I presume that nitrogen is absorbed by the glands; but the modified, brownish, more or less shrunk, and aggregated contents of the oblong glands were never seen by me or by my son to undergo those spontaneous changes of form characteristic of protoplasm. On the other hand, the contents of the larger spherical glands often separated into small hyaline globules or irregularly shaped masses, which changed their forms very slowly and ultimately coalesced, forming a central shrunken mass. Whatever may be the nature of the contents of the several kinds of glands, after they have been acted on by foul water or by one of the nitrogenous solutions, it is probable that the matter thus generated is of service to the plant, and is ultimately transferred to other parts.

The glands apparently absorb more quickly than do the quadrifid and bifid processes; and on the view above maintained, namely that they absorb matter from putrid water occasionally emitted from the bladders, they ought to act more quickly than the processes; as these latter remain in permanent contact with captured and decaying animals.

Finally, the conclusion to which we are led by the foregoing experiments and observations is that the bladders have no power of digesting animal matter, though it appears that the quadrifids are somewhat affected by a fresh infusion of raw meat. It is certain that the processes within the bladders, and the glands outside, absorb matter from salts of ammonia, from a putrid infusion of raw meat, and from urea. The glands apparently are acted on more strongly by a solution of urea, and less strongly by an infusion of raw meat, than are the processes. The case of urea is particularly interesting, because we have seen that it produces no effect on Drosera, the leaves of which are adapted to digest fresh animal matter. But the most important fact of all is, that in the present and following species the quadrifid and bifid processes of bladders containing decayed animals generally include little masses of spontaneously moving protoplasm; whilst such masses are never seen in perfectly clean bladders.

Development of the Bladders.—My son and I spent much time over this subject with small success. Our observations apply to the present species and to *Utricularia vulgaris*, but were made chiefly on the latter, as the bladders are twice as large as those of *Utricularia neglecta*. In the early part of autumn the stems terminate in large buds, which fall off and lie dormant during the winter at the bottom. The young leaves forming these buds bear bladders in various stages of early development. When the bladders of *Utricularia vulgaris* are about $\frac{1}{100}$ inch (·254 mm.) in diameter (or $\frac{1}{200}$ in the case of *Utricularia neglecta*), they are circular in outline, with a narrow, almost closed, transverse orifice, leading into a hollow filled with water; but the bladders are hollow when much under $\frac{1}{100}$ of an inch in diameter. The orifices face inwards or towards the axis of the plant. At this early age the bladders are flattened in the plane in which the orifice lies, and therefore at right angles to that of the mature bladders. They are covered exteriorly with papillæ of different sizes, many of which have an elliptical outline. A bundle of vessels, formed of simple elongated cells, runs up the short footstalk, and divides at the base of the bladder. One branch extends up the middle of the dorsal surface, and the other up the middle of the ventral surface. In full-grown bladders the ventral bundle divides close beneath the collar, and the two branches run on each side to near where the corners of the valve unite with the collar; but these branches could not be seen in very young bladders.

The accompanying figure (fig. 23) shows a section, which happened to be strictly medial, through the footstalk and between the nascent antennæ of a bladder of *Utricularia vulgaris*, $\frac{1}{100}$ inch in diameter. The specimen was soft, and the young valve became separated from the collar to a greater degree than is natural, and is thus represented. We here clearly see that the valve and collar are infolded prolongations of the walls of the bladder. Even at this early age, glands could be detected on the valve. The state of the quadrifid processes will presently be described. The antennæ at this period consist of minute cellular projections (not shown in the above figure, as they do not lie in the medial plane), which soon bear incipient bristles. In five instances the young antennæ were not of quite equal length; and this fact is intelligible if I am right in believing that they represent two divisions of the leaf, rising from the end of the bladder; for, with the true leaves, whilst very young, the divisions are never, as far as I have seen, strictly opposite; they

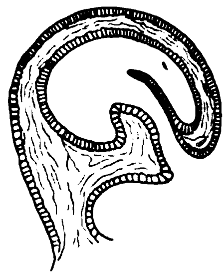

FIG. 23.
(*Utricularia vulgaris.*)
Longitudinal section through a young bladder, $\frac{1}{100}$ of an inch in length, with the orifice too widely open.

must therefore be developed one after the other, and so it would be with the two antennæ.

At a much earlier age, when the half formed bladders are only $\frac{1}{300}$ inch (·0846 mm.) in diameter or a little more, they present a totally different appearance. One is represented on the left side of the accompanying drawing (fig. 24). The young leaves

FIG. 24.
(*Utricularia vulgaris.*)
Young leaf from a winter bud, showing on the left side a bladder in its earliest stage of development.

at this age have broad flattened segments, with their future divisions represented by prominences, one of which is shown on the right side. Now, in a large number of specimens examined by my son, the young bladders appeared as if formed by the oblique folding over of the apex and of one margin with a prominence, against the opposite margin. The circular hollow between the infolded apex and infolded prominence apparently contracts into the narrow orifice, wherein the valve and collar will be developed; the bladder itself being formed by the confluence of the opposed margins of the rest of the leaf. But strong objections may be urged against this view, for we must in this case suppose that the valve and collar are developed asymmetrically from the sides of the apex and prominence. Moreover, the bundles of vascular tissue have to be formed in lines quite irrespective of the original form of the leaf. Until gradations can be shown to exist between this the earliest state and a young yet perfect bladder, the case must be left doubtful.

As the quadrifid and bifid processes offer one of the greatest peculiarities in the genus, I carefully observed their development in *Utricularia neglecta*. In bladders about $\frac{1}{100}$ of an inch in diameter, the inner surface is studded with papillæ, rising from small cells at the junctions of the larger ones. These papillæ consist of a delicate conical protuberance, which narrows into a very short footstalk, surmounted by two minute cells. They thus occupy the same relative position, and closely resemble, except in being smaller and rather more prominent, the papillæ on the outside of the bladders, and on the surfaces of the leaves. The two terminal cells of the papillæ first become much elongated in a line parallel to the inner surface of the bladder. Next, each is divided by a longitudinal partition. Soon the two half-cells thus formed separate from one another; and we now have four cells or an incipient quadrifid process. As there is not space for the two new cells to increase in breadth in their original plane, the one slides partly under the other. Their manner of growth now changes, and their outer sides, instead of their apices, continue to grow. The two lower cells, which have slid partly beneath the two upper ones, form the longer and more upright pair of processes; whilst the two upper cells form the shorter and more horizontal pair; the four together forming a perfect quadrifid. A trace of the primary division between the two cells on the summits of the papillæ can still be seen between the bases of the longer processes. The development of the quadrifids is very liable to be arrested. I have seen a bladder $\frac{1}{50}$ of an inch in length including only primordial papillæ; and another bladder, about half its full size, with the quadrifids in an early stage of development.

As far as I could make out, the bifid processes are developed in the same manner as the quadrifids, excepting that the two primary terminal cells never become divided, and only increase in length. The glands on the valve and collar appear at so early an age that I could not trace their development; but we may reasonably suspect that they are developed from papillæ like those on the outside of the bladder, but with their terminal cells not divided into two. The two segments forming the pedicels of the glands probably answer to the conical protuberance and short footstalk of the quadrifid and bifid processes. I am strengthened in the belief that the glands are developed from papillæ like those on the outside of the bladders, from the fact that in *Utricularia amethystina* the glands extend along the whole ventral surface of the bladder close to the footstalk.

UTRICULARIA VULGARIS.

Living plants from Yorkshire were sent me by Dr. Hooker. This species differs from the last in the stems and leaves being thicker or coarser; their divisions form a more acute angle with one another; the notches on the leaves bear three or four short bristles instead of one; and the bladders are twice as large, or about $\frac{1}{5}$ of an inch (5·08 mm.) in diameter. In all essential respects the bladders resemble those of *Utricularia neglecta*, but the sides of the peristome are perhaps a little more prominent, and always bear, as far as I have seen, seven or eight long multicellular bristles. There are eleven long bristles on each antenna, the terminal pair being included. Five bladders, containing prey of some kind, were examined. The first included five Cypris, a large copepod and a Diaptomus; the second, four Cypris; the third, a single rather large crustacean; the fourth, six crustaceans; and the fifth, ten. My son examined the quadrifid processes in a bladder containing the remains of two crustaceans, and found some of them full of spherical or irregularly shaped masses of matter, which were observed to move and to coalesce. These masses therefore consisted of protoplasm.

