THE COMMON TEASEL AS A CARNIVOROUS PLANT.

By Miller Christy, F.L.S.

I have always felt a special interest in the Common Teasel (*Dipsacus sylvestris*), as an exceptionally handsome and (in its cultivated form) an extremely useful plant. Moreover, I have long been convinced, as a result of observation, that the Teasel ought to be regarded as a carnivorous plant, and have felt surprise that it has never been generally recognized as such. Yet, for some reason which is not obvious to me, it never has been so recognized, as is shown by the fact that it is not mentioned as carnivorous by Sachs, Pfeffer, Goodale, Jost, Clements, Reynolds Green, Haberlandt, nor (so far as I have been able to discover) by any other writer on plant-physiology; nor does Darwin mention it as such in his 'Insectivorous Plants' (1875). An accidental occurrence has led me recently to examine the point with some care, and the following remarks are the outcome.

Every botanist is aware that the Teasel has, on its main stem, certain cup-like receptacles, formed by the bases of its large, obovate-lanceolate, connate-perfoliate leaves; also that, during the time when the plant is in perfection and flowering (that is, from the beginning of July onwards for about six or seven weeks), these receptacles are usually more or less full of water containing dead and putrefying insects and other small creatures.

It must be remembered that the Teasel (a biennial plant) produces, in its first year, nothing but radical leaves, which, though large, scarcely rise above the surface of the ground and form no cups, and that it does not produce its familiar tall stem with water-cups until its second year. The first-year procumbent leaves differ in various ways from the second-year cup-forming leaves described above. First, they are remarkably wrinkled, the corrugations in their upper surface serving, perhaps, to retain rain-water for the plant's sustenance; for these leaves possess pores or stomates on both surfaces. Secondly, they are provided both above and below with numerous spines sufficiently hard and sharp to protect them from being eaten during winter by browsing animals; for these leaves persist until the spring, when they die off completely. On their upper surfaces are a number of short, stout, straight, white spines, arranged chiefly in two well-defined rows, one on each side of and about a quarter of an inch from the midrib. Each of these spines is set on the top of a curious, raised, pustule-like inflation of the leaf, which readily gives when pressed; an arrangement which probably serves to prevent the spine being broken when the leaf is trodden upon, as it is very liable to be. There are also, nearer the margins of the leaves, other less well-defined rows of smaller spines, not set on pustules. Below, a number of sharp semi-hooked spines are set close together along the entire length of the midrib, and smaller spines along each of the branch side-ribs.

The plant's habit of catching and retaining water in its cups was definitely recorded by a British botanist nearly four centuries ago, when Turner wrote (*Herbal* [o. iiij.], 1551) that the leaves "have an hollow thyng at the cummyng out of the two leues, whyche cum one furthe agaynste an other: wher in is gathered water, both of the rayne and also of the dew." Gerard, more precise, wrote (*Herbal*, p. 1005, 1597):—"The leaves growe foorth of the iointes by couples, not onely opposite or set one against an other, but also compassing the stalke about, and fastened togither, and so fastened that they hold deaw and raine water in manner of a little bason."

These "basons" or "cups" are entire and hold water perfectly, unless punctured or broken. There are generally three or four of them, one above the other, on the stem of each plant of average height, which is often six or seven feet, though most of our botany books give the height as five or six feet. There are also usually smaller and less perfect cups on some of the lateral branches. This collection of water in the cups is a regular and every-day occurrence, not a casual or occasional phenomenon. There is *always* a certain amount of water in the cups, unless in times of very exceptional drought. Indeel, the very name of the genus, *Dipsacus* (from the Greek διψίος, thirsty), is derived from this characteristic habit, though some members of the genus do not possess it. There are, of course, other plants with connate leaves which similarly form cups round their stems and catch water in them, as, for instance, *Silphium perfoliatum*, a North American plant belonging to the Compositæ. There are also plants the leaves of which, though not connate, form receptacles that, though not perfect cups, hold water effectively, as, for instance, *Billbergia*, mentioned hereafter.

