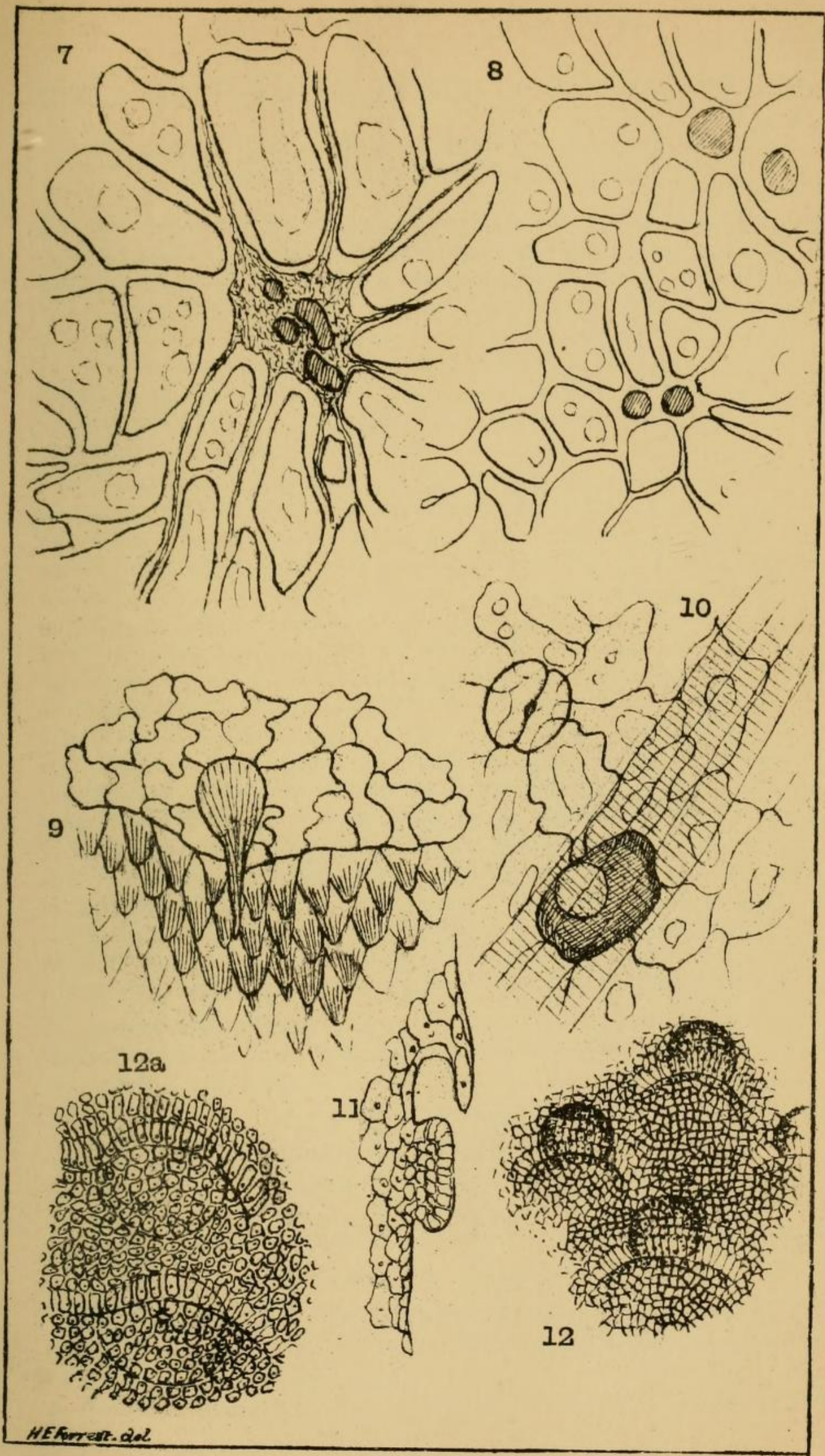


Structures of Pitcher Plants, &c.



H.E. Forrest. del.

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NOTES ON THE STRUCTURES OF PITCHER PLANTS.

BY LAWSON TAIT, F.R.C.S., PROFESSOR OF ANATOMY TO THE
BIRMINGHAM ROYAL SOCIETY OF ARTISTS, ETC.