UTRICULARIA MINOR.

This rare species was sent me in a living state from Cheshire, through the kindness of Mr. John Price. The leaves and bladders are much smaller than those of *Utricularia neglecta.* The leaves bear fewer and shorter bristles, and the bladders are more globular. The antennæ, instead of projecting in front of the bladders, are curled under the valve, and are armed with twelve or fourteen extremely long multicellular bristles, generally arranged in pairs. These, with seven or eight long bristles on both sides of the peristome, form a sort of net over the valve, which would tend to prevent all animals, excepting very small ones, entering the bladder. The valve and collar have the same essential structure as in the two previous species; but the glands are not quite so numerous; the oblong

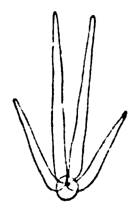

FIG. 25.
(*Utricularia minor.*)
Quadrifid process; greatly enlarged.

ones are rather more elongated, whilst the two-armed ones are rather less elongated. The four bristles which project obliquely from the lower edge of the valve are short. Their shortness, compared with those on the valves of the foregoing species, is intelligible if my view is correct that they serve to prevent too large animals forcing an entrance through the valve, thus injuring it; for the valve is already protected to a certain extent by the incurved antennæ, together with the lateral bristles. The bifid processes are like those in the previous species; but the quadrifids differ in the four arms (fig. 25) being directed to the same side; the two longer ones being central, and the two shorter ones on the outside.

The plants were collected in the middle of July; and the contents of five bladders, which from their opacity seemed full of prey, were examined. The first contained no less than twenty-four minute fresh-water crustaceans, most of them consisting of empty shells, or including only a few drops of red oily matter; the second contained twenty; the third, fifteen; the fourth, ten, some of them being rather larger than usual; and the fifth, which seemed stuffed quite full, contained only seven, but five of these were of unusually large size.. The prey, therefore, judging from these five bladders, consists exclusively of fresh-water crustaceans, most of which appeared to be distinct species from those found in the bladders of the two former species. In one bladder the quadrifids in contact with a decaying mass contained numerous spheres of granular matter, which slowly changed their forms and positions.

UTRICULARIA CLANDESTINA.

This North American species, which is aquatic like the three foregoing ones, has been described by Mrs. Treat, of New Jersey, whose excellent observations have already been largely quoted. I have not as yet seen any full description by her of the structure of the bladder, but it appears to be lined with quadrifid processes. A vast number of captured animals were found within the bladders; some being crustaceans, but the greater number delicate, elongated larvæ, I suppose of Culicidæ. On some stems, "fully nine out of every ten bladders contained these larvæ or their remains." The larvæ "showed signs of life from twenty-four to thirty-six hours after being imprisoned," and then perished.

CHAPTER XVIII.

UTRICULARIA (*continued*).

Utricularia montana — Description of the bladders on the subterranean rhizomes — Prey captured by the bladders of plants under culture and in a state of nature — Absorption by the quadrifid processes and glands — Tubers serving as reservoirs for water — Various other species of Utricularia — Polypompholyx — Genlisea, different nature of the trap for capturing prey — Diversified methods by which plants are nourished.

UTRICULARIA MONTANA.—This species inhabits the tropical parts of South America, and is said to be epiphytic; but, judging from the state of the roots (rhizomes) of some dried specimens from the herbarium at Kew, it likewise lives in earth, probably in crevices of rocks. In English hothouses it is grown in peaty soil. Lady Dorothy Nevill was so kind as to give me a fine plant, and I received another from Dr. Hooker. The leaves are entire, instead of being much divided, as in the foregoing aquatic species. They are elongated, about 1½ inch in breadth, and furnished with a distinct footstalk. The plant produces numerous colourless rhizomes, as thin as threads, which bear minute bladders, and occasionally swell into tubers, as will

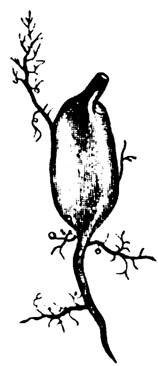

FIG. 26.
(*Utricularia montana.*)
Rhizome swollen into a tuber; the branches bearing minute bladders; of natural size.

hereafter be described. These rhizomes appear exactly like roots, but occasionally throw up green shoots. They penetrate the earth sometimes to the depth of more than 2 inches; but when the plant grows as an epiphyte, they must creep amidst the mosses, roots, decayed bark, &c., with which the trees of these countries are thickly covered.

As the bladders are attached to the rhizomes, they are necessarily subterranean. They are produced in extraordinary numbers. One of my plants, though young, must have borne several hundreds; for a single branch out of an entangled mass had thirty-two, and another branch, about 2 inches in length (but with its end and one side branch broken off), had seventy-three bladders.* The bladders are compressed and rounded, with the ventral surface, or that between the summit of the long delicate footstalk and valve, extremely short (fig. 27). They are colourless and almost as transparent as glass, so that they appear smaller than they really are, the largest being under the $\frac{1}{20}$ of an inch (1·27 mm.) in its longer diameter. They are formed of rather large angular cells, at the junctions of which oblong papillæ project, corresponding with those on the surfaces of the bladders of the previous species. Similar papillæ abound on the rhizomes, and even on the entire leaves, but they are rather broader on the latter. Vessels, marked with parallel bars instead of by a spiral line, run up the footstalks, and

* Prof. Oliver has figured a plant of *Utricularia Jamesoniana* ('Proc. Linn. Soc.' vol. iv. p. 169) having entire leaves and rhizomes, like those of our present species; but the margins of the terminal halves of some of the leaves are converted into bladders. This fact clearly indicates that the bladders on the rhizomes of the present and following species are modified segments of the leaf; and they are thus brought into accordance with the bladders attached to the divided and floating leaves of the aquatic species.

just enter the bases of the bladders; but they do not bifurcate and extend up the dorsal and ventral surfaces, as in the previous species.

The antennæ are of moderate length, and taper to a fine point; they differ conspicuously from those before described, in not being armed with bristles. Their bases are so abruptly curved that their tips generally rest one on each side of the middle of the bladder, but

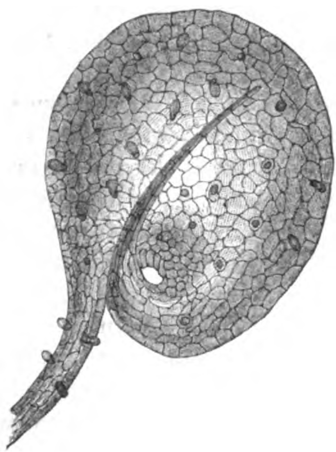

FIG. 27.
(*Utricularia montana.*)
Bladder; about 27 times enlarged.

sometimes near the margin. Their curved bases thus form a roof over the cavity in which the valve lies; but there is always left on each side a little circular passage into the cavity, as may be seen in the drawing, as well as a narrow passage between the bases of the two antennæ. As the bladders are subterranean, had it not been for the roof, the cavity in which the valve lies would have been liable to be blocked up with earth and rubbish; so that the curvature of the antennæ is a serviceable character. There are no bristles on the outside of the collar or peristome, as in the foregoing species.

The valve is small and steeply inclined, with its free posterior edge abutting against a semicircular, deeply depending collar. It is moderately transparent, and bears two pairs of short stiff bristles, in the same position as in the other species. The presence of these four bristles, in contrast with the absence of those on the antennæ and collar, indicates that they are of functional importance, namely, as I believe, to prevent too large animals forcing an entrance through the valve. The many glands of diverse shapes attached to the valve and round the collar in the previous species are here absent, with the exception of about a dozen of the two-armed or transversely elongated kind, which are seated near the borders of the valve, and are mounted on very short footstalks. These glands are only the $\frac{3}{4000}$ of an inch (·019 mm.) in length; though so small, they act as absorbents. The collar is thick, stiff, and almost semi-circular; it is formed of the same peculiar brownish tissue as in the former species.

