On the Protrusion *of* Protoplasmic Filaments *from the* Glandular Hairs *on the* Leaves *of the* Common Teasel (*Dipsacus sylvestris*). By Francis Darwin, M.B. (With Plate XIX.)

The connate leaves of the common teasel (*Dipsacus sylvestris*) form, as is well known, cup-like receptacles surrounding the stem of the plant. In the rain-water accumulating in these cups numerous insects are drowned, and their dead bodies convert the water in which they lie into a strongly animalised fluid.

In the autumn of 1875 I examined the leaves of the teasel, in the expectation of finding the same evidence of the absorption of the products of decay as may be observed in the remarkable trichomes lining the bladders of Utricularia.[1] The glandular hairs or trichomes on the leaves of the teasel proved, however, to be too much shrivelled for the experiment, although the leaves were not themselves withered. In the summer of 1876 I recommenced the investigation by examining transverse sections of teasel leaves mounted in dilute ammoniacal solutions such as those which are absorbed by the glands of Drosera, Pinguicula, &c., and by the trichomes of Utricularia, and which my father has shown to give rise to the remarkable phenomena of "aggregation."

While examining the transverse section of a teasel leaf (under Hartnack's objective No. 8) I observed a translucent, somewhat highly refracting mass seated on the summit of one of the glands. I imagined it to be resin, excreted in the form of a filamentous mass. I was therefore astonished to observe a few moments later that its shape had distinctly altered. On finding similar filaments on several neighbouring glands I became convinced that the subject was well worth investigation.

The first idea that presented itself was that the filaments were protoplasmic organs specially adapted for the absorption of the fluid containing decayed animal matter collected in the teasel cups. This theory was overthrown by the following facts. The teasel is a biennial, and during its first year's growth consists of a mere rosette of radical leaves, the cup-bearing stem being formed during the second year. But the supposed pseudopodia are found not only on the connate leaves of the second year's growth but on the radical ones produced during the first season. They are also found in *Dipsacus pilosus*, whose leaves are not sufficiently connate to retain water, and which can therefore capture no insects. These facts prove conclusively that, whether

[1] 'Insectivorous Plants,' p. 418.

or not the glands have anything to do with the absorption of the putrescent fluid in the cups of *D. sylvestris*, some other function must also be performed by them in the economy of the plant. Another idea which occurred to me was that the filaments might be low organisms of the nature of a Myxomycetes, living parasitically on the summits of the glands. The reasons for discarding this view will be fully given in the sequel.

The trichomes on the connate leaves of the second year's growth all have the shape of glandular hairs (except a double row of simple multicellular hairs on the midrib); the seedlings possess in addition numerous long hairs or prickles, the chief portion of which consists of a single large conical cell, sometimes ·85 millimeter in length, and ·09 millimeter in breadth at the base. The *glandular* trichomes are of two kinds, exemplified by figs. 1 and 13. The trichomes of the fig. 1 type are of no further interest, as they do not produce motile filaments. The other variety (fig. 13 and the other drawings) consist of a pear-shaped multicellular head, about ·05 millimeter in length, and a unicellular cylindrical stalk a little over ·03 millimeter in length, supported on a cushion-like cell projecting to a variable extent above the level of the epidermis; the whole trichome is about $\frac{1}{10}$th millimeter ($\frac{1}{250}$th of an inch) in height. In the glands on the second year's leaves the cells forming the pear-shaped head usually contain a few bright spheres of a resinous substance: the latter may be removed by alcohol, and then the nuclei of the cells become clearly visible. These large drops of resin are often absent, especially from the glands of the seedling leaves; in this case the cells contain merely granular and cloudy protoplasm. The drops of resin are, however, sometimes to be found in the seedling's leaf-glands, as shown in fig. 13. Both the trichomes of the fig. 1 type, and also those which produce filaments, occasionally contain a good deal of starch.

The stalk-cell exhibits a simple network of streaming protoplasm and a large nucleus. I have once or twice observed streams of protoplasm in the transparent cells forming the pear-shaped head of very young glands. The glands are often capped by accumulations of resinous secretion, and this is more frequently the case with the second-year leaves than with the seedlings. These secreted masses agree with the bright spheres found within the cells in exhibiting the following reactions, which show them both to be of a resinous nature. They are soluble in ether or alcohol, are coloured pink by tincture of alkanet; they are not blackened by osmic acid, as would be the case with a fatty substance. The crusts on the outside of the glands, contrary to what might be expected, are stained yellow with iodine. It appears, therefore, that the resinous secretion is formed in drops in a vacuolated protoplasm in the gland-cells of the trichomes, and, passing *through the cell-walls*, collects on the external surface of the gland. In his paper on glandular trichomes Hanstein[1] describes a method of secretion in which the product collects in a blister-like cavity beneath the cuticle, which bursts and allows it to escape. On dissolving the resinous crusts from the teasel glands I have occasionally seen a similar bladder of cuticle subsiding or bursting. Martinet[2] describes a similar process, and considers it pathological and of only occasional occurrence. I imagine that in the case of the teasel the essential act of secretion, *i.e.* the elimination of a resinous product from the cells in which it is formed, is a normal process; but possibly the method of elimination may vary, so that a bladder may or may not be formed. The resinous matter is secreted only by the trichomes of the types shown in figs. 2, 3, 4, 13, &c., that is to say, only by those from which the motile filaments are produced.

The motile filaments.—Various forms assumed by these remarkable bodies are shown in figs. 2, 3, 6, 7, 8, 9, and 16.

The typical form consists of a simple thread-like body slightly clubbed at its free end. The filament shown in fig. 3 was nearly ·1 millimeter in length, and about ·0012 millimeter in breadth at the thickest place. The dimensions vary extremely; for instance, the thickness may be reduced to that of the very delicate filament seen in fig. 6, whose length cannot be estimated because of the complicated tangle in which it is arranged. Another and far more elaborate knot of filaments measured ·2 millimeter in length; if it was composed of a single filament, which is quite possible, the latter would certainly have been 2 millimeters in length when uncoiled. Even the comparatively thick filament in fig. 2 measures ·4 millimeter in length. These entanglements are of common occurrence, and usually consist of a labyrinth of sweeping curves lying close up to the gland. Fig. 6 was selected from the curious angular disposition of the coils. Again, the thickness may be larger when compared with the length, as in the smaller masses in figs. 2 and 3; and thick, partly dumb-bell shaped masses may be combined so as to produce a branched filament, as in fig. 16. In fig. 4 an almost spherical filament[3] is seen. In fig. 16, again, rather thick filaments are seen, one of which forms a loop by having its distal end attached or closely applied to the summit of the gland. The formation of loops is an extremely common phenomenon; they do not seem to be

[1] 'Bot. Zeitung,' 1868.
[2] 'Annales des Sc. Nat.,' 1865.
[3] The word filament is used to express any motile mass, of whatever shape it may be, arising from a gland.

formed by the distal end of the filament becoming attached to the gland, but I believe that they *arise* as loops, or that two filaments unite and form a loop immediately after emerging from the gland. Variously beaded forms are shown in fig. 9, and a crowd of irregularly shaped masses in fig. 7.