The following notes comprise a series of jottings on the structures of these interesting plants, made whilst I was investigating, at the suggestion of Mr. Darwin, their digestive powers. Some of the observations are, I know, not new, and others I am equally certain will not be admitted without further corroboration. They were made at a time when leisure was more abundant to me than it is now, and I may therefore be excused if I say that I am not likely to travel over the ground again, and shall therefore leave any corrections which may be necessary to be made by future observers.

Mr. Darwin was the first to use the term "quadrifid" to describe certain structures inside the pitcher, which I think he shows are associated with the process of absorption. The term is a very useful one, and I have adopted it, and modifications of it, to describe certain epithelial structures which are of very frequent and constant occurrence in pitcher plants. They consist merely of modified epithelial cells, the walls of which are lined with a thin layer of protoplasm and divided into arms, so that the cell is composed of a set of branching tubes, conducting to one stem, in which is placed the cell nucleus. The number of arms is very various, and therefore I generally speak of these bodies as multifids. They are most numerous, and are most fully developed on the outsides of pitchers covered by the lid from the access of rain, and they are especially large and numerous on those parts of the pitcher where water is most apt to lodge. Thus, in a pitcher of a young plant of *Nepenthes Rafflesiana* they are largest at the point where the stem bends at the base of the pitcher, and in the curvature; the spot where of course water would be longest in evaporating from the surface of the pitcher. Over the general surface of the pitcher they are much smaller, and indeed are mostly to be found only as aborted buds. (Plate VII., Fig. 1.)

In the reversed coriaceous pitchers of an old plant (*N. Rafflesiana*) they are often to be found only as buds slightly raised above the general

REFERENCES TO PLATE VII.

- Fig. 1.—Multifid and bud from *Nepenthes Rafflesiana*.
 Fig. 2.—Included gland, *Drosera rotundifolia*.
 Fig. 3.—" " *Pinguicula alpina*.
 Fig. 4.—" " *Sarracenia flava*.
 Fig. 5.—Ostiole from pedicel of *Drosera* gland.
 Fig. 6.—Tubular trichome from fourth zone of young pitcher of *Sarracenia purpurea*.

REFERENCES TO PLATE VIII.

- Fig. 7.—Glandulous lacuna infested with fungous growth, *Sarracenia rubra*.
 Fig. 8.—Nucleated lacunar expansion from lip of *Darlingtonia*.
 Fig. 9.—First and second zones of *Sarracenia purpurea*, showing sudden transition.
 Fig. 10.—Nectaries of *Darlingtonia*.
 Fig. 11.—Secreting gland of *Nepenthes distillatoria*, in section, showing the hood.
 Fig. 12.—Ditto, at upper part of glandular zone.
 Fig. 12A.—Ditto, at lower part of glandular zone.

epithelial surface, and not dipping under it. Their contents consist of light brown protoplasm lining the walls, somewhat viscid, and within that a more fluid and slightly darker substance. When a piece of the pitcher on which they are situated is snipped off they rapidly shrivel, and the arms separate. But if a drop of water be placed on the fragment and then gently shaken off it will be found that while it does not adhere to the general surface, some of it has been retained by the arms, which have gathered together, just like the hairs of a brush wetted with water, and in a few minutes they become quite plump.

When this experiment was performed with water containing phosphate of ammonia (after Darwin's plan, but not with such extremely dilute solutions,) the protoplasm was found in some instances, but not in all, to become turbid and to separate into ill-defined masses, and the nucleus went through slow changes in outline. Decaying or digested animal matter did not, in any of my experiments, produce these changes. The distribution of these structures, which will be given more in detail when speaking of individual pitcher plants, and the result of my experiments induce me to believe that they are absorbents of water and such nutrient material as may be dissolved in water without special preparation.

In certain pitchers the multifid buds, instead of appearing wholly above the epithelial surface, are seen to dip partially under it, and this may be seen in favourable instances to advance till the epithelium almost meets over the top of the bud. In this case the protoplasm of the bud may be seen marked by distinct divisions, varying in number from two to nine, the latter being the largest number which I have seen. These divisions of the cell seem to send up processes which appear at the surfaces between the interstices of the epithelium, and such modifications are generally associated with a peculiar system of intercellular canals to be afterwards described. This involution of multifid buds is seen in many surfaces, but it is especially associated with the absorption of decayed or digested animal matter. When the epithelium completely covers these structures I propose to call them included glands, for similar, if not absolutely identical glands, are found in the tissues of many plants, some of which are already known as digesters, (*Drosera*, Fig. 2, *Pinguicula*, Fig. 3,) whilst others are not suspected to have such functions.