The bladders are filled with water, and sometimes include bubbles of air. They bear internally rather short, thick, quadrifid processes arranged in approximately concentric rows. The two pairs of arms of which they are formed differ only a little in length, and stand in a peculiar position (fig. 28); the two longer ones forming one line, and the two shorter ones another parallel line. Each arm includes a small spherical mass of brownish matter, which, when crushed, breaks into angular pieces. I have no doubt that these spheres are nuclei, for closely similar ones are present in the cells forming the walls of the bladders. Bifid processes, having rather short oval arms, arise in the usual position on the inner side of the collar.

These bladders, therefore, resemble in all essential respects the larger ones of the foregoing species. They differ chiefly in the absence of the numerous glands on the valve and round the collar, a few minute ones of one kind alone being present on the valve. They differ more conspicuously in the absence of the long bristles on the antennæ and on the outside of the collar. The presence of these bristles in the previously mentioned species probably relates to the capture of aquatic animals.

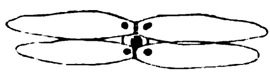

FIG. 28.
(*Utricularia montana.*)
One of the quadrifid processes; much enlarged.

It seemed to me an interesting question whether the minute bladders of *Utricularia montana* served, as in the previous species, to capture animals living in the earth, or in the dense vegetation covering the trees on which this species is epiphytic; for in this case we should have a new sub-class of carnivorous plants, namely, subterranean feeders. Many bladders, therefore, were examined, with the following results:—

(1) A small bladder, less than $\frac{1}{30}$ of an inch (·847 mm.) in diameter, contained a minute mass of brown, much decayed matter; and in this, a tarsus with four or five joints, terminating in a double hook, was clearly distinguished under the microscope. I suspect that it was a remnant of one of the Thysanoura. The quadrifids in contact with this decayed remnant contained either small masses of translucent, yellowish matter, generally more

or less globular, or fine granules. In distant parts of the same bladder, the processes were transparent and quite empty, with the exception of their solid nuclei. My son made at short intervals of time sketches of one of the above aggregated masses, and found that they continually and completely changed their forms; sometimes separating from one another and again coalescing. Evidently protoplasm had been generated by the absorption of some element from the decaying animal matter.

(2) Another bladder included a still smaller speck of decayed brown matter, and the adjoining quadrifids contained aggregated matter, exactly as in the last case.

(3) A third bladder included a larger organism, which was so much decayed that I could only make out that it was spinose or hairy. The quadrifids in this case were not much affected, excepting that the nuclei in the several arms differed much in size; some of them containing two masses having a similar appearance.

(4) A fourth bladder contained an articulate organism, for I distinctly saw the remnant of a limb, terminating in a hook. The quadrifids were not examined.

(5) A fifth included much decayed matter apparently of some animal, but with no recognisable features. The quadrifids in contact contained numerous spheres of protoplasm.

(6) Some few bladders on the plant which I received from Kew were examined; and in one, there was a worm-shaped animal very little decayed, with a distinct remnant of a similar one greatly decayed. Several of the arms of the processes in contact with these remains contained two spherical masses, like the single solid nucleus which is properly found in each arm. In another bladder there was a minute grain of quartz, reminding me of two similar cases with *Utricularia neglecta.*

As it appeared probable that this plant would capture a greater number of animals in its native country than under culture, I obtained permission to remove small portions of the rhizomes from dried specimens in the herbarium at Kew. I did not at first find out that it was advisable to soak the rhizomes for two or three days, and that it was necessary to open the bladders and spread out their contents on glass; as from their state of decay and from having been dried and pressed, their nature could not otherwise be well distinguished. Several bladders on a plant which had grown in black earth in New Granada were first examined; and four of these included remnants of animals. The first contained a hairy Acarus, so much decayed that nothing was left except its transparent coat;

also a yellow chitinous head of some animal with an internal fork, to which the œsophagus was suspended, but I could see no mandibles; also the double hook of the tarsus of some animal; also an elongated greatly decayed animal; and lastly, a curious flask-shaped organism, having the walls formed of rounded cells. Professor Claus has looked at this latter organism, and thinks that it is the shell of a rhizopod, probably one of the Arcellidæ. In this bladder, as well as in several others, there were some unicellular Algæ, and one multicellular Alga, which no doubt had lived as intruders.

A second bladder contained an Acarus much less decayed than the former one, with its eight legs preserved; as well as remnants of several other articulate animals. A third bladder contained the end of the abdomen with the two hinder limbs of an Acarus, as I believe. A fourth contained remnants of a distinctly articulated bristly animal, and of several other organisms, as well as much dark brown organic matter, the nature of which could not be made out.

Some bladders from a plant, which had lived as an epiphyte in Trinidad, in the West Indies, were next examined, but not so carefully as the others; nor had they been soaked long enough. Four of them contained much brown, translucent, granular matter, apparently organic, but with no distinguishable parts. The quadrifids in two were brownish, with their contents granular; and it was evident that they had absorbed matter. In a fifth bladder there was a flask-shaped organism, like that above mentioned. A sixth contained a very long, much decayed, worm-shaped animal. Lastly, a seventh bladder contained an organism, but of what nature could not be distinguished.

Only one experiment was tried on the quadrifid processes and glands with reference to their power of absorption. A bladder was punctured and left for 24 hrs. in a solution of one part of urea to 437 of water, and the quadrifid and bifid processes were found much affected. In some arms there was only a single symmetrical globular mass, larger than the proper nucleus, and consisting of yellowish matter, generally translucent but sometimes granular; in others there were two masses of different sizes, one large and the other small; and in others there were irregularly shaped globules; so that it appeared as if the limpid contents of the processes, owing to the absorption of matter from the solution, had become aggregated sometimes round the nucleus, and sometimes into separate masses; and that these then tended to coalesce. The primordial utricle or protoplasm lining the processes was also thickened here and there into irregular and variously shaped specks of yellowish translucent matter, as occurred in the case of *Utricularia neglecta* under similar treatment. These specks apparently did not change their forms.

The minute two-armed glands on the valve were also affected by the solution; for they now contained several, sometimes as many as six or eight, almost spherical masses of translucent matter, tinged with yellow, which slowly changed their forms and positions. Such masses were never observed in these glands in their ordinary state. We may therefore infer that they serve for absorption. Whenever a little water is expelled from a bladder containing animal remains (by the means formerly specified, more especially by the generation of bubbles of air), it will fill the cavity in which the valve lies; and thus the glands will be able to utilise decayed matter which otherwise would have been wasted.

Finally, as numerous minute animals are captured by this plant in its native country and when cultivated, there can be no doubt that the bladders, though so small, are far from being in a rudimentary condition; on the contrary, they are highly efficient traps. Nor can there be any doubt that matter is absorbed from the decayed prey by the quadrifid and bifid processes, and that protoplasm is thus generated. What tempts animals of such diverse kinds to enter the cavity beneath the bowed antennæ, and then force their way through the little slit-like orifice between the valve and collar into the bladders filled with water, I cannot conjecture.

Tubers.—These organs, one of which is represented in a previous figure (fig. 26) of the natural size, deserve a few remarks. Twenty were found on the rhizomes of a single plant, but they cannot be strictly counted; for, besides the twenty, there were all possible gradations between a short length of a rhizome just perceptibly swollen and one so much swollen that it might be doubtfully called a tuber. When well developed, they are oval and symmetrical, more so than appears in the figure. The largest which I saw was 1 inch (25·4 mm.) in length and ·45 inch (11·43 mm.) in breadth. They commonly lie near the surface, but some are buried at the depth of 2 inches. The buried ones are dirty white, but those partly exposed to the light become greenish from the development, of chlorophyll in their superficial cells. They terminate in a rhizome, but this sometimes decays and drops off. They do not contain any air, and they sink in water; their surfaces are covered with the usual papillæ. The bundle of vessels which runs up each rhizome, as soon as it enters the tuber, separates into three distinct bundles, which reunite at the opposite end. A rather thick slice of a tuber is almost as transparent as glass, and is seen to consist of large angular cells, full of water and not containing starch or any other solid matter. Some slices were left in alcohol for several days, but only a few extremely minute granules of matter were precipitated on the walls of the cells; and these were much smaller and fewer than those precipitated on the cell-walls of the rhizomes and bladders. We may therefore conclude that the tubers do not serve as reservoirs for food, but for water during the dry season to which the plant is probably exposed. The many little bladders filled with water would aid towards the same end.