On 3rd July 1883, when in an open part of a wood at Chignal St. James, near Chelmsford, which had been cut down, I believe, two years earlier, I noticed a large number of Teasels with their cups full of water—the result of heavy rain which had fallen about five o'clock that morning, there having been none for several days previously; and, as the cups seemed to be unusually full, the idea occurred to me that it would be of interest to ascertain what total quantity of water an average plant is capable of holding in its cups at one time. Thereupon, by the best means available (which were, I admit, somewhat rough and ready), I measured the water in the cups of eight average-sized plants, with the following results:—

No. of Plant.	Height of Plant.	Quantity of Water.
1	6 ft. 6 ins.	$\frac{3}{4}$ pint.
2	6 ft. 0 ,,	$\frac{5}{8}$ pint.
3	6 ft. 0 ,,	$\frac{1}{2}$ pint.
4	6 ft. 0 ,,	$\frac{1}{2}$ pint.
5	5 ft. 9 ,,	$\frac{3}{4}$ pint.
6	5 ft. 4 ,,	$\frac{1}{3}$ pint.
7	5 ft. 0 ,,	$\frac{1}{2}$ pint.
8	5 ft. 0 ,,	$\frac{1}{2}$ pint.
Averages ...	5 ft. $8\frac{1}{2}$ ins.	About $\frac{1}{2}$ pint.

It will be seen that the water-cups on the eight plants held altogether a little less than four pints and a half of water, or an average of rather over half-a-pint each plant. Unfortunately I neglected to note the number of water-cups borne by each individual plant; had I done so, it would probably have explained why the quantity of water per plant bore, as will be seen, no regular relation to the height of the plant.

Erasmus Darwin's statement, made nearly a century and a half ago (Bot. Gard. ii. 30 n.; 1789), that "There is a cup around every joint of the stem of this plant, which contains from a spoonful to half-a-pint of water," is incredible, if he means (as apparently he does) that any *single cup* is capable of holding the last-named quantity. Much more nearly correct is the estimate of Sir Francis Darwin, who says (Q. Journ. Microscop. Soc. xvii. 269; 1877) that the cups hold "from 12 to 100 cc. of fluid," the larger quantity being equal to about one-sixth of a pint; which, reckoning three cups to a plant, agrees approximately with my own observations given above. Barthelémy has stated (*Comptes-rendus* Acad. Sci. lxxxvii. 1878, p. 609) that the cups of the var. *fullonum* are larger and more numerous than those of *D. sylvestris*. On one plant of the former, 1 m. 60 cm. high, he counted 15 cups, which contained 280 grammes of water; and he estimates that a fine plant when in perfection might hold from 300 to 350 grammes.

The source of this water has been investigated by French botanists. As long ago as 1863, Charles Boyer made observations (Bull. Soc. Bot. France, x. 746; 1863) on plants growing in his garden at St. Remy, near Montbard; but his results are not very conclusive. "L'eau s'amasse la nuit," he declares; adding that the quantity accumulated during one night, by excretion from the plant itself, might be from half to one-fifth of the capacity of any cup, the amount varying according to the position of the cup. The sun and wind cause, he says, considerable evaporation of the liquor. His conclusion is "que la sécrétion joue le principal rôle dans la production de l'eau, et que la rosée n'y contribue guère que pour un huitième. Le siége de la sécrétion doit être dans les tiges, puisqu'elle persiste après l'ablation de la presque totalité du limbe des feuilles. Pendant la période de grande végétation, la tige est gorgée de sêve, qui, sous forme de goutelettes, s'échappe à l'instant de la moindre blessure."

Fifteen years later, A. Barthelémy (*op. cit.*), as a result of observations extending over several years, arrived at conclusions totally different from those of Boyer. The cups of some plants he grew under cover remained dry; from which he concludes that the water is due neither to dew nor to secretion from the plant itself, but is provided by the rain alone. He had watched plants during heavy rain and had seen the water gathering rapidly in the upper cups; then overflowing their capacity; next, trickling down the stem; and finally filling the lower cups. The latter are filled in the same way from the upper cups when the plant is shaken during a high wind.

There can be no doubt, I think, that in the main Barthelémy was right; for I have notes that on 6 June 1882 and 3 July 1883 I found the cups exceptionally full immediately after heavy rain, and I have seen the same thing many times since. Yet there seems considerable probability that Boyer was right in part, and that the liquor found in the cups may be due to some small extent to excretion from the plant itself. This seems the more probable in that, during active growth, the stem of the plant is gorged with a colourless slightly viscous sap, which appears to be under some pressure; for directly the stem is cut, it oozes copiously from the pores, as Boyer observed.