Dr. John Lindley described these structures in *Nepenthes* as long ago as 1848, and Mr. A. W. Bennet has also described them in *Drosera* and *Pinguicula* under the term *ganglia*, but without entering into any explanation of their function. ("Popular Science Review," Oct., 1875.) In very many cases where they are included they may be seen to occupy lacunar enlargements in the system of intercellular canals, and even where no such canals can be seen they occupy the spaces between the large cells of the parenchyma (as in *Pinguicula*) in a position where their aid would be almost as effectual. In some cases, as in the lids of some *Sarracenias* (*rubra* and *flava*, see Fig. 4) and in the pedicels of *Droseraceæ*, they have intimate relations with the intercellular canals

without being included by the epithelium, and then I give to them the name of *ostioles*. On the pedicels of the Droseraceæ they are seen to be papillary in some instances. (Fig. 5.) These ostioles never have air bubbles in them as the stomata invariably have, unless they have been removed by maltreatment; and they are smaller than stomata, being $\cdot 035$ mm. in their largest measurement, whilst the latter are almost uniformly $\cdot 05$. Cells do not radiate from stomata as they do from ostioles. Their relations to other parts, their special distribution, and the fact that I have seen their contents undergo changes when the fragment of leaf has been bathed in a solution of phosphate of ammonia, and once in the case of *Drosera intermedia*, when the leaf was bathed in a solution of peptone, the result of digestion in a *Nepenthes* pitcher, make me certain that their function is the absorption of the food of the plant.

Another variety of epithelial absorbent is the tubular trichome found in certain pitchers. It is always associated with a system of intercellular canals, and seems really to be developed from the protoplasm contained in these canals more than from a cell, the cell wall apparently going to constitute the lining membrane of the tube, its protoplasm disappearing. At the upper side of the margin of the base of the trichome its protoplasm can be seen to be continuous with that of the intercellular canals; and in the growth of the hairs this can be seen to be deepening in colour and increasing in quantity at the lower part, so as to form the process of the trichome. This observation can be best made at the lower part of the fourth zone of a young pitcher of *S. purpurea* (Fig. 6.) At the free extremity of these tubular trichomes there must be a true stoma, though I cannot pretend to have seen it. But I have seen a bubble of air enter at the extremity of the tubule, and I have traced its slow passage, coincident with the shrivelling of the fragment examined; and the air bubbles may be made to alternate with short columns of water by alternately wetting and drying the surface.

The systems of intercellular canals to which I have referred are best seen on such surfaces as absorb digested food. Thus on the inner surface of a *Nepenthes* pitcher examination by high powers will demonstrate these canals beyond dispute. They are walled and contain protoplasm, for its columns may be seen broken at irregular spots. They are undoubtedly absorbents, for I have repeatedly satisfied myself that they were larger in pitchers which had been fed, had digested and were absorbing their food, than they were in virgin or starved pitchers of the same plant; and the fact that the tubular trichomes of *Sarracenia* are developed from the protoplasm contained in these canals is a further argument in favour of this view. The most complete proof of the actual existence of these canals is to be obtained from diseased epithelial surfaces where fungous growth is found to be extending into them from an ostiole and distending them. In several pitchers of *S. flava* and also of *S. rubra*, I have found the ostioles so infected that their characteristic protoplasm had been destroyed, but their canals were so dilated that the connecting systems between the ostioles could easily be traced and

canals could also be seen dipping deeply down into the parenchyma of the lid. The appearances seen strongly reminded me of the effects of a poisoned wound of the finger upon the superficial lymphatics of the forearm. (Plate VIII., Fig. 7.)

In the lip of *Darlingtonia* I have seen them with nucleated lacunar expansions (Fig. 8) quite identical with similar appearances which I have already described in the human umbilical cord, (Proceedings Roy. Soc., No. 163, 1875.) In many cases, however, they do not possess distinct walls, but seem to be mere tubular interspaces between cells.

The last structure found in pitcher plants to which I shall make special reference is the secreting gland. These are limited to the *Cephalotus* and *Nepenthes*. In the former they are buried in a pit excavated in the parenchyma and lined by epithelium. They are constructed of modified epithelium, arranged very much like the elements of the glands of the *Drosera* and *Dionæa* as described by Darwin. They are probably also absorbents, their two actions alternating; but of this I have no evidence save the analogy with the glands of *Drosera*.