To test the correctness of this view, a small plant, growing in light peaty earth in a pot (only $4\frac{1}{2}$ by $4\frac{1}{2}$ inches outside measure) was copiously watered, and then kept without a drop of water in the hothouse. Two of the upper tubers were beforehand uncovered and measured, and then loosely covered up again. In a fortnight's time the earth in the pot appeared extremely dry; but not until the thirty-fifth day were the leaves in the least affected; they then became slightly reflexed, though still soft and green. This plant, which bore only ten tubers, would no doubt have resisted the drought for even a longer time, had I not previously removed three of the tubers and cut off several long rhizomes. When, on the thirty-fifth day, the earth in the pot was turned out, it appeared as dry as the dust on a road. All the tubers had their surfaces much wrinkled, instead of being smooth and tense. They had all shrunk, but I cannot say accurately how much; for as they were at first symmetrically oval, I measured only their length and thickness; but they contracted in a transverse line much more in one direction than in another, so as to become greatly flattened. One of the two tubers which had been measured was now three-fourths of its original length, and two-thirds of its original thickness in the direction in which it had been measured, but in another direction only one-third of its former thickness. The other tuber was one-fourth shorter, one-eighth less thick in the direction in which it had been measured, and only half as thick in another direction.

A slice was cut from one of these shrivelled tubers and examined. The cells still contained much water and no air, but they were more rounded or less angular than before, and their walls not nearly so straight; it was therefore clear that the cells had contracted. The tubers, as long as they remain alive, have a strong attraction for water; the shrivelled one, from which a slice had been cut, was left in water for 22 hrs. 30 m., and its surface became as smooth and tense as it originally was. On the other hand, a shrivelled tuber, which by some accident had been separated from its rhizome, and which appeared dead, did not swell in the least, though left for several days in water.

With many kinds of plants, tubers, bulbs, &c. no doubt serve in part as reservoirs for water, but I know of no case, besides the present one, of such organs having been developed solely for this purpose. Prof. Oliver informs me that two or three other species of Utricularia are provided with these appendages; and the group containing them has in consequence received the name of *orchidioides*. All the other species of Utricularia, as well as of certain closely related genera, are either aquatic or marsh plants; therefore, on the principle of nearly allied plants generally having a similar constitution, a never failing supply of water would probably be of great importance to our present species. We can thus understand the meaning of the development of its tubers, and of their number on the same plant, amounting in one instance to at least twenty.

UTRICULARIA NELUMBIFOLIA, AMETHYSTINA, GRIFFITHII, CÆRULEA, ORBICULATA, MULTICAULIS.

As I wished to ascertain whether the bladders on the rhizomes of other species of Utricularia, and of the species of certain closely allied genera, had the same essential structure as those of *Utricularia montana,* and whether they captured prey, I asked Prof. Oliver to send me fragments from the herbarium at Kew. He kindly selected some of the most distinct forms, having entire leaves, and believed to inhabit marshy ground or water. My son, Francis Darwin, examined them, and has given me the following observations; but it should be borne in mind that it is extremely difficult to make out the structure of such minute and delicate objects after they have been dried and pressed.*

Utricularia nelumbifolia (Organ Mountains, Brazil).—The habitat of this species is remarkable. According to its discoverer, Mr. Gardner,† it is aquatic, but "is only to be found growing in the water which collects in the bottom of the leaves of a large Tillandsia, that inhabits abundantly an arid rocky part of the mountain, at an elevation of about 5000 feet above the level of the sea. Besides the ordinary method by seed, it propagates itself by runners, which it throws out from the base of the flower-stem; this runner is always found directing itself towards the nearest Tillandsia, when it inserts its point into the water and gives origin to a new plant, which in its turn sends out another shoot. In this manner I have seen not less than six plants united." The bladders resemble those of *Utricularia montana* in all essential respects, even to the presence of a few minute two-armed glands on the valve. Within one bladder there was the remnant of the abdomen of some larva or crustacean of large size,

* Prof. Oliver has given ('Proc. Linn. Soc.' vol. iv. p. 169) figures of the bladders of two South American species, namely, *Utricularia Jamesoniana* and *peltata;* but he does not appear to have paid particular attention to these organs.

† 'Travels in the Interior of Brazil, 1836–41,' p. 527.

having a brush of long sharp bristles at the apex. Other bladders included fragments of articulate animals, and many of them contained broken pieces of a curious organism, the nature of which was not recognised by anyone to whom it was shown.

Utricularia amethystina (Guiana).—This species has small entire leaves, and is apparently a marsh plant; but it must grow in places where crustaceans exist, for there were two small species within one of the bladders. The bladders are nearly of the same shape as those of *Utricularia montana*, and are covered outside with the usual papillæ; but they differ remarkably in the antennæ being reduced to two short points, united by a membrane hollowed out in the middle. This membrane is covered with innumerable oblong glands supported on long footstalks; most of which are arranged in two rows converging towards the valve. Some, however, are seated on the margins of the membrane; and the short ventral surface of the bladder, between the petiole and valve, is thickly covered with glands. Most of the heads had fallen off, and the footstalks alone remained; so that the ventral surface and the orifice, when viewed under a weak power, appeared as if clothed with fine bristles. The valve is narrow, and bears a few almost sessile glands. The collar against which the edge shuts is yellowish, and presents the usual structure. From the large number of glands on the ventral surface and round the orifice, it is probable that this species lives in very foul water, from which it absorbs matter, as well as from its captured and decaying prey.

Utricularia griffithii (Malay and Borneo).—The bladders are transparent and minute; one which was measured being only $\frac{28}{1000}$ of an inch (·711 mm.) in diameter. The antennæ are of moderate length, and project straight forward; they are united for a short space at their bases by a membrane; and they bear a moderate number of bristles or hairs, not simple as heretofore, but surmounted by glands. The bladders also differ remarkably from those of the previous species, as within there are no quadrifid, only bifid, processes. In one bladder there was a minute aquatic larva; in another the remains of some articulate animal; and in most of them grains of sand.

Utricularia cærulea (India).—The bladders resemble those of the last species, both in the general character of the antennæ and in the processes within being exclusively bifid. They contained remnants of entomostracan crustaceans.

Utricularia orbiculata (India).—The orbicular leaves and the stems bearing the bladders apparently float in water. The bladders do not differ much from those of the two last species. The antennæ, which are united for a short distance at their bases, bear on their outer surfaces and summits numerous, long, multicellular hairs, surmounted by glands. The processes within the bladders are quadrifid, with the four diverging arms of equal length. The prey which they had captured consisted of entomostracan crustaceans.

Utricularia multicaulis (Sikkim, India, 7000 to 11,000 feet).—The bladders, attached to rhizomes, are remarkable from the structure of the antennæ. These are broad, flattened, and of large size; they bear on their margins multicellular hairs, surmounted by glands. Their bases are united into a single, rather narrow pedicel, and they thus appear like a great digitate expansion at one end of the bladder. Internally the quadrifid processes have divergent arms of equal length. The bladders contained remnants of articulate animals.

POLYPOMPHOLYX.

This genus, which is confined to Western Australia, is characterised by having a "quadripartite calyx." In other respects, as Prof. Oliver remarks,* "it is quite a Utricularia."

Polypompholyx multifida.—The bladders are attached in whorls round the summits of stiff stalks. The two antennæ are represented by a minute membranous fork, the basal part of which forms a sort of hood over the orifice. This hood expands into two wings on each side of the bladder. A third wing or crest appears to be formed by the extension of the dorsal surface of the petiole; but the structure of these three wings could not be clearly made out, owing to the state of the specimens. The inner surface of the hood is lined with long simple hairs, containing aggregated matter, like that within the quadrifid processes of the previously described species when in contact with decayed animals. These hairs appear therefore to serve as absorbents. A valve was seen, but its structure could not be determined. On the collar round the valve there are in the place of glands numerous one-celled papillæ, having very short footstalks. The quadrifid processes have divergent arms of equal length. Remains of entomostracan crustaceans were found within the bladders.