This conclusion seems to be confirmed by the fact that on 18th June 1921, when examining a number of teasels growing in the huge chalk-pits at Grays Thurrock, Essex, I noticed that nearly all the cups of those which grew among grass and bushes on a steep chalk slope contained a little liquor, while all the cups on other plants growing in the open, on the bare and drier floor of the pit exposed to the sun, were empty or practically so. As this was during a period of very exceptional drought (only 3·94 in. of rain having fallen there since the 18th January, a period of 22 weeks*), it seemed remarkable that any of the cups should have held any water at all. It seemed clear, therefore, that the small amount of water met with must (unless derived from dew) have been excreted by the plants themselves; in which case it must first have been absorbed by their roots from the chalk in which they grew. Now chalk retains at all times a certain amount of moisture; and that the plants growing among grass and bushes should have held more water than those growing in the open was due, no doubt, to the fact that chalk covered with herbage would retain more moisture than chalk exposed to the full rays of the sun, which had been very hot for some weeks previous to the date named. Five weeks later, on 25 July (there having been no more than 0·08 in. of rain in the interval, making 4·4 ins. only in 27 weeks*), all cups were absolutely dry.

The water which gathers in the cups of the Teasel may very likely serve to succour the plant in time of drought, by being absorbed (perhaps in part re-absorbed) into the tissues of the plant, as has been held by many who have written on the subject. Thus, in 1789, Erasmus Darwin (*l. c.*) wrote that it "serves . . . . for the nutriment of the plant in dry seasons." Pfeffer, more cautious, says (Physiol. Plants, transl. A. W. Ewart, i. 160; 1900) that "a little of the water collected . . . . may be absorbed, although these plants do not normally require any supply of water from this source." Kerner (Nat. Hist. Pl. i. 240) also expresses doubt whether the water collected is absorbed to any great extent. Barthelémy reached, however, a totally different conclusion (*op. cit.* 609); plants the cups of which he kept empty of water attained (he says) no more than a third or a quarter of their normal height and their lateral shoots failed to develop. He declares explicitly that "l'eau joue un rôle considérable dans la phase du végétation de cette plante"; and his conclusion seems justified, so far as it goes, though there may be another interpretation of the evidence on which he relies. On the other hand, Boyer denies altogether that the water nourishes the plant (*op. cit.* 647): "Le séjour de l'eau dans les feuilles est sans influence sur la végétation des *Dipsacus*. Un *Dipsacus* dont je

* For these figures, I am indebted to the kindness of Mr. A. C. James, M.Inst.C.E., of Grays.

trouais successivement toutes les feuilles n'en a pas paru souffrir dans sa végétation."

On the whole, it seems probable that the Teasel does derive some direct benefit from the water it catches in its cups. At the same time, it may be recognized that the plant is one not likely to be often in serious need of such succour; for it grows as a rule in fairly damp situations, not particularly likely to be affected by drought. Without doubt, therefore, the plant's habit of collecting and storing water in its cups is also of use to it in some other and more specialised way or ways.

One such use of the water-cups has been suggested by many writers: namely, that of protecting the nectar or pollen of the plant against wingless robber-insects, which, were the water absent, might crawl up the stem and steal either or both. In much the same way, the nectar of *Lychnis*, *Silene*, *Hyoscyamus*, and many other "catch-fly" plants is protected by a sticky exudation on the stem or leaves, which catches and holds small crawling insects. As long ago as 1789, Erasmus Darwin asserted (*l. c*) that the water-cups of the Teasel served "to prevent insects from creeping up to devour its seed [meaning pollen]." Since his time, many other botanists have accepted the same idea:—see, for example, Kirchner (*Flora von Stuttgart*, pp. 678–679: 1888), Francis Darwin (*op. cit.*), Lubbock (*Ants, Bees, and Wasps*, 8th ed., p. 52: 1886), and Ainsworth-Davis (*The Flowering Plant*, p. 112: 1890).

That the water-cups of the Teasel are capable of serving this purpose effectively is certain. Yet, for several reasons, one may doubt whether, in fact, they really do so serve to more than a very small extent, if at all.

In the first place, the stem of the plant is so tall, so smooth, and so well provided with thorn-like downward-pointing prickles, that the number of insects capable of crawling up it and reaching the flowers, six or seven feet above the ground, must be infinitesimally small. In the second place, of the very few small creeping insects capable of achieving this feat, few or none would be able to benefit by it; for the flowers of the Teasel (which are adapted for pollination, and are visited freely by long-tongued lepidopterous and hymenopterous insects—see Muller, *Fertilization of Flowers*, 308, and Knuth, *Pollination*, ii. 557) have corolla-tubes from 10 to 13 mm. in length, about 2 mm. in width at the entrance, and taper at the bottom to so narrow a point that no insect, however small, likely to be capable of crawling up the stem and reaching the flowers could enter, and none but flying insects having a tongue almost or quite 10 mm. in length could possibly reach the nectar.