[TO BE CONTINUED.]

SCIENTIFIC NAMES.—II. PRONUNCIATION.

BY W. B. GROVE, B.A.

(Continued from Vol. I., p. 152.)

The rules concerning the pronunciation of words come under two heads, (1) as to the sound of single letters, (2) as to the syllable upon which the accent falls. Upon the second head, in the case of Latin, at least, there is very little difference of opinion, but with regard to the first the ideas of many persons are in a transition state. The old-established idea was that each nation should follow the precedent of *its own* language in determining the sound of the various letters in Latin words. But, though this was the theory, the practice, at least among ourselves, was very different, and the accepted model was a combination of diverse styles, together with a little of no style at all.

In the case of scientific nomenclature the confusion is worse confounded on account of the medley of sources from which it is derived. Sometimes when a native name of a plant or animal formed part of the scientific name, or when some discoverer with an appellation full of unclassical consonants and diphthongs was to be immortalised, an attempt was made to diminish the incongruity by Latinising the word on the same principle on which the Romans themselves converted the words which they adopted from other nations, as when they changed Caradoc into Caractacus. But this is seldom done now, and the practice sometimes leaves the original form of the altered name uncertain, and thereby fails after all to immortalise anybody in particular. No apology is now thought needful for placing a word which is pure Greek side by side with one which is pure Javanese, *e.g.*, *Strychnos Tieuté*, a tree which grows in Java. The old principles will no longer suffice, and any change will most likely

A short distance further on our diggers bring from their hiding-places three beautiful specimens of the rather rare *Trechus brunneus*.

Our time has now nearly run out and we must think of returning. Before leaving this spot, however, we turn over one of the drowned dogs lying about, and pick out a supply of the Histers and other Clavicorns that have taken possession of his carcass. But though there are plenty of beetles we are soon glad to retreat, the "high" state of our quarry being too much for at least one of our five senses. We therefore hasten towards Brownhills Railway Station, with the view of catching the next train homeward. On the way we capture *Carabus arvensis* running on the heath, *C. catenulatus* under a stone, and a single specimen of a pine-feeding weevil—*Hylobius abietis*—which seems to be altogether out of his reckoning here. This beetle suggests a topic for conversation, and our journey home is bereft of much of its tediousness by an animated discussion on the migrations (both local and general) of insects. Our second Ramble thus ends as happily as did the first, and our party separates with evident signs of unabated energy, indicated by the eager enquiry, "Where shall we go next, and when?"

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(Continued from page 268.)

SARRACENIE.

Of this family Dr. Hooker makes two groups, in the first of which the lid does not cover the mouth of the pitcher, whilst in the second the lid does not admit rain to the pitcher. These groups are united by the fact that in some of the first the lid covers the mouth of the pitcher in the young state of the plant, but does not do so when the plant is old.

In *S. purpurea* the lid never covers the pitcher, and to this plant I first directed my attention, for it seemed to me that it would prove to be in organisation the least removed from a mere water pitcher. I examined many specimens of this plant, some grown under glass in this country, and some brought living from its native soil. My observations on the structure may be summed up in the description of a mature pitcher of a native-grown plant, nine centimetres in length. The outer surface was scattered with stomata and multifid buds. From the margin of the lip down the inner surface of the true pitcher, for a distance varying between two and three centimetres, the epithelium is of peculiar shape, known as sinuous. On this zone stomata are very abundant. There are numerous stiff hairs, not tubular, but made up of long rod-like cells. (Plate VIII., Fig. 9.) These setæ are all pointed downwards, towards the cavity of the pitcher, and must, evidently, be of service in preventing the egress of insects who may wish to travel outwards. It would be very interesting to know what special appliances enable