Polypompholyx tenella.—The bladders are smaller than those of the last species, but have the same general structure. They were full of débris, apparently organic, but no remains of articulate animals could be distinguished.

* 'Proc. Linn. Soc.' vol. iv. p. 171.

GENLISEA.

This remarkable genus is technically distinguished from Utricularia, as I hear from Prof. Oliver, by having a five-partite calyx. Species are found in several parts of the world, and are said to be "herbæ annuæ paludosæ."

Genlisea ornata (Brazil).—This species has been described and figured by Dr. Warming,* who states that it bears two kinds of leaves, called by him spathulate and utriculiferous. The latter include cavities; and as these differ much from the bladders of the foregoing species, it will be convenient to speak of them as utricles. The accompanying figure (fig. 29) of one of the utriculiferous leaves, about thrice enlarged, will illustrate the following description by my son, which agrees in all essential points with that given by Dr. Warming. The utricle (*b*) is formed by a slight enlargement of the narrow blade of the leaf. A hollow neck (*n*), no less than fifteen times as long as the utricle itself, forms a passage from the transverse slit-like orifice (*o*) into the cavity of the utricle. A utricle which measured $\frac{1}{36}$ of an inch (·705 mm.) in its longer diameter had a neck $\frac{15}{36}$ (10·583 mm.) in length, and $\frac{1}{100}$ of an inch (·254 mm.) in breadth. On each side of the orifice there is a long spiral arm or tube (*a*); the structure of which will be best understood by the following illustration. Take a narrow ribbon and wind it spirally round a thin cylinder, so that the edges come into contact along its whole length; then pinch up the two edges so as to form a little crest, which will of course wind spirally

* "Bidrag til Kundskaben om Lentibulariaceæ," Copenhagen, 1874.

round the cylinder like a thread round a screw. If the cylinder is now removed, we shall have a tube like one of the spiral arms. The two projecting edges are not actually united, and a needle can be pushed in easily between them. They are indeed in many places a little separated, forming narrow entrances into the tube; but this may be the result of the drying of the specimens. The lamina of which the tube is formed seems to be a lateral prolongation of the lip of the orifice; and the spiral line between the two projecting edges is continuous with the corner of the orifice. If a fine bristle is pushed down one of the arms, it passes into the top of the hollow neck. Whether the arms are open or closed at their extremities could not be determined, as all the specimens were broken; nor does it appear that Dr. Warming ascertained this point.

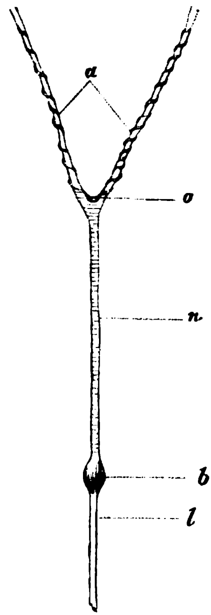

FIG. 29.
(*Genlisea ornata.*)
Utriculiferous leaf; enlarged about three times.

l Upper part of lamina of leaf.
b Utricle or bladder.
n Neck of utricle.
o Orifice.
a Spirally wound arms, with their ends broken off.

So much for the external structure. Internally the lower part of the utricle is covered with spherical papillæ, formed of four cells (sometimes eight according to Dr. Warming), which evidently answer to the quadrifid processes within the bladders of Utricularia.

These papillæ extend a little way up the dorsal and ventral surfaces of the utricle; and a few, according to Warming, may be found in the upper part. This upper region is covered by many transverse rows, one above the other, of short, closely approximate hairs, pointing downwards. These hairs have broad bases, and their tips are formed by a separate cell. They are absent in the lower part of the utricle where the papillæ abound. The neck is likewise lined throughout its whole length with transverse rows of long, thin, transparent hairs, having broad bulbous (fig. 30) bases, with similarly constructed sharp points. They arise from little projecting ridges, formed of rectangular epidermic cells. The hairs vary a little in length, but their points generally extend down to the row next below; so that if the neck is split open and laid flat, the inner surface resembles a paper of pins,—the hairs representing the pins, and the little transverse ridges representing the folds of paper through which the pins are thrust. These rows of hairs are indicated in the previous figure (29) by numerous transverse lines crossing the neck. The inside of the neck is

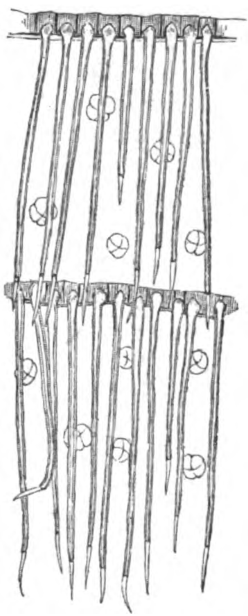

FIG. 30.
(*Genlisea ornata.*)
Portion of inside of neck leading into the utricle, greatly enlarged, showing the downward pointed bristles, and small quadrifid cells or processes.

also studded with papillæ; those in the lower part are spherical and formed of four cells, as in the lower part of the utricle; those in the upper part are formed of two cells, which are much elongated downwards beneath their points of attachment. These two-celled papillæ apparently correspond with the bifid process in the upper part of the bladders of Utricularia. The narrow transverse orifice (*o*, fig. 29) is situated between the bases of the two spiral arms. No valve could be detected here, nor was any such structure seen by Dr. Warming. The lips of the orifice are armed with many short, thick, sharply pointed, somewhat incurved hairs or teeth.

The two projecting edges of the spirally wound lamina, forming the arms, are provided with short incurved hairs or teeth, exactly like those on the lips. These project inwards at right angles to the spiral line of junction between the two edges. The inner surface of the lamina supports two-celled, elongated papillæ, resembling those in the upper part of the neck, but differing slightly from them, according to Warming, in their footstalks being formed by prolongations of large epidermic cells; whereas the papillæ within the neck rest on small cells sunk amidst the larger ones. These spiral arms form a conspicuous difference between the present genus and Utricularia.

Lastly, there is a bundle of spiral vessels which, running up the lower part of the linear leaf, divides close beneath the utricle. One branch extends up the dorsal and the other up the ventral side of both the utricle and neck. Of these two branches, one enters one spiral arm, and the other branch the other arm.

The utricles contained much débris or dirty matter, which seemed organic, though no distinct organisms could be recognised. It is, indeed, scarcely possible that any object could enter the small orifice and pass down the long narrow neck, except a living creature. Within the necks, however, of some specimens, a worm with retracted horny jaws, the abdomen of some articulate animal, and specks of dirt, probably the remnants of other minute creatures, were found. Many of the papillæ within both the utricles and necks were discoloured, as if they had absorbed matter.

From this description it is sufficiently obvious how Genlisea secures its prey. Small animals entering the narrow orifice—but what induces them to enter is not known any more than in the case of Utricularia—would find their egress rendered difficult by the sharp incurved hairs on the lips, and as soon as they passed some way down the neck, it would be scarcely possible for them to return, owing to the many transverse rows of long, straight, downward pointing hairs, together with the ridges from which these project. Such creatures would, therefore, perish either within the neck or utricle; and the quadrifid and bifid papillæ would absorb matter from their decayed remains. The transverse rows of hairs are so numerous that they seem superfluous merely for the sake of preventing the escape of prey, and as they are thin and delicate, they probably serve as additional absorbents, in the same manner as the flexible bristles on the infolded margins of the leaves of Aldrovanda. The spiral arms no doubt act as accessory traps. Until fresh leaves are examined, it cannot be told whether the line of junction of the spirally wound lamina is a little open along its whole course, or only in parts, but a small creature which forced its way into the tube at any point, would be prevented from escaping by the incurved hairs, and would find an open path down the tube into the neck, and so into the utricle. If the creature perished within the spiral arms, its decaying remains would be absorbed and utilised by the bifid papillæ. We thus see that animals are captured by Genlisea, not by means of an elastic valve, as with the foregoing species, but by a contrivance resembling an eel-trap, though more complex.