It seems clear, therefore, that the primary object of the collection of water in the cups is neither the succour of the plant in time of drought nor the protection of its nectar against predatory insects. It appears more probable, from facts to be given hereafter, that the main object of the plant in collecting water is the catching and drowning therein of the many small creatures already mentioned, and that their juices, after putrefaction, are digested (or, at any rate, absorbed) by the plant. Other members of the genus *Dipsacus*, but not all, also possess this insect-catching habit.

The most superficial observation suffices to show that the water in the cups is never pure, except when quite freshly accumulated: it is always of a dirty coffee-colour, of an oily consistency, and smells very offensively as a result of the putrefaction of the bodies of the many small creatures which have crawled or fallen into it and been drowned. How offensively the liquor smells will be realized fully only by one who, after having gathered some of it in order to examine the creatures contained in it, has been obliged to deodorize his fingers. In short, the presence of many small putrefying creatures in the liquor in the cups is practically invariable—as much a matter of course as the presence of water in the cups.

It has been stated that in early times this foul stinking liquor was collected and used as a cosmetic, as a cure for inflamed eyes, and otherwise. This is probable enough; for our ancestors had a strong belief in nasty medicines: Ray himself wrote of the Teasel (Cat. Plant. Cantabr. p. 45: 1660): "Aqua pluvia in alis foliorum hujusce plantæ stagnans commendatur ad verrucas abigendas, si manus eâ aliquoties laventur. Atque hinc fortasse Labri Veneris nomen obtinuit." It was probably the use anciently of this foul liquor as a cosmetic which gained for the plant the name "Venus's Bath." Pliny wrote of the Teasel as *Labrum Venereum* (Nat. Hist. bk. xxv. ch. 108).

Whether or not this use of the fetid liquor found in the cups of the Teasel survives in England, both Boyer and Barthelémy state that the country people of France, especially those of the centre and east, still attribute marvellous curative properties to it, regarding it as a cure for sore eyes and eruptions on the face: hence they speak of the Teasel cup as "*une fontaine de Venus*."

It has also been suggested that, during July, a thirsty traveller might refresh himself from the water in the cups of the Teasel; but one might almost as well drink crude sewage. As Parkinson remarked (Theatr. Bot. p. 985: 1640), sensibly enough (alluding to a statement by earlier writers who had spoken of the liquor as thirst-quenching):—"The water conteined in these leaves groweth bitter by standing in them and [is], therefore, not fit to quench but to encrease thirst rather." Nevertheless, the water, when quite freshly-caught, is clear, limpid, and not altogether undrinkable. At this stage, says Barthelémy (*op. cit.* p. 609), chemical analysis shows no impurities except traces of bicarbonates and of soil blown in by the wind. Mr. A. J. Wilmott informs me that years ago, when he was a boy, being in a large wood on a hot day and very thirsty, he actually drank from the cups of some teasels (which were quite full, as a result of recent heavy rain) and was refreshed. He drank, however, only the upper and sweeter portion of the liquor. Moreover, one of the names by which, according to Barthelémy, French country people speak of the Teasel cup—namely, "cabaret des oiseaux"—implies their belief that birds are accustomed to drink therefrom.

The belief that the water was drinkable seems to have been fairly general; thus the younger Withering, in his (the seventh) edition of his father's *Arrangement of British Plants* (ii. 216: 1830), says that in desert countries the traveller "would often exchange the whole of his property for the luxury of a draught from one of these water-lodging plants," adding that "this curious structure would appear to be rather destructive than preservative of animal life, for in the basins formed by these connate leaves many insects are drowned; so that *Dipsacus* may rank among the vegetable *Muscicapæ.*"

As to the particular small animals usually found putrefying in the cups: examination shows that they are not only very numerous individually, but that they belong to a great variety of widely-differing species and even classes *, but usually in such an advanced stage of decomposition that they are difficult to identify. My own observations show that the majority are Insects, chiefly flies (Diptera) of many kinds—blue-bottle, green-bottle, large horse, and numerous others. Beetles, too, of many species (Coleoptera), are frequent. Less common, but still often met with, are lady-birds, plant-lice, spiders, earwigs, caterpillars, moths, and butterflies—even such large species as the Cabbage White (*Pieris brassicæ*). Mollusca, too, are not infrequent. I have identified the slug *Limax agrestis* several times. Further, at Grays Thurrock, on the occasion referred to above (that is, during the great drought), I found dead in the cups a considerable number of *Helix hispida* (or its var. *concinna*) and at least a dozen *H. cantiana.* The latter is a surprisingly large and heavy creature to be captured by any carnivorous plant; for the adult animal weighs about 75 cg. On a later occasion, also during the great drought, I found several adult living individuals of *H. aspersa* sheltering in the empty cups, which they had entered, no doubt, for the sake of the slight moisture (scarcely more than dampness) remaining in their bottoms: but these had not been "captured" by the plant.