The filaments are with the very rarest exceptions attached to the summit of the gland; and when the actual place of attachment can be made out, it is found to be at the point where the radiating cells meet in the centre of the dome-like surface of the gland, or at least on the junction line between at least two cells. The substance of which the filaments are composed is translucent, highly refracting, and quite free from granules. The filaments are in constant tremulous Brownian movement, showing that they are of a gelatinous consistence. I hope to prove that they consist in part at least of protoplasm, but I have not succeeded in showing the presence of albuminoids by any of the usual micro-chemical tests. Neither the rose-red colour with syrup and sulphuric acid, nor the xanthoprotein test with nitric acid and ammonia succeeded properly, though a distinct faint tinge was produced by the latter means. The filaments, however, assume a bright yellow colour with iodine, but I presume that no great weight ought to be attached to this reaction. The filaments are not stained by ordinary colouring fluids, such as logwood, anilin, &c. It will be shown that the substance of which they are composed consists in large measure of a resinous substance mingled in some way with the protoplasm, and I presume that it is this circumstance which interferes with the above reactions.

Protrusion of the motile filaments from inside the glandular trichomes.—I have hitherto spoken of the filaments as merely attached to the surface of the glands, but they are in fact protruded from the inside. There can be no doubt of this, for glands may be observed whose dome-like summits are quite naked and bare, but which may be seen after a few moments to be surmounted by a minute projection which grows up into a normal filament by visible increments in length. I cannot positively state by what means the filaments traverse the external cell-walls. It might be supposed that apertures would be found to allow of their transmission. By stripping off the epidermis a bird's-eye view of the summits of the trichomes is obtained, and if any apertures exist they would be probably visible in this way, but no such appearance can be seen. But the tops of the trichomes ought to be cut off by sections parallel to the surface of the leaf, to decide the point with certainty. It is extremely unlikely that apertures should exist, and the protrusion of the filaments can be explained without assuming their existence, for semifluid secretions undoubtedly pass through cell-walls, and there is no difficulty in believing that gelatinous protoplasm may do the same.[1] The migration of blood-corpuscles occurs where no special apertures exist for their transmission.

The protrusion of filaments was first observed in sections of leaves mounted in a dilute solution of carbonate of ammonia; but the presence of this salt is not necessary, as the filaments issue forth vigorously in distilled water. A very slight film of moisture on the surface of gland is sufficient to allow of protrusion taking place. For I have seen filaments protruded when looking vertically down on to the surface of a damp leaf. Whether they are protruded from a perfectly dry leaf I cannot ascertain.

Movements of the filaments.—The most remarkable movement exhibited by the filaments is a violent contraction. This is especially well seen by irrigating a preparation with dilute acetic acid (2 or 3 %). In figs. 3 and 4 a filament is shown before and after treatment with dilute acetic acid. The contraction is often so energetic that the whip-like filament seems suddenly to be replaced by a ball seated on the summit of the gland. After the act of contraction the substance of the filament is denser and more highly refracting. When the contraction is not so violent its course may be watched. It usually begins at the free end of the filament; a ball appears at the distal extremity and increases in size as it rapidly approaches the gland, being connected with it by the remaining uncontracted portion of the filament, which of course quickly diminishes in length. I have also seen the contraction begin at the proximal or attached end of the filament; a ball forms on the surface of the gland, and increases as the extended portion diminishes. These violent alterations in form are frequently preceded by a most beautiful phenomenon which I have called "moniliform" contraction. This appearance is shown in fig. 9; here the filament retained this form for some time, and was in fact in a chronic state of contraction. The "acute" moniliform contraction presents the same appearance, but lasts only a few seconds. Sometimes the moniliform contraction invades the whole filaments so rapidly that it seems simultaneous; in other cases it is distinctly seen spreading along the filament. When the constrictions between the "beads" are not especially deep, the beads and the spaces between them appear alternately light and dark as the focus is changed. I have occasionally seen a momentary appearance of alternate light and dark bars throughout the whole length of the filament, instantly followed by violent

[1] See a paper by Max Cornu, "Sur le cheminement du plasma au travers des membranes vivantes non perforées," 'Comptes rendus,' Jan. 15th, 1877.

contraction. This appearance may be due to a moniliform contraction in which the outlines of the beads and constrictions are not perceptible, or may possibly be due to the contraction occurring at a series of equidistant points, the refractive index being raised at each point in consequence of the increased density of the tissue. It should be added that contraction frequently occurs without being preceded by moniliform appearance.

I have hitherto spoken as if after the completion of the act of contraction the filament were always found massed into a spherical body on the gland from which it took its origin. This is normally the case, but in rare instances a long filament becomes entangled with a neighbouring gland, and when contraction takes place the filament snaps in two, one portion remaining attached to its own gland and the remainder actually contracting on to the foreign surface by which it had been entangled. It must be noted that filaments frequently break loose from their attachment, and while in this free state are capable of contracting and exhibit other signs of vitality. These two observations are important because they throw some light on the nature of the act which I have called contraction. A friend suggested that possibly the filament may not undergo a true contraction, but that its movements may be governed by changes occurring within the gland, so that the filament itself is merely passively acted on by these internal agencies. But it is evident that this cannot be the case, because freely floating filaments are capable of contracting, and because the distal portion of a filament exhibits the same power independently of the proximal portion.

Causes inducing contraction.—In the present section I shall examine only those causes which produce the violent changes of form which I have hitherto called "contraction." Under certain conditions the filaments assume an amœboid state in which gradual alterations in shape spontaneously occur; it is obvious that these movements may quite as justly be supposed to be due to contractility; but these movements are excluded from the present discussion, and will be considered in the sequel.

Acetic acid.—The contraction caused by this reagent has already been described. The filaments are very sensitive to its action, and contract violently when exposed to a solution of 1 per cent. Also distinctly with a much weaker solution, ·2 per cent.; but on the other hand some filaments were found in a half expanded state after three hours' immersion in ·4 per cent. acetic acid.

After the protoplasm of the filament has been killed by the action of acetic acid, a remarkable change occurs. The contracted mass swells and becomes more transparent, and produces a pile of polyhedral vesicles, whose shape is determined by mutual pressure, so that it somewhat resembles in appearance a heap of soap-bubbles, as shown in fig. 5. I may remind the reader that when a colourless blood-corpuscle dies it swells up into a transparent sphere, owing to the imbibition of water,[1] and I believe that the formation of the soap-bubble mass is due to the protoplasm of the filament imbibing water at a number of different points.[2] This soap-bubble appearance is not specially connected with death by acetic acid; it appears to be a result of any kind of death, and may be seen where the filament has been killed by other reagents (such as $\frac{1}{2}$ per cent. solution of chloride of gold) or by heat. On the other hand it is not the invariable accompaniment of any kind of death, simple balloon-like masses being often produced by the swelling of the protoplasm in a single mass.

Sulphuric acid.—By irrigating with 2 per cent. solution of sulphuric acid contraction was several times produced. Weaker solutions were not tried.

Hydrochloric acid.—As my father found this acid not poisonous to Drosera, a dilute solution (2 per cent.) was tried with the teasel. Contrary to my expectations, it proved poisonous, always causing contraction and death of the filament.

Boracic acid.—This acid is not poisonous in a weak solution. Several long and delicate filaments were found protruded after being immersed all night in ·2 per cent. solution, and they contracted at once with dilute acetic acid. In this case the teasel agrees with Drosera, as boracic acid is not poisonous to the latter.[3]

Citric acid.—This acid is not poisonous to Drosera,[4] and is so to the teasel, but I cannot speak decisively as to how poisonous it is. A solution of 1 per cent. rapidly causes contraction. A solution of ·5 per cent. usually produces contraction after a time, and also kills the glands. But two filaments withstood a solution of this strength for between seventeen and eighteen hours; two others were not made to contract by five hours' immersion in the same solution.