Genlisea africana (South Africa).—Fragments of the utriculiferous leaves of this species exhibited the same structure as those of *Genlisea ornata.* A nearly perfect Acarus was found within the utricle or neck of one leaf, but in which of the two was not recorded.

Genlisea aurea (Brazil).—A fragment of the neck of a utricle was lined with transverse rows of hairs, and was furnished with elongated papillæ, exactly like those within the neck of *Genlisea ornata.* It is probable, therefore, that the whole utricle is similarly constructed.

Genlisea filiformis (Bahia, Brazil).—Many leaves were examined and none were found provided with utricles, whereas such leaves were found without difficulty in the three previous species. On the other hand, the rhizomes bear bladders resembling in essential character those on the rhizomes of Utricularia. These bladders are transparent, and very small, viz. only $\frac{1}{100}$ of an inch (·254 mm.) in length. The antennæ are not united at their bases, and apparently bear some long hairs. On the outside of the bladders there are only a few papillæ, and internally very few quadrifid processes. These latter, however, are of unusually large size, relatively to the bladder, with the four divergent arms of equal length. No prey could be seen within these minute bladders. As the rhizomes of this species were furnished with bladders, those of *Genlisea africana, ornata,* and *aurea* were carefully examined, but none could be found. What are we to infer from these facts? Did the three species just named, like their close allies, the several species of Utricularia, aboriginally possess bladders on their rhizomes, which they afterwards lost, acquiring in their place utriculiferous leaves? In support of this view it may be urged that the bladders of *Genlisea filiformis* appear from their small size and from the fewness of their quadrifid processes to be tending towards abortion; but why has not this species acquired utriculiferous leaves, like its congeners?

Conclusion.—It has now been shown that many species of Utricularia and of two closely allied genera, inhabiting the most distant parts of the world—Europe, Africa, India, the Malay Archipelago, Australia, North and South America—are admirably adapted for capturing by two methods small aquatic or terrestrial animals, and that they absorb the products of their decay.

Ordinary plants of the higher classes procure the requisite inorganic elements from the soil by means of their roots, and absorb carbonic acid from the atmosphere by means of their leaves and stems. But we have seen in a previous part of this work that there is a class of plants which digest and afterwards absorb animal matter, namely, all the Droseraceæ, Pinguicula, and, as discovered by Dr. Hooker, Nepenthes, and to this class other species will almost certainly soon be added. These plants can dissolve matter out of certain vegetable substances, such as pollen, seeds, and bits of leaves. No doubt their glands likewise absorb the salts of ammonia brought to them by the rain. It has also been shown that some other plants can absorb ammonia by their glandular hairs; and these will profit by that brought to them by the rain. There is a second class of plants which, as we have just seen, cannot digest, but absorb the products of the decay of the animals which they capture, namely, Utricularia and its close allies; and from the excellent observations of Dr. Mellichamp and Dr. Canby, there can scarcely be a doubt that Sarracenia and Darlingtonia may be added to this class, though the fact can hardly be considered as yet fully proved. There is a third class of plants which feed, as is now generally admitted, on the products of the decay of vegetable matter, such as the bird's-nest orchis (Neottia), &c. Lastly, there is the well-known fourth class of parasites (such as the mistletoe), which are nourished by the juices of living plants. Most, however, of the plants belonging to these four classes obtain part of their carbon, like ordinary species, from the atmosphere. Such are the diversified means, as far as at present known, by which higher plants gain their subsistence.

INDEX.

Letter 2951—Darwin to Daniel Oliver
17 Oct [1860]

15 Marine Parade | Eastbourne
Oct 17th

My dear Sir

I am infinitely obliged for your mass of interesting facts & extracts.—f1 The only at all full account which I have seen of Dionæa is by Mr Curtus, quoted by author (Lindley?) in Penny Encyclopædia.f2 Lindley also refers to Dionæa having been fed & flourished on chopped m eat.— I think you could see with lens on growing plant whether colour in Sensitive Hairs becomes broken after being touched; that experiment & effect of C. of Ammonia on disc could be very interesting. A good dissector, I daresay could follow the cells with red matter from base of sensitive Hair, & thus follow its *nerves*!—

Many thanks about stomata; it was uncommonly stupid in me not to think of your explanation, which I have hardly a doubt is right;f3 for it was after removing the tortoise-like glands, which are mounted on *very* short footstalks, that I saw the appearance of stoata: I have hardly a doubt that my so-called stomata are 2 cells of the footstalk.—

Thanks for your various analogies & co parisons about the moving red matter: it is beyond me; I shall just publish what I saw.—f4 I think that you have is understood me in supposing that this appearance follows only from C. of Ammonia.— it is *better* seen in the Hairs which have naturally contracted over a fly or other object; & this it is, which seem s to me to make the case curious.— I have been ascertaining this morning how quickly C. of Ammonia acts; & certainly 13 seconds suffice for the absorption & for a marked change in structure in the glands; in one minute the action reaches the upper part of footstalk.— No other substance (such as Acetate, Oxalate, nitrate of Ammonia &c &c) acts nearly so quickly, though they do act after some time; the acetate of Ammonia is next in quickness.— I *suspect* that m ilk, urine &c & these salts do not act until they have become decomposed, & yield C. of Ammonia.—I cannot avoid suspecting that we see in the action of these substances on the leaves of Drosera what chemists believe takes place with organic manures on the roots of other plants.—f5 I am going to try tomorrow C. of Ammonia on the root of Drosera & on some other common plant.—f6

Thanks about Elatine—& for Goodenia Plants.— Pray thank Crokerf7 for all great trouble which he has taken.—

I have told Murray to send you copy of m y Journal,f8 which I am very glad you did not possess.—

Yours very truly | C. Darwin

The day after tomorrow I shall begin & draw up m y paper on Drosera; for I have wasted a shameful lot of time on it—& **yours** also.f9

The leaves of D. spathulata will not open.—

Footnotes

f1 See preceding letter. The letter that apparently accompanied the note has not been found.

f2 Moses Ashley Curtis, a resident of North Carolina where *Dionaea* is native, was quoted by John Lindley in [Lindley] 1837, p. 508. CD cited Curtis 1834 in *Insectivorous plants*, p. 301 n.

f3 The stomata of *Dionaea muscipula* were apparently discussed in the missing portion of the preceding letter. For CD's views on the fine structure of the leaves, see the letter to Daniel Oliver, 14 October [1860].

f4 CD described the phenomenon of aggregation in *Insectivorous plants*, chapter 3.

f5 CD was familiar with the prevailing view of agricultural chemists that the roots of plants absorbed nitrogen derived from the decay of animal matter. A copy of Liebig 1840, which discusses this point, is in the Darwin Library–CUL. For CD's reading of the works of Justus von Liebig, see *Correspondence* vol. 4, Appendix IV.

f6 CD's experiments on the absorption of carbonate of ammonia by the roots of *Drosera rotundifolia* were given in *Insectivorous plants*, pp. 141–2. Further experiments on the roots of other plants were ultimately given in his paper on `The action of carbonate of ammonia on the roots of certain plants' (1882) (*Collected papers* 2: 236–56). By that time, CD had decided that aggregation was the result of an accumulation of waste products in the cells at the tip of the root.

f7 Charles William Crocker. See letter to Daniel Oliver, 5 October [1860].

f8 *Journal of researches* (1860). See second letter to Daniel Oliver, 12 [October 1860].

f9 Although CD did not publish the results of his study of *Drosera* until 1875 (*Insectivorous plants*), he delivered a paper on the subject on 21 February 1861 at a meeting of the Philosophical Club of the Royal Society (Bonney 1919, p. 154). The index to his `Eastbourne paper' is in DAR 54: 1.