Sir Francis Darwin records (*l. c.*) that he found the following in the cups of some wild Teasels:—"In one cup, six large malacoderm beetles, from half to three-quarters of an inch in length, one fair-sized caterpillar, and two flies; in another [cup], seven of the same beetles, one earwig, a blue-bottle fly, besides many smaller flies and much debris. A much larger number of insects were counted in some other teasel-cups, but the notes were lost."

Sir Francis also met with some "large slugs" (? *Limax arborum, L. flavum,* or *Arion ater*) in the liquor. The occurrence of these is surprising; for they are much larger and heavier animals than even *Helix cantiana*, and one would have thought that they, above all other crawling creatures, would have been stopped in their ascent of the stem by the many sharp, downward-pointing, thorn-like prickles. As these prickles would hardly serve to stop smaller creatures, such as ants (which could easily pass between them), and are not stiff enough to keep off large browsing animals, they appear functionless. Yet they are so numerous and form so striking a feature of the plant that one can scarcely regard them as vestigial merely.

* So many of the creatures found in the cups are not true insects that I prefer to speak of the Teasel as a "carnivorous," rather than an "insectivorous," plant.

In addition to the many small animals mentioned, various extraneous objects also frequently find their way into the cups. Thus Kerner (*op. cit.* i. p. 156) writes that in them "there is invariably a collection of dust-particles, small dead animals, pollen-grains, etc., which have been blown in by the wind; whilst rain, trickling down the stems, brings very various objects with it from higher up and washes them into these reservoirs in the leaves. Sometimes, too, a few animals are drowned in the receptacles."

Mr. Robert Paulson informs me that he has observed in the cups fungus-spores, unicellular algæ, pollen-grains, and seeds of a grass (*Holcus lanatus*), some of these latter actually germinating therein in the autumn. In late summer and autumn, I have often found in the cups a considerable number of the plant's own corolla-tubes, which fall as the flowering-season advances.

There is, however, one Order of Insects of which one might, at first sight, expect to find examples in the cups of the Teasel, but which are practically never found therein — namely, the bees (Hymenoptera). This is, in one way, surprising; for, as stated already, the pollination of the flowers is effected largely by these insects, which are to be seen constantly visiting its flowers and might easily fall in. Yet their absence from the cups is not really surprising; for these bees are clean feeders and are, therefore, not at all likely to be attracted by the fetid liquor, as the foul-feeding flies (Diptera) seem to be. In any case, I have only once found a bee dead in the liquor—an individual of *Bombus derhamellus* ♂ (identified by Mr. C. Nicholson), which I found in one of the cups of a plant growing in the Grays chalk-pits on 17th August 1922. I assume that it had fallen in accidentally whilst visiting the flowers of the plant. Sir Francis Darwin does not mention having met with any bees in the cups.

The water-cups offer, one would have thought, ideal breeding-places for mosquitoes; but these creatures never use them as such in this country, so far as my observations go. The late Mr. Arthur Bacot, who had given much attention to the breeding of mosquitoes, informed me, shortly before his recent death, that he knew of no instance of their so doing. Yet in America a species of mosquito and certain other insects elsewhere are known to breed in very similar situations. Thus, there are various species which lay their eggs habitually and exclusively in the pitchers of certain species of both *Nepenthes* and *Sarracenia*, the grubs, when hatched, living in and upon the putrescent liquor existing therein, subsequently eating their way through the walls of the pitchers and pupating in the earth. The first to call attention to this curious fact was Dr. Charles V. Riley, who recorded the habit in connection with a Flesh-fly (*Sarcophaga sarraceniæ* Riley), which thus uses the pitchers of *Sarracenia flava* and *S. variolans* (see Trans. Acad. Sci. St. Louis, iii. pp. 235–240: 1875). At least two other species of Flesh-fly (*S. rileyi* Aldrich and *S. jonesi* Aldrich) are known to do the same (see Aldrich in *Publications of the Thomas Say Foundation*, i. pp. 86, 241, and 242: La Fayette, Ind. 1916). An American species of mosquito (*Wyeomia smithii*) makes a similar and exclusive use of the pitchers of a *Sarracenia* (? sp.) growing in New Jersey (see Howard, Dyar, and Knab, Mosquitos N. and Centr. America, iii. (1), pp. 97–101: 1915). Again, J. C. H. de Meijere has described seven species of Diptera which, in Java, make exactly the same use of the pitchers of *Nepenthes* (see Ann. Jard. Bot. Buitzenzorg, 2nd ser. Supp. iii. pp. 917–940: Leyden, 1910). Hepburn and Jones have shown that the larvæ of *Sarcophaga sarraceniæ* (and probably those of the other two species named above) are able to live in the digestive fluid in the pitchers of *Sarracenia* because their bodies contain certain "anti-proteases," or digestion-resisting compounds (see Contrib. Bot. Laboratories Univ. Pennsylv. iv. pp. 460–463: 1919). It is, perhaps, because these substances are absent from the bodies of the larvæ of our English mosquitoes that these latter cannot (or, apparently, do not) live in the putrescent liquor in the cups of the Teasel.