Osmic acid.—The action of this highly poisonous acid has surprised me much. As is well known, its usual effect on protoplasm is to kill it instantaneously without altering its appearance. This is not the case with the filaments of the teasel, at least with weak solutions of the acid, which act like acetic or sulphuric acids, but not so vigorously, and sometimes not completely. I record in my notes that on irrigating with $\frac{1}{4}$ per cent. solution of osmic acid a whip-like filament "contracted into a barred and knobbed cylinder." I then irrigated with water, and

[1] 'Handbook for the Physiological Laboratory,' p. 12.
[2] Perhaps this may be connected with the filament's power of contracting at a number of equidistant points.
[3] 'Insectivorous Plants,' p. 191. [4] Ditto, p. 194.

the filament subsequently showed itself to be still alive by changing its form and contracting with dilute acetic acid. This filament was therefore made to partially contract without being killed, instead of the normal effect of the poison being produced, viz. death without contraction. After numerous trials I conclude that irrigation with acid of this strength either causes complete or almost complete contraction, or else no effect is produced and the filament withstands the poison. This is a remarkable fact, as the *glands* are soon killed and blackened by ¼ per cent. osmic acid; it shows that the *filaments*, when once protruded, are independent of the life of the gland. With 1 per cent. osmic acid I succeeded in obtaining a different result; a filament began to contract and then died in a partially expanded state, and afterwards resisted the action of strong acetic acid. In another instance the filament was half poisoned by osmic acid and only contracted after prolonged irrigation with 20 per cent. acetic acid. In another case a filament contracted partially with osmic acid and then withstood 20 per cent. acetic acid, showing that it was killed by the osmic acid.

Various salts.—Carbonate of ammonia in dilute solutions, viz.: ½ per cent., causes moniliform contraction; the filament becomes partially concentrated into a ball, and then recovers, and extends itself again. The most interesting points in connection with this salt have no bearing on the simple contraction of the filaments, and will be discussed later. The same remark applies to the carbonates of potassium and sodium, both of which cause contraction in ½ per cent. solutions.

Chloride of gold in ½ per cent. solution causes rather languid contraction. But the filaments are killed by it, and become transformed into soap-bubble masses.

Nitrate of silver in ¼ per cent. solution has the same effect, viz. contraction and death, followed by the production of a soap-bubble mass.

Iodine.—A solution (Schacht's) composed of iodine 2 grains, iodide of potassium 6 grains, water 2 ounces, was employed. Violent moniliform contraction is produced, and the rounded mass into which the filament is transformed by contraction is stained yellow. In one instance the contracted mass consisted of two parts, a heap of transparent soap-bubbles and a yellow mass. There can be little doubt that the iodine and not the iodide of potassium is physiologically active in this solution. When diluted so that the iodine is about in the proportion $_{8}$ per cent., the solution is not poisonous, or only slightly so. It is known to have stimulating but not poisonous effects on germinating seeds.[1]

Alcohol.—Strong contraction is produced by irrigating with a

[1] Heckel, 'Comptes rendus,' 1875, p. 1170.

drop or two of methylated spirit. The subsequent effect of alcohol has puzzled and astonished me more than any other point in this research. First of all, the contracted mass seated on the top of the gland turns of a greenish colour. It then begins to diminish in size, and ultimately either almost or quite disappears. At first I was repeatedly deceived by this appearance, and believed that the filament was actually retracted within the gland. What really happens is that a great part of the filament is dissolved by the alcohol. The reaction with alkanet shows that resin is contained in the filaments. I presume that it is spread through the protoplasm of the filament, and corresponds to the metaplasm of Hanstein, or is intimately connected with the protoplasm in some other way. The results of treatment with alcohol seem to show that the quantity of resin is very large compared with that of the protoplasm. In some cases a minute shrivelled ball remains after treatment with alcohol; in other cases the contracted filament breaks loose and floats away before the alcohol has completed the solution of the resin contained in it; in a third set of cases the whole of the contracted filament disappears under the influence of alcohol. I know not how to explain this phenomenon. The summit of the gland is sometimes hollowed out slightly, and is difficult to examine accurately with high powers; it is possible that the minute remnant of protoplasm remaining after the resin is dissolved, and which would necessarily be shrunk by the alcohol, might be overlooked within the hollow on the summit of the gland. Again, it is conceivable that if the resin is very intimately distributed throughout the substance of the filament, its sudden removal by a powerful solvent might cause the disintegration of the remnant of protoplasm.

In a filament killed by osmic acid in an extended condition, and which was certainly dead (as it did not contract with 20 per cent. acetic acid), an effect of alcohol was seen which I cannot explain. The specimen was irrigated with methylated spirit with the intention of dissolving the resin of the filament and leaving a protoplasmic skeleton in an extended position. But the filament ran together in a manner which could not be verbally distinguished from contraction, although it had more the appearance of a filament of spun glass melting into a button than the normal act of contraction.

Chloroform.—Applied in the form of a vapour, choroform causes contraction. A thin transverse section of a young leaf was suspended by means of a drop of water to the under surface of a thin glass cover, forming the roof of a gas chamber. The chamber had the usual arrangement of tubes, one being connected with a washing bottle (in which the chloroform is placed, covered by a layer of water), the other either with the mouth of the observer or with an aspirator. Observations made in this way established the fact that the vapour of chloroform causes contraction of the filaments. I recorded in one case that the filament under observation "did not contract directly I tasted the chloroform." The following observations show that chloroform produces a temporary narcosis of the filaments:—August 9th, 4.30 p.m. A filament was made to contract by the vapour of chloroform; by next morning at 9 a.m. it had altered in shape, being more elongated than when it first contracted, although it had by no means recovered its original whip-like form. On drawing chloroform through the chamber it contracted again. During this aspiration, a fully extended filament was seen to contract;[1] this filament had escaped the effect of the previous day's chloroform, as it had not then been protruded. Pure air was then rapidly drawn through the chamber, and by one o'clock the second contracted filament had partially assumed an elongated form, and was again made to contract by aspiring the chloroform.[2]

Glycerine.—A preparation was irrigated with glycerine, and a filament was seen to contract slowly, a sluggish-looking beading making its appearance. It ultimately became spherical, and remained unaltered for half an hour; it was then thoroughly irrigated with water, and still continued unchanged in appearance.

Syrup of sugar also produces contraction.

Quinine.—An aqueous solution of $\frac{1}{10}$ % of sulphate of quinine was employed, and contraction was observed in several cases. This result agrees with my father's observation that quinine is poisonous to Drosera.[3]

Camphor.—This substance was tried because my father has shown it to be a powerful stimulant to Drosera.[4] The washing bottle connected with the gas-chamber was half filled with water, in which a few lumps of camphor were floating; an atmosphere strongly impregnated with camphor was thus produced. The filament could not be made to contract by drawing the camphor-laden air through the chamber. A $\frac{1}{10}$ % (*i.e.* natural) solution of camphor was prepared, and by irrigating with this fluid contraction was distinctly and repeatedly produced. Conwentz has shown that camphor is a poison to the cells of *Cladophera fracta*[5].

[1] Contraction was here preceded by an unusual appearance which may be best described as a wrinkling, and is different from the moniliform contraction.

[2] There is nothing very special in the narcotizing influence of chloroform, for filaments half killed by dilute acids have occasionally been observed in a sluggish, narcotized state.

[3] 'Insectivorous Plants,' p. 201.

[4] Ibid., p. 209.

[5] 'Bot. Zeitung,' 1874, pp. 401, 417. Göppert seems first to have observed the poisonous effect of camphor on plants.

It is certainly poisonous to the glands and filaments of the teasel; but the latter are not excited by it as is the protoplasm in the tentacles of Drosera.