Letter 3853—Darwin to John Scott
11 Dec [1862]

Down Brom ley Kent
Decr. 11th.—

Dear Sir

I have read your paper with much interest.f2 You ask for rem arks on matter, which is alone really important, shall you think me impertinent (I am sure I do not mean to be so) if I hazard a rem ark on style, which is of more importance than some think? In my opinion (whether or no worth much) your paper would have been much better if written more simply & less elaborated,—m ore like your letters. It is a golden rule always to use, *if possible*, a short old Saxon word. Such a sentence as “so purely dependent is the incipient plant on the specific morphological tendency”f3—does not sound to my ears like good m other English—it wants translating.—

Here & there you might, I think, have condensed some sentences: I go on plan of thinking every *single* word which can be omitted without actual loss of sense as a *decided* gain.— Now perhaps you will think me a muddling intruder; Anyhow it is the advice of an old hackneyed writer who sincerely wishes you well.—

Your rem arks on the two sexes counteracting variability in product of the one is new to me.f4 But I cannot avoid thinking that there is something unknown & deeper in seminal generation. Reflect on the long succession of embryological changes in every animal. Does a bud ever produce cotyledons or embryonic leaves? I have been much interested by your remarks on inheritance at corresponding ages; I hope you will, as you say, continue to attend to this.f5 Is it true that fem ale plants always produce female by parthenogenesis?f6 If you can answer this I shd. be glad; it bears on my Primula work: I thought on subject but gave up investigating what had been observed, because fem ale Bee by parthenogenesis produces *males* alone. Your paper has told me much that in my ignorance was quite new to me.— Thanks about P. Scotica. If any *important* criticism s are made on Primula to Bot. Soc. I shd. be glad to hear them .f7 If you think fit, you m ay state that I repeated the crossing experiments on P. Sinensis & Cowslip with the same result this Spring as last year—indeed with rather more marked difference in fertility of the two crosses.f8 In fact had I then proved Linum case I would not have wasted time in repetition.— I am determined I will at once publish on Linum .—f9

We seem predestined to work on same subjects: for 3 or 4 summers I have worked *hard* at Drosera & Dionæa & have almost a volume of materials, which I suppose some day I shall publish; ie if ever I have time to work m y materials into shape.f10 Irritability of plants has been a hobby-horse to me. I **suspect** it will turn out that irritability of same nature, only intensified in Dionæa &c. is very com m on with plants.—f11 If your paper on Drosera is published, I shd. be grateful for a copy.—f12 Two Germ an papers have been written on subject, but I now forget where; & there is good French paper on Structure, which I daresay you knowf13 I was right to be cautious in supposing you in error about Siphocampylus (no flowers were enclosed):f14 I hope that you will make out whether the pistil presents two *definite* lengths; I shall be astounded if it does.—

I do not fully understand your objections to N. Selection;f15 if I do, I presume they would apply with *full* force to, for instance, Birds. Reflect on modification of Arab- Turk Horse with our English Race-Horse.—f16

I have had satisfaction to tell m y publisher to send m y Journal & Origin to your address.—f17

I suspect with your fertile mind, you would find it far better to experiment on your own choice; but if on reflection you would like to try some which interest me, I shd. be truly delighted, & in this case would write in some detail.f18 If you have means, to repeat Gärtners experiments on vars. of Verbascum or on Maize (see Origin) such experiments would be preeminently important.—f19 I could never get vars. of Verbascum .f20 I could suggest experiments on Potatoes analogous with case of Passiflora; even this case of Passiflora, often as it has been repeated, might be with advantage repeated.f21

I have worked like a slave (having counted about 9000 seeds) on Melastomas on meaning of the two sets of very different stamens, & as yet have been shamefully beaten, & I now cry for aid.—f22

I could suggest what I believe very good scheme (at least Dr. Hooker thought so) for systematic degeneration of culinary plants & so find out their origin; but this would be laborious & work of years.—f23

I am tired, so pray believe me, yours very faithfully | Ch. Darwin

P.S. I have been thinking that if you do not complete your beginning on the nondimorphic Primula, I should like *extremely* to do so & would of course fully acknowledge your work.f24 What I shd. do would be to fertilise a dozen or score of flowers with own pollen & another score of flowers with pollen of others, the most different, & count the seed of each capsule.—

Now could you aid me (unless you resolve to do the work yourself) & procure me from any Edinburgh nursery-garden 1⁄2 a dozen plants (or fewer, if so m any could not be got) & 1⁄2 dozen of any of the other non-dim orphic species. They could be sent in pots in box addressed. "C. Darwin care of Down Postman, Bromley Kent" & I could pay by P.O.— They give or lend me all plants at Kew; but they are very weak in Primulas. I am sick of ordering plants at London nurseries; I so often get wrong thing. Could you aid me in this?—

Footnotes

f1 The year is provided by the relationship to the letter from John Scott, 6 December [1862].

f2 Scott 1862a. See letter from John Scott, 6 December [1862]. CD's annotated copy of this paper is in the Darwin Pamphlet Collection–CUL.

f3 Scott 1862a, p. 216.

f4 In his paper, Scott aimed, by analysing the nature of fern spores, to shed new light on their `apparently anomalous properties', and particularly on `that peculiar facility afforded by spores for the reproduction and perpetuation of any accidental variation of the parts upon which they originate' (Scott 1862a, p. 210). Scott contrasted the reproductive organs in ferns with those in higher plants. Since in the latter the embryo was `the *modified resultant* of two originally distinct organs' (p. 214), there would, he claimed, `necessarily be a greater tendency to efface any individual peculiarities of these than would have been the case, had the embryo been the product of a single organ.' See also letter from John Scott, 6 December [1862] and n. 15.

f5 Scott 1862a, pp. 217–8. Scott prefaced his remarks by quoting CD's statement (*Origin*, p. 13): `That at whatever period a peculiarity first appears, it tends to appear in the offspring at a corresponding age, *though sometimes earlier.*'

f6 Scott 1862a, p. 219.
f7 CD refers to the Botanical Society of Edinburgh (see letters from John Scott, 6 December [1862] and 17 December [1862]).

f8 See letter to J. D. Hooker, 23 June [1862], n. 4.

f9 Having discovered in 1861 that certain species of *Linum* were dimorphic, CD carried out crossing experiments in the summer of 1862 on *L. perenne* and *L. grandiflorum*. According to his `Journal' (*Correspondence* vol. 10, Appendix II), CD wrote his paper, `Two forms in species of *Linum*', between 11 and 21 December 1862.

f10 See letter from John Scott, 6 December [1862]. In 1860, CD began to experiment on the sensitivity to various substances of the insectivorous plants, *Drosera rotundifolia* and *Dionaea muscipula* (see *Correspondence* vol. 8). He had hoped to continue and complete the experiments in the summer of 1861, but subsequently decided to postpone them (see *Correspondence* vol. 9, letter to J. D. Hooker, 4 February [1861], and letter to Daniel Oliver, 11 September [1861]). He carried out further experiments in May and September 1862 (see DAR 54: 29–49, 74–5). However, he did not again work extensively on this subject until 1872 (*LL* 3: 322); his findings were published in 1875 as *Insectivorous plants.*

f11 See also letter to J. D. Hooker, 26 September [1862].

f12 Scott read his paper on *Drosera* and *Dionaea* (Scott 1862b) before the Botanical Society of Edinburgh on 11 December 1862. CD cited Scott's paper in *Insectivorous plants*, pp. 1 n.–2 n.

f13 In a brief overview of the literature on insectivorous plants in *Insectivorous plants*, p. 1 n., CD referred to five papers on *Drosera rotundifolia* published by German and French writers before 1862: Milde 1852 and Nitschke 1861a and 1861b (in *Botanische Zeitung*), and Grönland 1855 and Trécul 1855 (in *Annales des Sciences Naturelles* (*Botanique*)).

f14 See letter to John Scott, 3 December [1862], and letter from John Scott, 6 December [1862]. See also letter from John Scott, 17 December [1862].

f15 See letter from John Scott, 6 December [1862].

f16 CD apparently refers to the fact that an objection to natural selection based on the effect of blending inheritance on incipient varieties, would be particularly telling in cases where individuals paired for life (as with birds). CD had cited the gradual improvement of `the whole body of English racehorses' by selection and training in *Origin* p. 35, noting that they had come to surpass the parent Arab stock. See also *Correspondence* vol. 10, Appendix VI.