It is clear from what has been said that insects and many other small creatures are captured and drowned, at all times and in large numbers, in the water-cups of the Teasel. It is necessary, therefore, to enquire *how* this is effected and *why*.

That the formation of the cups is well adapted to retain any small creatures which may enter them is obvious. First, the sides of the cups are sloped very steeply, the leaves forming them being set at an angle of about 30 degrees with the stem and about 60 degrees with the surface of the ground, while the wing which connects the bases of the leaves is sloped at an even sharper angle with the stem. Secondly, the surface of the stem and the interior surface of the cups are both extremely smooth and glossy, rendering it likely that any small creatures which may have been induced, by whatever means, to enter or approach the cups will slip down into the liquor in their bottoms and be drowned therein. As Sir Francis Darwin has remarked (*op. cit.* 270): "The plant is well adapted for catching and drowning insects. . . . The cups undoubtedly form most efficient traps. . . . I have seen a beetle struggling to get out and observed his tarsi slipping, over and over again, on the smooth stalk."

There is, however, nothing in the foregoing, and apparently nothing in connexion with the structure of the plant or its water-cups, to suggest, at first sight, *why so many small creatures should enter the cups at all* (unless, perhaps, to drink in time of exceptional drought); still less why they should get drowned therein so frequently.

Both Boyer and Barthelémy took the view that the many small creatures found in the cups had all "fallen" in (*tombent*). Kerner (*l. c.*) clearly shares that view. Yet the presence in the cups of numerous dead insects is (as has been shown) almost invariable. This cannot be due solely to accidental causes; for it is impossible to suppose that the presence of so many dead creatures in such comparatively minute areas of water can be due merely to wind-transport, rain-wash, accidental falls, or other such casual causes. There must surely be something which *definitely attracts* the creatures in question: otherwise, they would not be found in the water so invariably and in such numbers.

Subject to careful chemical investigation, I can only explain the phenomenon by hazarding the surmise that the plant exudes into the water, when accumulated, some strong-smelling or sweet-tasting toxic substance which first attracts insects and other small creatures and then narcotizes or intoxicates them, leading them to fall in and get drowned. Their subsequent putrefaction is, doubtless, due (in the main, at any rate) to bacterial infection from the air.

That insects really are both attracted and stupefied in some way by the liquor seems proved by an observation I made on 25 August 1916. Early in the morning of that day, I happened to notice a newly-dead individual of the Large White Butterfly (*Pieris brassicæ*) floating in the putrescent liquor in one of the upper cups of one of a group of plants of the cultivated Teasel* growing in my garden. Whilst I was fishing out and examining the insect, I was surprised to see two other White Butterflies, till then unnoticed, fly up from one of the lower cups, having been disturbed, no doubt, by the slight shaking I had given the whole plant. That these two butterflies had become, in some way, more or less stupefied through imbibing the liquor seems to me certain; for they did not fly up till some time (perhaps a quarter of a minute) after I had begun my examination; whereas, had they been normally alert, they would have taken flight immediately I began my examination of the plant, or even before I had approached it closely, being, like all butterflies, very shy by nature.

Further evidence to the same effect seems to be provided by the fact, already cited, that I have found slugs (generally, I believe, *Limax agrestis*) and several species of snail (including *Helix cantiana*) dead in the cups; while Sir Francis Darwin found "large slugs" in them. Now all these molluscs (which find no difficulty in crawling up a perpendicular glass window-pane) could surely, in ordinary circumstances, have crawled with ease up the sides of the Teasel-cups, in spite of their exceedingly steep and smooth sides. Indeed, Sir Francis says: "I find that slugs, if dropped into the teasel-cups, can crawl up the smooth leaves [*i. e.*, the sides of the cups]." The obvious conclusion is, therefore, that those molluscs which failed to crawl out, had been stupefied or intoxicated in some way and drowned through imbibing the liquor.