Curare.—A solution which had been used for curarizing frogs was employed to irrigate preparations with; it made the filament become slightly transparent, as if effected by ammonia, but did not paralyse or kill them. Curare is not poisonous to Drosera.[1]

Cobra poison.—A solution of about ¼ % was used for irrigation; it produces a peculiar form of contraction, with an intense wrinkling, and zig-zag appearance of little darting side filaments. It is not poisonous, and the filament shoots out again; it appears to be a powerful stimulant to the filaments, and this agrees with my father's observations on its extraordinary exciting effects on the protoplasm in the tentacles of Drosera.

Strychnine.—A solution of 1 % of acetate of strychnine was prepared, but the salt was not all dissolved, and the solution used was probably ·75 %. In some of the experiments, simple contraction was the result. But in several instances a remarkable phenomenon occurred. The filament began to contract, and then suddenly became motionless, being killed in a partly extended condition. The filaments were certainly dead, for they could not be made to contract by subsequent irrigation with *strong* acetic acid. This fact is important, for it shows that the contraction ordinarily due to acetic acid is not a chemical effect on the substance of which the filament is composed. For it is extremely unlikely that both osmic acid and strychnine should possess the power of hindering the *chemical* effect of acetic acid. On the other hand, the behaviour of the filaments with strychnine agrees to some extent with that of the tentacles of Drosera. My father found that a solution of acetate of strychnia (stronger than ¼ %), when applied to tentacles which had begun to move, allowed the latter to go on bending for a short time, and then killed them in a semi-contracted state.[2] In a few cases the filaments were rendered sluggish, without being killed by the strychnia solution, and a parallel effect was noted by my father in Drosera. Strychnine has the same power as ammonia of causing the appearance of drops of resin in the epidermic cells.

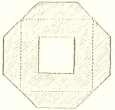
Heat.—In 'Flora' of last year (1876, p. 177) there is a careful research by Velten on the effect of heat on the streaming of protoplasm. He discusses various instruments for the examination of microscopic objects at different temperatures. He concludes that the most accurate are Sachs' heating-box ('Warmkasten'), and a modification of an apparatus of Nägeli's. The

[1] 'Insectivorous Plants,' p. 205.
[2] Ibid., p. 200.

'Warm-kasten'[1] is described in Sachs' 'Text-book of Botany,' Eng. Tr. p. 658. Velten's instrument is fully described and figured in 'Flora' (loc. cit.)

In my observations on the filaments of the teasel I have made use of both of the above apparatus; in this way, no serious error can occur. If the filaments were liable to contract spontaneously it would, of course, be impossible to make any trustworthy experiments, but this is distinctly not the case; the filaments remain extended with great constancy for long periods of time. Again, if they contracted when washed to-and-fro by

[1] Mr. Hawksley has constructed a box of this description for me, which answers admirably. At his suggestion it was made of carefully soldered tin-plate, which is said to be more durable than zinc if care is taken to drain the water out thoroughly after use. Mr. Hawksley has also substituted tin-plate lined with felt for the cardboard cover. According to Velten, the projecting portion of the tube of the microscope ought to be enveloped in felt to prevent undue cooling of the objective. Velten's apparatus is more simple than Sachs', and can be fitted up by any one for himself. A small glass vessel is placed on the stage of the microscope, the object to be examined is supported on a wooden frame, so that when the vessel is filled with water the object is surrounded by it on all sides, and the objective has to dip beneath the surface of the water like an immersion lens. The temperature is regulated by a current of hot water flowing in at the bottom, and a siphon carrying off the surface-water at the opposite edge of the vessel. Both tubes are provided with taps, and the water should be made to flow by drops and not in a quick continuous current. A thermometer is kept in the water close to the object. Velten cemented his thin cover-glass to prevent the preparation under observation being disturbed. I have found it more convenient to employ the following device:—A piece of stout lead-foil is cut into the shape shown in the woodcut. The object is



Lead-foil clamp for holding a microscopic object between two thin glass covers.

mounted between two thin glass covers and placed over the square aperture in the lead-foil; the four flaps are then gently bent up (the hinge-lines are dotted on the figure) so as to clamp the glass slides together, and the object can now be placed in water without any danger of the cover-glasses separating. This plan has the advantage of leaving the preparation accessible to re-agents after the heating experiment has been concluded, and from being between two thin glasses the object is rapidly affected by the changes in temperature of the surrounding water.

currents in the water in which they are mounted, observation would be difficult, at least, with Velten's apparatus; but this is not the case, for I have often seen the filaments violently shaken by the current without contracting. In the following experiments I thought it necessary to give the time at which the various temperatures were attained, because Kühne[1] has shown that time is an important element in heat experiments on protoplasm.

Experiments with Velten's apparatus.

In both 1 and 2 the record of experiment begins when the vessel had been filled with warm water.

Experiment 1.—Aug. 19th.

Time.	Temperature. C.	
4.26 p.m.	34°	Filament extended.
4.36	40	„
4.44	45	„
4.58	56	Filament contracted.

Experiment 2.—Aug. 20th.

12 noon	39	Filament extended.
12·5′ 30″ p.m.	43	„
12.8′ 15″	45	„
12.15′	49	„
12.20	52	Filament partially contracted. Observation continued on a different filament in same preparation.
12.35	56·5	Filament extended.
1.?′	57	Filament contracted.

Experiment 3.—Nov. 27th.

9.35 a.m.	12	Specimen mounted in cold water, a current of cold water flowing through vessel. Filament extended.
10.15	12	Filament still extended.
10.20	31·5 or 32	Filament and another on neighbouring trichome contracted; vessel of water was then allowed to cool somewhat.
10.25		The filament extended again.
10.37	28·5	Filament contracted.
11.29	19	Filament appeared again. Between 10.37 and 11.29 it had been subjected to the temperatures shown in Experiment 4.
11.41	17·4	Filament still extended.
11.43	27	
11.44	30·5	Filament contracted.
11.47	45·2	After 11.47 vessel allowed to cool slightly.
11.50	38	A fresh filament found in the same preparation, still extended.
11.52	41·7	

[1] 'Das Protoplasma,' 1864, p. 103.

Time.	Temperature. C.	
11.53′ 30″	44	Filament contracted; as are all the filaments in this preparation.
11.59	50	After 11.59 vessel allowed to cool.
12.20 p.m.	25	All the filaments (2 in number) contracted.
		Nov. 28th.
5 p.m.	cold	Two filaments slightly re-extended; they were therefore not killed by temperature of 50°.
		Experiment 4.—Nov. 27th.
10.38′ 15″	30·5	A filament in the preparation used in Experiment 3 still *extended*.
10.41′ 15″	35·5	Filament contracted. Nineteen filaments on this section of leaf contracted, but one is found still extended.
10.43	34	Filament extended.
10.45	32	,,
10.46′ 30″	36	,,
10.48′ 45″	39	,,
10.51	40	,,
10.52	41	
10.54′ 30″	42·5	Filament contracted.
		Experiment 5.
3.20	cold	A number of filaments extended.
3.32	,,	Filaments still extended.
3.34	17	,,
3.37	38·5	,,
3.39	47	Several filaments contracted.
3.40	47·5	More filaments contracted.
3.40′ 25″	48·5	All contracted. Vessel of water allowed to cool.
5.53	12·8	A single thick, partially expanded filament.
5.56	21·2	Filament still extended.
5.58′ 30″	27	Filament contracted.
		Experiment 6.
6.3	16·2	No filaments visible.
6.24	11·8	A filament extended.
6.26′ 30″	18	
6.35	23·5	Filament contracted. Observation immediately transferred to another filament (extended) in the same preparation.
6.36′ 30″	23·2	
6.43	27	This, the second filament, contracted. Observation transferred to third filament.
6.45	27	Third filament extended.
6.52′ 20″	30	,,
6.55	32·8	,,
6.57	35	,,
6.59′ 20″	37	Third filament contracted.
7	36·2	Extended again.
7.4′ 30″	42	Contracted (owing to a mistake in observing, it may have contracted at a few degrees lower), water having cooled since 7.5. Filament still contracted.
7.49	12	

The important result derived from these experiments is that, although there is most remarkable variability in the temperatures at which contraction took place, *yet no filament withstood without contraction a temperature of more than* 57° *C.* No increased activity was observed at lower temperatures.