f17 John Murray. See letter to John Scott, 3 December [1862], and letter from John Scott, 6 December [1862].

f18 See letter from John Scott, 6 December [1862].

f19 The references are to *Origin*, pp. 269–71, and Gärtner 1844 and 1849; CD's extensively annotated copies of the latter works are in the Darwin Library–CUL (see *Marginalia* 1: 248–98). CD considered the experiments particularly important because of their bearing on an objection raised against natural selection by Thomas Henry Huxley (see letter to T. H. Huxley, 18 December [1862] and nn. 8–12, and *Correspondence* vol. 10, Appendix VI).

f20 See, for example, *Correspondence* vol. 9, letters to J. D. Hooker, 28 September [1861], 18 October [1861], 23 October [1861], and 1 November [1861], and this volume, letter to C. C. Babington, 20 January [1862], and letter to W. E. Darwin, 4 [July 1862] and n. 4.

f21 The reference is to the fact that in *Passiflora* it had been found that plants could be `much more easily fertilised by the pollen of a distinct species, than with its own' (*Natural selection*, p. 400; see also *Origin*, p. 251). Scott reported the results from a series of experiments on sterility and hybridisation in *Passiflora*, begun in 1863, in Scott 1864b.

f22 See letter to J. D. Hooker, 14 [October 1862], n. 7.

f23 Hooker discussed this project with CD during a visit to Down House in April 1860 (see *Correspondence* vol. 8, letter to Asa Gray, 25 April [1860]). See also letter from C. W. Crocker, 31 October 1862 and n. 12.

f24 Scott had apparently sent CD an account of his experiments on *Primula* in the missing portion of his letter of [20 November -- 2 December 1862]). After further research, Scott wrote a paper on the subject (Scott 1864c), which CD later cited in *Forms of flowers.*

Letter 8113—Mary Treat to Charles Darwin f1
20 December 1871

Vineland, New Jersey,

Dec. 20, 1871

Mr. Darwin:

Dear Sir,

Experimenting with Papilio asterias, Cramer, I learned to distinguish the sex in the larva state—the female being larger than the male—and this led me to try to control the sex.

My first experiments were a year ago last summer, some three or four hundred miles inland, where I had much better success than I had here last summer near the coast.

The larvae of my first experiment were of the first brood, so that I only had to wait a few days for their final transformation. These larvae fed on two quite dissimilar Umbelliferous plants—the Poison Hemlock (*Conium maculatum*), and the Caraway of the gardens (*Carum Carni*). I could always distinguish the larvae that fed on the Poison Hemlock from those that fed on the Caraway; but with the butterflies there was little or no marked difference in their general appearance.

I noticed that the female larva fed longer than that of the male. So taking several larvae of the same age, I found some specimens were inclined to leave their food several days earlier than others, and these always proved to be males. It then occurred to me to try to induce some of these male larvae to feed longer; so, after they had wandered from their food, and even selected places for their transformations, (of course not *fixed*), if I disturbed them, made them leave their places, and coaxed them with a fresh supply of their favorite food, I could almost invariably induce them to eat from ten days to two weeks longer, when all such ones would be females—If it was a larva that fed on Caraway, I tempted it with the tenderest, and freshest leaves and flowers of the same plant. It was never hungry enough at that stage to be induced to change its food, —though they will change in their earlier stages rather than starve, but evidently they do not like to change even then, and frequently fail to transform when their food is thus changed. They can be induced to change their food to the nearest allied species of plants with less difficulty—

On the other hand, when a larva had become the right size to produce a male, if I cut off its supply of food, even when it was eating greedily, it would wander about perhaps a little longer, as if in search of food, but finally it almost always changed to the chrysalis, and such a chrysalis always produced a male butterfly.

Last summer a fit of sickness prevented my experimenting with the first brood of these butterflies; and with the second brood—although I procured many specimens before the first moult—I was only able to rear about one in ten. An unnamed tiny Microgaster was their fatal enemy. But the few larvae that I succeeded with, behaved precisely as those of the previous year. Their food plant was *Archangelica hirsuta*. I have the chrysalids of my last experiment carefully marked, and am fully confident that I know which will produce the different sexes.

Now that I am writing I will give you my observations on *Drosera*, which have escaped the notice of botanists. I had two or three species of these pretty plants growing for window ornaments; and soon saw that *D. longifolia* was a fly—trap of considerable power. The unlucky fly—a common house fly—would no sooner be caught by the sticky glands of the leaf, than the blade would at once commence to fold about its victim; it folded from the apex to the stem of the leaf, after the manner of its vernation.

Closer and closer it held the poor fly in its embrace, until it ceased its struggles, when it soon became partly absorbed by the plant —Prof. Gray will give my observations on this plant in his new edition of "*How Plants Grow*".

I do not know that my experiments can be of use to you, but I thought perhaps they might interest you. A life time of observation and experiments could not repay the debt of gratitude we owe you.

Yours most respectfully,   Mrs. Mary Treat.

Footnotes

f1 This letter is not yet published in the edition of The correspondence of Charles Darwin; it will appear in volume 19, due to be published in 2011. The text is being made available here ahead of print publication as part of the 'Darwin and Gender' project funded by The Bonita Trust.

Letter 9005—Darwin to Mary Treat
12 Aug 1873

Down, | Beckenh am, Kent.
Aug. 12. 1873

Dear Madam

I am very much obliged to you for having so kindly sent me an account of *Drosera filiform* is.

Your statements will be very useful to me in my short account of this species. I am familiar with what you state about *D. longifolia* & *rotundifolia*.

I have just lately been working hard for the last 2 months on the latter species; & before long shall draw up an account of their digestive powers & action under various stimulants. If I were in your place I should be afraid to publish the statement about the *Drosera* bending towards flies or m eat which they did not touch; unless I had tried the experiment m any times, under the most rigorous precautions; for I am convinced that no botanist w[d] believe the statement unless all the precautions taken were described in detail.

With my best thanks, I remain dear Madam | yours faithfully & obliged | Ch. Darwin

Whenever m y little book is published I will do myself the pleasure to send you a copy; it will be on the genera *Drosera*, *Dionœa* & *Drosophyllum* with the republication of m y paper on Climbing Plants.

Footnotes

f1 This letter is not yet published in the edition of *The correspondence of Charles Darwin*; it will appear in volume 21. The text is being made available here ahead of print publication as part of the `Darwin and Gender' project funded by The Bonita Trust.

INSECTIVOROUS PLANTS[1]

SINCE the appearance of Mr. Darwin's work on "Insectivorous Plants" the want of direct proof that the plants profit by their carnivorous habits has been somewhat widely felt. Thus we find expressions to this effect by MM. Cassimir de Candolle, Cramer, Duchartre, Duval-Jouve, Faivre, Göppert, E. Morren, Munk, Naudin, W. Pfeffer, Schenk, &c., &c.

The assent which many naturalists have given to Mr. Darwin's explanation of the meaning of the structure and physiological properties of carnivorous plants rests on a sound basis, namely, the impossibility of believing that highly specialised organs are unimportant to their possessor, and the difficulty of giving any rational explanation except the one proposed in "Insectivorous Plants." Mr. Darwin himself felt the desirableness of direct evidence on this head, and the experiments intended to

[1] From a paper "On the Nutrition of *Drosera rotundifolia*," by Francis Darwin, M.B., read before the Linnean Society, January 17, 1878.

decide the question only failed through an accident. The present research by Dr. F. Darwin is practically a repetition of the same experiments.

The widely-spread belief that insectivorous plants thrive equally well when deprived of animal food rests on very insufficient grounds. Many observers have based their opinion on the general appearance of the plants, and in no case has observation been sufficiently extended in point of time or details of comparison. The plan of the present research was therefore (1) To cultivate a large number of plants. (2) To continue observation for a considerable space of time, during which artificial starving and feeding of two sets of plants was to be kept up. (3) To compare the starved and fed plants in a variety of ways and especially as to the production of seed.