The presence in the fluid of some such intoxicating element was suspected, many years ago, by Sir Francis, who says:—"I tried a number of experiments by taking a large number of . . . malacoderm beetles and placing one half in water, the other in the fluid of the Teasel-cups. The result showed that beetles are drowned much more readily in the Teasel fluid than in pure water. Whether there is a narcotising poison in the fluid or whether, as is far more probable, the oiliness or stickiness of the decaying fluid causes the insects' spiracles to be blocked up, I cannot say."

In this connexion, it may be noted again that most of the small creatures commonly found in the cups are notoriously addicted to foul feeding—the Diptera and some Coleoptera, in particular. Even the

* This, though generally spoken of as a distinct species (*D. fullonum*, the "Fuller's Teasel"), is probably no more than a variety of *D. sylvestris*, slightly altered by long cultivation.

dainty Lepidoptera are not free from the habit, as shown by the old method used for taking the Purple Emperor Butterfly (*Apatura iris*)—that of placing in its haunts the putrid carcase of an animal. Again, it is well known that these insects are extremely fond of fermenting liquors. On 17th October 1878, at Portslade, Sussex, I watched for some time a Red Admiral Butterfly (*Pyrameis atalanta*) fluttering persistently round a wine-merchant's delivery-van laden with spirits, which had been left standing in a road. Again, in "sugaring" for moths, the attraction provided is not so much the sugar as the rum or gin mixed with it. Further, it is very well known that butterflies and other insects frequently suck the fermenting sap which exudes from injured trees *. Clearly, therefore, such insects are liable to be attracted and intoxicated by the fermenting liquor usually found in Teasel cups. On the other hand, the Hymenoptera are clean feeders, so that the putrid liquor can have no attractions for them: consequently, they are very rarely found dead in the cups.

In view of all the foregoing, it is hard to doubt that some constituent of the liquor in the teasel-cups *definitely attracts and stupefies* these many small creatures, causing them to drown. It is equally hard to doubt that, this being accomplished, the plant does actually derive benefit *from the absorption of the highly-nitrogenous liquor* which must result from their putrefaction in the cups.

This latter conclusion was, indeed, reached definitely by Sir Francis Darwin forty-five years ago, and his conclusion was endorsed explicitly by his father, Charles Darwin. Sir Francis, in the course of an article † on certain "protoplasmic filaments" he had observed protruding from the glandular hairs on the leaves of the Teasel, writes (*op. cit.* 270–2):—

"I believe that the plant does profit by the insects caught in the cups. . . . But, whether or not the glands which find themselves immersed in the putrid fluid of the teasel-cups take advantage of their position to absorb nitrogenous matter, there is no doubt.—That the protrusion of filaments is not a habit originally developed for this special purpose; for . . . the glands on the seedlings, which do not form cups and therefore catch no insects, have well-developed filaments. . . . That the function of the protoplasmic portion of the filament was originally to assist in the act of secretion, but that it has been subsequently utilized by the plant as a mode of nutrition. That the protoplasmic filaments have the power of absorbing nitrogenous matter and that, in the seedlings, they probably absorb ammonia from the rain-water and dew. In the adult plants, they absorb the products of the decaying insects for the capture of which the plant is adapted."

Later observations raise doubt as to the part played by the "protoplasmic filaments," but Sir Francis's main conclusion still stands, and has been held more or less vaguely by others since he

* For a summary of observations thereon, see Charles Nicholson in Essex Nat. xix. (1920) pp. 12–14, 170–171.

† See Proc. Roy. Soc. xxvi. (1878) pp. 4–8, and Quart. Journ. Microscop. Sci. n. s. xvii. pp. 169–174; also, much more fully, in Quart. Journ. Microscop. Sci. n. s. xvii. (1877) pp. 245–272.

wrote. The nature and functions of the filaments are now being investigated carefully by Mr. Robert Paulson, who believes them to be separate organisms, probably Rhizopods.

That absorption does take place seems highly probable in view of the fact that stomates or pores of some kind are known to exist in the cuticle of those portions of the stem and the inner walls of the cups which are submerged when the cups are full of water, and also of the leaves. These stomates were observed by Barthelémy in 1878. They also are now undergoing investigation by Mr. Paulson, who finds that those upon the stem vary in some points of detail from those on the upper side of the leaves. Either or both of these kinds may serve either as excretion-glands or as absorption-glands, or as both. It is necessary, however, to await Mr. Paulson's further results before speaking positively as to their functions.