The following experiments were made with Sachs' heating box:

Experiment 7.

Time.	Temperature. C.	
12.26	47	Filament extended.
12.37	55	Filament contracted. The microscope was then removed, another specimen mounted and then replaced.
12.45	56·8	Filament extended.
12.54	56·9	Filament contracted.

Experiment 8.

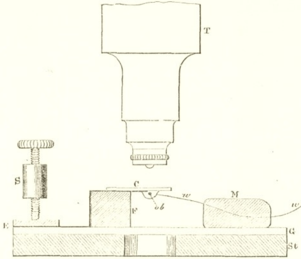
10.55 a.m.	T. of room.	Filament extended.
11.1′ 30″	36·5	,,
11.18	35	Filament contracted; microscope removed and replaced. Fresh filament observed.
11.23	38	
11.35	37	Fresh filament contracted. Microscope removed and new filament (3rd) observed.
11.40′ 30″	40	
12.1	43·5	Filament contracted.

The average temperature of contraction from the experiments with Sachs' box is 45·4°, the average for the series with Velten's apparatus being 38·7°, the average of the whole of both series being 42° C.

Electrical stimulation.—By using a modification[1] of the electrodes usually employed in microscopical work the filaments were easily subjected to the influence of the induced current. Clear and unmistakeable contraction was thus produced, and the observation was several times repeated. No contraction was produced until the current was approaching the strength at which water is decomposed. The filaments were not thrown into a state of activity by weaker currents; and this agrees with Heidenhain's observations on the hairs of Tradescantia (quoted by Sachs, 'Physiologie Végétale,' p. 85). He found that weak currents produced no effect *on the protoplasm*, while strong currents rapidly stopped all movement. On the other hand, Brücke and Max Schultze (quoted in Sachs, 'Phys. Vég.', p. 86)

[1] I succeeded so easily with this modified arrangement, when I failed with the ordinary form of microscopic electrodes, that it seems worth describing. I am indebted for the suggestion to Prof. E. Ray Lankester. He pointed out that the object to be examined might be placed in a drop of water hanging from the under surface of a thin glass cover, just as in the gas-chamber. One electrode is fixed to the under surface of the thin glass, the other is movable and is brought cautiously into the field of vision until it closely approaches the object. This arrangement is shown in the accompanying woodcut, which gives the instrument in section.

found that delicate trembling filaments darted out from the



Microscope electrodes.

St, stage of microscope; G, glass slip; F, block of cork; M, lump of modelling wax; *w*, *w*, fine wire passing through M; B, end of *w* connected with battery; E, the other electrode fixed to F; *ob.*, the object to be examined hanging in a drop of water; C, thin glass; T, tube of microscope with objective; S, a Stricker's binding screw; G is an ordinary glass slip, to which is cemented a cubical block of cork, F, which supports the *fixed* electrode. The latter is represented by the black line, E. It consists of a sheet of platinum foil nearly as wide as the glass slip to whose upper surface it is cemented, reaching from E to the fixed block, F, it then passes up the vertical external face of F, and bending at right angles ends in a point, and is cemented to the upper surface of F and the under surface of the thin glass-cover, C. The movable electrode consists of a block of modelling wax, M, pierced by a finely pointed wire, *w* (such as is used for clearing the canula of a hypodermic syringe). To use the instrument, the object is placed at *ob*, suspended in a drop of water, and *w* and E are connected with the battery or Du Bois coil. For connecting the platinum plate E with the coil a single one of Stricker's binding screws may be used. The point *w* ought to stand up like a spring, so that by sliding up M, and slipping *w* beneath the glass cover C, the point of *w* presses gently against the under surface of C (*w* does not touch the under surface of C in the figure). Supposing that a section of a teasel leaf is hanging at *ob*, the point of *w* can be made to approach any desired filament; when this is effected the cube of modelling wax, M, is fixed by a little firm pressure, to the glass slide, and on closing the key the filament is subjected to the action of the current.

streaming protoplasm in the hairs of the nettle when subjected to an induced current.

Mechanical stimulation.—By getting a filament exactly into the centre of the field of vision, and screwing the objective down so as to press on the cover-glass, the filament can be made to contract. This observation was repeated several times, and in some cases, by focussing up rapidly, the filament was observed in the act of contraction from the effect of the previous pressure.

Amœboid or aggregation movements.—This term is applied to a series of appearances which, though not essentially differing from the moniliform contraction already described, are more conveniently considered separately. It would, perhaps, be better to call them simply aggregation movements, since they more closely resemble the changes observed in the tentacles of Drosera when excited by the absorption of nitrogenous matter than any other phenomena.

The most striking variety of aggregation-change which occurs in the filament is due to the action of dilute solutions of carbonate of ammonia, or of an infusion of meat, and is partially produced by weak solutions of carbonate of potassium and sodium. A detailed experiment will best illustrate the nature of the phenomenon in question. July 10th, 1 p.m., a young teasel "cup" was cut from the plant by severing, both below and above the bases of the leaves, the stalk which passes like a vertical axis through the cup. The small section of the stalk, thus freed from its attachment to the plant, was divided in a median plane in such a way that one half of the stalk remained attached to each leaf; one half was placed in a solution of carbonate of ammonia ($\frac{1}{4}$ %), and the other in distilled water. On July 11th, at 8 a.m., transverse sections were cut from both specimens and examined. In the water specimen the filaments were long and delicate threads, whereas in the sections taken from the half immersed in the ammonia solution they presented a totally different appearance. The glands were surmounted by transparent sausage-shaped and rounded masses of low refractive index. Subsequently sections were cut from the water specimen and were irrigated with $\frac{1}{4}$ % of carbonate of ammonia. A filament was seen to undergo moniliform contraction, and then became partially extended; nearly all the filaments in the preparation became changed into variously shaped transparent masses, and distinct changes of shape were seen. A few transparent masses produced by immersion for an hour, in $\frac{1}{4}$ % solution of carbonate of ammonia, are seen in fig. 7. Remarkable changes of form occur; large bulging masses quite alter their shapes, snake-like filaments disappear and others appear, spheres coalesce with one another, and, in fact, the mass of filaments is in the course of an hour or so completely transformed and altered in appearance. The glands are coloured of a faint green by the ammonia solutions. The results obtained with fresh and putrid infusions of raw meat have surprised me still more than the changes produced by ammoniacal solutions.

July 18th, 10.50 a.m.—Sections cut from a young leaf of second year's growth were mounted on slides, some in distilled water, others in an infusion of raw meat; owing to a mistake in the notes I cannot say whether it was a fresh or putrid infusion. The specimens were examined at 3.30; those mounted in water showed only fine whip-like filaments, whereas in the meat specimens there were found enormously long and bulky filaments, something like those shown in fig. 11. The same kind of result was obtained by five hours' immersion in *fresh* infusion of meat, also in the following instance with putrid infusion.

July 20th (between 11 and 12 noon).—A young 'cup' was divided in the manner described above, one half being placed in distilled water the other in putrid meat infusion. July 23rd, 10 a.m. (about seventy hours after immersion).—Sections were cut from both halves and examined. In the meat specimens there were astonishing masses of spherical and pear-shaped transparent filaments with some rope-like ones as much as ·96 mm. ($\frac{1}{26}$ inch) in length. Changes in form and in position were seen to take place. The masses exactly resembled in appearance the transparent filaments which are seen attached to glands after irrigation with dilute solution of carbonate of ammonia, but here they were attached to no glands; they seemed to have been poured out in enormous quantities and to have freed themselves from all attachment. Unfortunately no record was kept of the condition of the corresponding half of the 'cup' which had been in distilled water; but from this fact it is probable that they presented the normal appearance with thread-like or slightly moniliform filaments. On July 26th, at noon, the glands appeared to be dead, but the protoplasmic masses (which were not attached to glands) were still in movement. Fig. 11 was sketched with the camera lucida. The masses were bright and highly refracting. A curiously moniliform mass (not figured in the plate) was also seen in very rapid movement. One mass was made to run into a sphere and was almost or entirely dissolved by methylated spirit. As I found that an infusion of putrid meat was faintly alkaline it appeared possible that the results obtained with ammonia, with carbonates of potassium and sodium, and with meat infusions, were all due to their alkalinity. But this is certainly not the case, as precisely the ordinary results were obtained with meat infusions carefully neutralised with dilute citric acid. Why solutions of carbonate of potassium and sodium should have the same effect as nitrogenous or ammoniacal solutions, I cannot say. These salts produce aggregation in Drosera and in this way they again resemble ammonia in action.

It will be seen from the above account that the effect of infusions of meat is to cause an enormous and probably abnormal production of filaments which usually free themselves from their attachment. In some cases the filaments are very transparent, like those produced by ammoniacal solutions; in other cases they do not differ in refractive index from the ordinary filaments, which are usually bright and highly refracting. In the latter case the filaments resemble those shown in figs. 8, 9, and 15; in fig. 15 are represented the rapid movements of a free and unattached filament. The change from fig. 8 to fig. 9 took place in about half an hour; the curiously beaded filament in fig. 8 had doubtless originally issued from the trichome as a simple whip-like body. The aberrant forms produced by slow contraction are exemplified in fig. 12, for in this case also there is little doubt that the mass was originally a simple filament. I am, unfortunately, unable to say to what cause this latter kind of movement is due. I have seen curiously shaped or actively moving filaments *in fresh specimens mounted in distilled water*; this seems to negative the view that the changes in question are due to the absorption of nitrogenous matter. But it must be remembered that a transverse section of a young leaf mounted in water is practically exposed to a nitrogenous fluid owing to the death of the protoplasm killed in the young leaf-cells in making the sections. I can only repeat that these changes do under *some unknown conditions certainly occur*, and that somewhat similar changes are certainly brought about by immersion in infusions of meat and solutions of carbonate of ammonia.

Nature and physiological relations of the filaments.—I have now given some account of the physiological behaviour of these remarkable filaments. Before proceeding further it will be well to attempt the discussion of the question, what relation does the power of protruding filaments bear to other processes of vegetable physiology? When I first observed the filaments I found it extremely difficult to believe that they were protoplasmic organs issuing from the glands. I was even inclined to suspect that they might be parasitic organisms of some unknown kind which merely fixed themselves on the summits of the trichomes to avail themselves of the putrescent fluid retained by the connate leaves of the plant. Such facts as those given in one of Mr. Dallinger's memoirs,[1] should make one cautious in rejecting such a theory, nevertheless I believe it may certainly be dismissed. It is impos-

[1] "Practical Notes on Heterogenesis," 'Popular Science Review,' Oct., 1876.

sible to believe that parasitic organisms would seat themselves almost without exception on the same part of the gland. Some of the very rare cases in which a filament was seen seated on the side of a trichome proved after all not to be exceptions to the rule; for, by making them contract, they proved to be attached by delicate connecting filaments with the summit of the gland. It is also a very convincing fact that the trichomes of the fig. 1 type never produce a filament, although they are apparently as well fitted as the fig. 2 type for the abode of a parasite. Again, the fact that filaments are found on the leaves of seedlings reared in a hot-house and far from their parent-plants (from which they might otherwise be infected with the supposed parasite) seems to me strongly against the parasite hypothesis.

Putting aside any view of this nature, we seem to be reduced to two theories—(1) That the filaments are protrusions of the resinous protoplasm of the glands. (2) That they consist of a resinous secretion of gelatinous consistence; and that the movements which occur are not due to vital activity inherent in the substance of the filaments, but are due to purely mechanical causes. The movements might be supposed to be similar in kind to those observed by Professor Ray Lankester[1] in the coloured blood-corpuscles. He found that the merest trace of the vapour of ammonia caused a wrinkled wave to travel over the surface of the corpuscle, simulating contraction. A stronger dose causes the protrusion from the corpuscle of processes which collapse when acetic acid is substituted for ammonia. These movements are believed by Professor Lankester to be purely mechanical in nature. As another instance of purely physical effects closely similar to "vital" movements may be cited Sachs' recent research, 'Ueber die Emulsion Figuren, &c.'[2] Previous investigators had believed the movements of swarm-spores in relation to light were truly vital in nature. Sachs has, however, proved, by obtaining similar phenomena with emulsions of oil, that they are the direct physical result of slight differences in the temperature of surrounding objects.

I shall now briefly consider the behaviour of the filaments in relation to the above-mentioned theories, which may be called (1) the vital; (2) the mechanical theory.

In favour of the mechanical *theory* we have the fact that the filaments undoubtedly contain a large percentage of resinous matter, which might conceivably give rise to mechanical pseudo-contractions. Again, it might seem that there is a greater *à priori* probability of such pseudo-contractions occurring than of the protrusion of a highly resinous protoplasm through the

[1] 'Quarterly Journal of Microscopical Science,' 1871, p. 376.
[2] 'Flora,' Nrs. 16, 17, 18, 1876.

cell-wall of one of the higher plants. But the balance of probabilities is reversed when we inquire into the causes that induce the movements. For it is inconceivable that violent contraction should be mechanically or chemically produced by such different reagents as very dilute acids, alkalies, solutions of chloride of gold, sulphate of quinine, camphor, or by a temperature below 57° C.

On the other hand, the whole behaviour of the filaments (except the results of irrigation with alcohol) points to the conclusion that the movements are connected with living matter. In this point of view the more important features in the behaviour of the filaments are the following:

1. The "spontaneous" movements.

2. Contraction being produced by various reagents, such as acetic acid or sulphate of quinine in very dilute solutions, and by the vapour of chloroform.

3. Death in an extended or not fully contracted condition being produced by solutions of osmic acid and acetate of strychnine.

4. Contraction being produced by subjecting the filaments to a temperature below 57° C.; to the action of the induced current; to mechanical violence.

5. Not only do these agencies cause contraction, but the filament is reduced by them to a motionless condition, in which no farther contraction can be induced, and in which the filament swells up in consequence of the imbibition of water.

On the whole, the balance of evidence seems to me to be strongly in favour of the view that the filaments of the teasel consist of protoplasm in which a large proportion of resin is in some way mingled.