Another matter which must be awaited is a careful analysis of the liquor found in the Teasel cup, both in its early freshness and in its later fetid condition. More than two years ago, I made arrangements for such analyses; but my plans have been defeated by the recent abnormal weather-conditions. In 1921, owing to the excessive drought, liquor was not obtainable in analyzable quantity: in 1922, though liquor was obtainable in sufficient quantity, the cold wet weather which prevailed at the critical season was so prejudicial to insect life that practically no insects were caught and the liquor never attained its normal putridity.

On the whole, however, if there is as yet no conclusive proof, there seems every reason to believe that the main use of the water-cups of the Teasel is the catching of small "insects"; that the plant exudes into the water which collects in the cups some narcotizing substance; that this both attracts and stupefies the "insects," causing them to drown; that, after drowning, they decompose in the fluid, causing it to become very highly charged with nitrogenous matter; that the plant then digests and absorbs this matter, deriving nutriment therefrom; and that the Teasel is, therefore, truly carnivorous, as suggested at the outset. It is difficult to see how any other conclusion can be reached; inasmuch as we find, in connection with the plant, practically all the characteristic features which occur, in one form or another, in connection with other plants which are recognized universally as carnivorous.

Assuming my contention to be proven, it may be said of the Teasel that it is one of the largest carnivorous plants known—certainly by far the largest in Britain; that it is capable of capturing and digesting larger and heavier creatures than any other; and that, in capturing its prey, it employs methods which differ considerably from those of nearly all other plants having similar habits.

Carnivorous plants may be divided roughly into four classes, according to the methods of capture they employ. Thus:—

(1)—*Dionæa*, *Pinguicula*, and *Drosera* all exude a sweet viscid substance on the surface of their leaves, which, when small insects have been attracted and caught thereby, curl or close over, cover, and digest them.

(2)—*Nepenthes* and *Sarracenia* both have deep "pitchers," containing a liquor, secreted by the plant itself, which attracts insects, whose escape is prevented by retaining-hairs at the entrance and by a more-or-less complete lid. The insects are then drowned and become putrid, after which their products are absorbed by the plant.

(3)—In *Utricularia*, a genus of small floating (rootless) aquatic plants of which two species are fairly common in Britain, the method employed is surprisingly ingenious. The plant has on its leaves many small bladders, each of which is provided at the entrance with a trap-door surrounded by hairs. When any wandering creature, however small, approaches the entrance, guided by the surrounding hairs, it touches one special hair which is sensitive. This, acting like a trigger, causes the trap-door to open suddenly inwards, thus causing a sharp current of water to enter the bladder, carrying with it the tiny creature in question. This is at once imprisoned and retained by the re-closing of the trap-door, and is then digested at leisure. Attention has been called only recently to the working of this highly-ingenious piece of mechanism by Mr. C. L. Withycombe (*Knowledge*, xxxix. 1916, pp. 238–241). Earlier observers, including Darwin, had supposed that the prey forced its way into the bladders, attracted by some sweet substance secreted inside.

(4)—In *Dipsacus* a totally-different and simpler method is employed. The plant has neither pitchers, nor bladders, nor any partially-closed receptacles provided with lids, trap-doors, or retaining-hairs at their entrances. On the contrary, its cups in which insects are captured are widely open at the top and the liquor contained in them is certainly derived—in the main, at any rate—from falling rain and dew. Yet it seems to contain some sweet toxic substance (excreted, apparently, by the plant itself) which attracts and stupefies many small creatures; while the structure of the cups is such as to facilitate their capture, drowning, and putrefaction, leading, ultimately, to the absorption by the plant of the resulting highly-nitrogenous product. A somewhat similar method is employed in *Billbergia* (Order *Bromeliaceæ*), of which there are many species, all epiphytic on trees, in the West Indies and northern South America. Water is caught and retained by the bases of the leaves, though these do not form true cups. In this, many insects and other creatures become drowned, and these putrefying, soon render it highly offensive. The extraordinary variety of creatures thus caught has been investigated by C. Picardo (Bull. Scient. France et Belg. xlvii. 1913, pp. 215–360), H. Scott (*Zoologist*, 1914, pp. 183–195), and D. J. Scourfield (Journ. Queckett Microscop. Club, ser. 2, viii. 1903, p. 539). Mr. J. L. North, Curator of the Royal Botanic Society, informs me he has heard a man relate how once, travelling in Brazil, he had passed beneath a tree the branches of which were covered with plants of *Billbergia* in full flower, and, reaching up with his riding-crop to pull down some blossoms, had been at once drenched with putrid evil-smelling liquor!