Probable functions of the filaments.—I shall now endeavour to connect the above-described phenomena with known facts in physiology, and to make a conjecture at what seems to be the most probable function of the filaments. The class of facts which appears to be most nearly related to the phenomena is that of secretion. There can be little doubt that the protrusion of filaments is closely related to the secretion of resin, for caps of accumulated resin are found on the summits of the glands, while inside the cells are spheres of the same substance. No one would hesitate to consider these crusts as resin secreted by the glands. But the filaments resemble these crusts in several ways, *e.g.* in refusing to be stained by ordinary dyes, in being coloured by alkanet and by iodine, and in being largely soluble in alcohol. Moreover, incrustations of resin are only found on that variety of gland from which filaments are protruded. The view is maintained by many physiologists that an act of secretion consists in the disintegration or death of protoplasm. Every mass of what is ordinarily called protoplasm, or *plasma*, is made up of two distinct portions: one of these is truly living matter, and should alone be called protoplasm; the other is not alive, and is called metaplasm (Hanstein)[1]. According to Beale, all metaplasm must pass through the stage of protaplasm. But whether or not this be so need not here be discussed. It will be granted in either case that secretions may be formed by the metaplasm increasing so that the protaplasm is annihilated. Dr. Creighton's recent work[2] renders it highly probable that the secretion of milk takes place on this principle; a new plastid arises within a mammary gland-cell, and is entirely converted into oil. I would suggest that the secretion of resin is an example of a somewhat different form of protoplasmic secretion. I believe that the portions of protoplasm destined to give rise by disintegration and death to the secreted resin does not proceed at once to the full limit of disintegration, but that it issues from the gland while still possessed of some vitality. I am aware that many weighty objections may be raised against this view. It may be said that protoplasm containing so large an amount of lifeless matter could not exhibit activity. In support of this it might be pointed out, that the accumulation of large quantities of food-yolk in ova is associated with quiescence. Secondly, it may be said that the protrusion of living protaplasm is an inconceivably wasteful method of getting rid of a secretion.

I will first consider the former of these objections. The process of aggregation, as it occurs in the tentacles of Drosera, affords an example of loss of motility connected with an increase of metaplasmic matter. The spontaneously-moving masses of coloured protoplasm in Drosera assume under certain conditions a spherical form in which motion ceases, and this condition is associated with an increase in density, probably owing to the condensation of the accumulated metaplasm into smaller compass. This phenomenon seems to negative the view that the filaments of Dipsacus could possibly be active while containing a large quantity of resin. But from another point of view, this argument is not quite fair. The motionless aggregated masses in Drosera are so dense that they crack into star-like forms[3] when pressure is made on the cover-glass. But before this intense condition of aggregation was reached the metaplasm must have been at least moderately condensed, and in this condition the masses were still motile. There is another possibility which

[1] 'Bot. Zeitung,' 1868, p. 710.

[2] 'Reports of the Medical Officer to the Privy Council,' 1875, No. vi, p. 171.

[3] 'Insectivorous Plants,' p. 47. For figures of these forms see 'Quart. Journ. of Micro. Science,' July, 1876.

should be considered, namely, that the filaments may consist of a liquid core of resinous matter, surrounded by a tubular shell of protoplasm. Professor Ray Lankester, who was kind enough to examine preparations of living glands, suggested this idea. He remarked that the moniliform contraction gave him more the impression of a tube closing on its contents than of any possible contraction of a solid body. I think this view ought to be considered, though I am not at present inclined to accept it.

To return to the second of the above objections—viz. that the protrusion of protoplasm is an incredibly wasteful method of secreting. Two answers may be made to this objection. It must be granted that if a wasteful, it is also a rapid way of secreting, and it is impossible to know of how great importance it may be that what is probably an excretion should be rapidly eliminated. In the second place, it is quite possible or probable that the filaments have not adhered to their original function of removing waste products, but have assumed other functions. It is perfectly conceivable that a protruded mass, consisting in part of true, living, protoplasm, should, on finding itself surrounded by a nitrogenous fluid, absorb and transmit nutriment to the leaf. We know from my father's observations on Utricularia that the trichomes lining the bladders are markedly affected by the absorption of nitrogenous fluids. And we have the same kind of evidence in the case of the teasel. My father found that a weak solution of the poison of the cobra-snake had a powerfully stimulating effect on the tentacles of Drosera. A solution of about $\frac{1}{4}$ % produced more active aggregation than can be produced by any other means, except, perhaps, a moderately high temperature. The same solution of cobra poison was tried with the teasel; it not only produced a state of activity in the filaments as already described, but was certainly absorbed by the trichomes. At 4 p.m., when the solution was applied, the contents of the trichomes were merely granular, next morning the cells contained definite masses, which slowly changed their forms. (See fig. 10.) This appearance must be considered as "aggregation"; and when it is remembered that aggregation only occurs in the glands of Drosera, Pinguicula, Utricularia, &c., when excited, it must be allowed that we have evidence of the excitement of the glands of the teasel by the absorption of the cobra solution. But too much stress must not be laid on this phenomenon, as on some occasions it entirely fails with cobra solution, and is a very rare occurrence under any circumstances, and fig. 10 was drawn from a specimen simply mounted in *water* for two or three days. Moreover, it seems to have nothing to do with the filaments, for I have seen it on two occasions in the glands of the fig. 1 type. I may here mention another phenomenon which I do not understand, but which is the almost universal result of treatment with ¼ or ½ % solution of carbonate of ammonia. It consists in the appearance of numerous bright, highly refracting drops of resin in the epidermic cells, which gradually run together and form large spheres. They are very easily soluble in methylated spirit, and, no doubt, consist of the same resinous matter secreted by the glands. A similar effect was extremely well marked, and repeatedly seen in preparations mounted in 75 % solution of acetate of strychnia. No other substances seem to have the same power, and the phenomenon must remain unexplained. At first sight the protrusion of filaments, and the changes which occur in them, appear to be isolated phenomena unrelated to any known physiological process, except in a certain way with secretion. I believe, however, that some relationship must exist between the protrusion and amœboid movements of the filaments, and the process of aggregation as it occurs, for example, in the tentacles of Drosera. The physiological meaning of the latter phenomenon is at present unknown; we know, at least, that variously shaped protoplasmic (?) masses make their appearance and undergo incessant movement. If these masses were to traverse the external cell-wall, and protrude into the surrounding medium, they would closely resemble the filaments of the teasel. The following are the points of resemblance between the protruded filaments of the teasel and the aggregated masses of Drosera:

(1.) Both consist of homogeneous, highly refracting masses of protoplasm, imbued with a large quantity of metaplasm; the latter being fatty (?) in Drosera, resinous in Dipsacus.

Both are connected with glandular organs, which not only secrete certain substances, but also absorb nitrogenous materials.

The comprehension of the relations between the processes of protrusion and aggregation is rendered more difficult by the fact that true aggregation takes place within the trichomes of the teasel.

The production of filaments is not an unknown occurrence in the ordinary protoplasmic contents of cells. Max Schultze[1] describes in the stinging hairs of the nettle the appearance of a certain number of threads projecting from the parietal protoplasm into the cell-sap; their free extremities are swollen or clubbed, and they are in a state of trembling movement. These appearances are only seen when the electric current to which the hair is subjected is nearly strong enough to kill the protoplasm.

I have occasionally seen these internal filaments, for instance in a gland which bore also an ordinary external filament. By careful

[1] Quoted by Sachs, 'Physiologie Végétale' (French translation), p. 86.

focussing with No. 9 Hartnack I made certain that there was a filament actually inside the gland; and it was proved not to be outside by irrigating with methylated spirit, by which means the external filament was made to contract while the internal one was unaffected. The same appearance of trembling clubbed filaments was seen in one of the large conical hairs on the seedling teasel-leaf. Three of such filaments are marked by crosses in fig. 12; the largest of the three waved to and fro, and reminded me closely of one of the ordinary external filaments.

Relation between the general structure of the Teasel and the protrusion of filaments.—The conclusion to which the study of the filaments and the glands seems to lead is, that they are both capable of absorbing nitrogenous fluids. It will be well to consider whether or not the general structure of the teasel is in any way co-ordinated with this power.

In the first place, it is quite certain that the plant is well adapted for catching and drowning insects.[1]

The connate leaves form cups holding from 12 to 100 c.c. of fluid; the leaves are smooth[2] (although those of the seedlings are rough, with large prickly hairs) and are inclined so as to form a large angle with the horizon and a small one with the vertical; they form, therefore, two steep and slippery slides, leading to a pool of water. The stalk of the plant is covered with sharp prickles, but these cease where the stalk dips into the water in the cup. If it were not for the loss of the prickles at this point, a ladder of escape would be provided for the drowning victims. I have seen a beetle struggling to get out, and observed his tarsi slipping over and over again on the smooth stalk. The cups undoubtedly form a most efficient trap. In some wild teasels the following insects were found:—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, seven of the same beetles, one earwig, a bluebottle fly, besides

[1] Prof. Kerner believes that the "cups" of the teasel are a protection to the flower against the attacks of ants and other wingless insects who might steal the nectar without benefiting the species. In his recent memoir, "Die Schutz-Mittel der Blumen gegen unberufene Gäste," in the 'Proceedings of the K. K. Zoolog. Botan. Gesellschaft, Vienna,' 1876, he supports, with strong arguments, the theory that many flowers are thus protected. He would, however, be the first to admit that a given structure may have developed through serving more than one useful purpose. It is curious that in the last century Erasmus Darwin should have remarked on the protective function of the "bason" formed by connate leaves of the teasel. He even alludes to nectar as one of the treasures to be guarded in this kind of way, although he was not, of course, aware of the true relations existing between flowers and insects. (See 'Loves of the Plants,' Note 6.)

[2] The glands do not make the leaves appreciably rough.

many smaller flies and much débris. A much larger number of insects were counted in some other teasel-cups, but the notes were lost, and the loss was only discovered when it was too late to make fresh observations. The water contained in the cups is almost always muddy from the débris of dead insects; and when the old leaves at the base of the stem wither, and can no longer hold water I have seen them swarming with Staphylinidæ and other refuse-eating beetles. I tried a number of experiments by taking a large number of the same kind 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 rapidly in the teasel fluid than in pure water. Whether there is a narcotizing poison in the fluid, or whether, as is far more probable, the oiliness or stickiness of the decaying fluid causes the insect's spiracles to be blocked up, I cannot say. The fact that large slugs are occasionally drowned in the cups is in favour of the poison hypothesis, for I find that slugs, if dropped into the teasel-cups, can crawl up the smooth leaves.

From these various considerations I believe that the plant does profit by the insects caught in the cups. This question I hope to decide by a comparative experiment, in which a number of teasels raised from seed under similar conditions will be divided into two lots, one half being starved and the other fed with insects or pieces of meat.

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, as above explained, the glands on the seedlings which do not form cups, and therefore catch no insects, have well-developed filaments. But it may be answered that they are developed in the seedlings by a kind of inheritance from the adult plant. Even if this reasoning were permissible the conclusion that the filaments are specially adapted in relation to the leaf-cups is demolished by the following fact, already alluded to. The other British species of teasel, *D. pilosus*, has no leaf-cups, and therefore cannot entrap insects, yet the leaves bear glands, and these produce contractile filaments. If we grant that the filaments have any power of absorbing nitrogenous fluids, and this can hardly be denied, the only theory that suggests itself is the following:—That the filaments absorb the salts of ammonia from the rain-water and dew which fall on the leaves, and that it is this power which is modified in the adult plant so as to enable the filaments to take advantage of the animalized fluid retained by the leaf-cups. It has been already stated that filaments can issue from the glands when the leaf is merely *damp*. It does not, therefore, seem impossible that an elongated filament should crawl or spread itself over the surface of the leaf, its proximal end remaining attached to the gland; and in this way ammonia might be absorbed and transmitted to the gland, from the dew or rain collected on the leaf. The following observation seems to show that the filaments can adhere to smooth surfaces; and this faculty, in conjunction with their powers of contraction and extension, would enable them to crawl on the surface of the leaf. A free or unattached filament being in the field of the microscope, the preparation was irrigated with methylated spirit. The filament did not float away with the current, but evidently adhered to the under surface of the cover-glass. When the alcohol reached it the filament actually contracted against the force of the current, showing how firmly it was attached to the glass.[1]

Schlösing[2] has shown that the leaves of the tobacco-plant, when supplied with the vapour of carbonate of ammonia, yield on analysis a greater amount of nitrogen than other plants not thus treated. My father remarks that the vapour may be, perhaps, absorbed by the glandular hairs on the leaves. Dr. Gilbert[3] also states that Adolph Mayer has "experimentally shown that plants can take up nitrogen by their leaves from ammonia supplied to them in the ambient atmosphere." There is, therefore, nothing extraordinary in the belief that the leaves of the teasel absorb ammonia from the atmosphere; the novelty is merely in the method of absorption, viz. by protoplasmic filaments.

It is therefore important to know whether the amount of available ammonia in the atmosphere is sufficient to be an item in the food of the plant. MM. Schlösing and Mayer (as quoted by Dr. Gilbert) appear to believe that the absorbing action "takes place in a very immaterial degree in natural vegetations." This may be from a lack of absorbing organs on the part of the leaves, or from the small quantity of ammonia which is available for

[1] This observation suggested that the filaments might in the adult plant crawl over the dead bodies of the drowned insects, and thus absorb a strongly nitrogenous nutriment. I therefore cut thin sections of roast meat across the fibres, and placed the minute fragments thus obtained round and among the glands on a section of a teasel-leaf. But not a single filament applied itself to a piece of meat. I also thought that the filaments might have the power of seizing minute granules floating in the muddy water of the cups. I tried a number of experiments in the hopes of deciding the question. Preparations were irrigated with finely divided carmine suspended in slightly ammoniacal fluid, but no particles were ever seized by the filaments.

[2] 'Insectivorous Plants,' p. 353; for the original see 'Comptes rendus,' June 15th, 1874.

[3] Address delivered at South Kensington at the Science Conferences, 1876.

absorption. Dr. Gilbert (p. 5) gives the amount of ammonia which falls in rain and minor aqueous deposits per acre at Rothamsted as 6·46 pounds per annum. Boussingault[1] found ·00079 grm. per litre of ammonia in rain water in the *country districts of France*. In dew he found as much as from ·001 to ·006 grm. per litre. The average of three analyses here given of the amount of organic matter *in rain water is ·028 grm. per litre.* Is it not possible that some of this organic matter (which causes rain water to putrify when kept) may be absorbed by the filaments? *On the whole, it does not seem impossible* that a plant should derive benefit from the nitrogen in the rain and dew which falls on its leaves.

Conclusions.

The following is a summary of the results which I believe to be established on a reasonable basis of probability :

1. That the filaments are not parasitic organisms, but are the normal productions of a particular form of glandular trichomes on the leaves of the seedling and second-year plants.
2. That they consist of protoplasm in some way intimately connected with resinous matter.
3. 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 utilised by the plant as a mode of nutrition.
4. 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 absord the *products of the decaying insects for the* capture of which the plant is adapted.
5. That some obscure correspondence may exist between the *protrusion* of the filaments and the *process* of aggregation.

Note to Mr. Francis Darwin's Paper.

I beg leave to say that I have witnessed almost all the facts described in the foregoing paper, and can vouch for their accuracy. To the best of my judgment, the whole case is a most remarkable one, and well deserves the attention of physiologists.

CHARLES DARWIN.

[1] 'Watts' Dict. of Chemistry,' v, p. 1014-15.