Xanthoptera semioceca and *Sarcophaga sarracenia*, said by Professor Riley to be the only two insects which can escape from the pitchers of the *Sarracenia*, to overcome this formidable *chevaux de frise*. In the case of the latter insect it is probable that the grub is deposited in the pitcher by the mother before the special armature of the first zone is developed. This development afterwards leads to the peculiar method of escape of the mature grub in a way serviceable to the plant in which it has fed. Sparsely scattered over this surface are multifid buds, raised above the epithelial level for the greater part of their bulk, but slightly dipping below it, being therefore transitions from the multifid bud to the ostiole. I have failed to find anything which I could regard as nectaries on this surface. It ends quite abruptly in a line of crescentic markings, armed with stunted setæ, and when wetted it does not throw off water. (Fig. 9.) The second zone presents to the naked eye a remarkable bald appearance, and when wetted it throws off the water, a circumstance which seems to be due to a peculiar arrangement of the epithelium. Each cell is produced into a mammillary process, (Fig. 9.) pointing downwards, and is marked by a number of flutings, like the back of a pecten shell, these flutings converging towards the apex of the process. The process of each cell overlaps the upper margin of the cell immediately below it, and in this way a subsidiary barrier is formed which must prevent the egress of insects small enough to creep between the large setæ of the first zone. On this surface the intercellular spaces are evidently canalicular, and multifid buds abound, but they are covered by the altered epithelium. Whether this covering means that they are only hidden by the peculiar development of the epithelium, or are really embedded, I am unable to say. This zone is about six millimetres wide, and ends as abruptly as it begins. I have failed to obtain any evidence of secretion from this surface, and therefore I regard its glandular structure as purely absorbent. Stomata are of very occasional occurrence on this surface. In the third zone the epithelium is of the sinuous pattern, with well marked intercellular canals and very abundant included glands. These bodies are entirely covered by the epithelium, the divisions of their protoplasm appearing, however, very close under the surface. They are about $\frac{1}{65}$ of a millimetre. There are no stomata on this surface. The transition from the third to the fourth and most extensive zone is rapid, but not quite sudden, and consists in an alteration of the cells of the epithelium from the sinuous shape into irregular polygons. The subepithelial cells are, however, of the sinuous shape, a fact which may account for the view expressed by Dr. Hooker, that this fourth zone has no cuticle. There are no stomata to be found in this zone, and no subepithelial glands, the place of the latter seeming to be taken by the tubular trichomes already described. These trichomes are not nearly so stiff and strong as the setæ on the first zone, and the surface on which they are situated is peculiarly retentive of water, the innumerable hairs taking it up between them like a sponge. I have not seen spiral vessels in the tissue of *Sarracenia purpurea*. All my efforts to discover the presence of any ferment having digestive properties in the fluid taken

from *S. purpurea* have failed. Fluid taken from pitchers containing insects generally gives a distinctly alkaline reaction, and in the few instances where I have obtained a faintly acid reaction, it has seemed to me to be due to the presence of ants. In virgin pitchers, fed with albumen, no acid reaction has ever been obtained, and the albumen rapidly decomposes. I may here state that the ordinary method of testing these fluids by litmus paper is crude enough not to be always trustworthy. A more delicate way is to make a concentrated solution of litmus in distilled water, and add to it about ten per cent. of absolute alcohol. A drop of this should be placed on a white porcelain plate, side by side with a drop of the fluid to be tested, and the drops then made to touch. An amount of acid may thus be detected which will escape the eye of the observer if litmus paper be used, and there can be no possibility of error. I draw the conclusion, therefore, that the glandular structure of *S. purpurea* is purely absorbent, that its pitchers are merely passive insect traps, and that the advantage gained for the plant by the destruction of flies is to be attributed entirely to their maceration. Another argument in favour of this, the importance of which will be seen by and by, is that flies continue to live an indefinite time after having been introduced into a *Sarracenia* pitcher containing fluid. The very interesting observation of Prof. Riley concerning the habits of the *Sarcophaga sarraceniæ* would show that considerable advantage is gained for the plant by the direct application of the insect debris to the roots of the plant. I am quite certain from my experiments with the nutrition of *Nepenthes* that if *S. purpurea* had a secretion at all like it, no insect could visit the latter with impunity. A series of experiments made during the summer with test tubes of various sizes and diameters, and containing fluids of various kinds, have convinced me that as far as the common house fly is concerned, no specially disguised or attractive form of trap is required. But there is no doubt that the addition of the coloured venation on the lip of the *S. purpurea* must make it more attractive to certain kinds of insects, as Sir John Lubbock has shown that bees are greatly influenced by colour. The armatures of the upper zones must also be advantageous by imprisoning the insects. It will be seen, then, that I differ from Dr. Hooker in that I regard the first and second zones of the *S. purpurea* as the truly detentive surfaces, and the third and fourth as absorbent.

S. flava.—I examined the pitchers of a young plant in which the lip covered the mouth of the pitcher. If I may argue from the facts observed in *Nepenthes* this ought to be the most active condition of the pitcher. I found spiral vessels in the lid, and numerous stomata and ostioles. The latter in this case suggested that they may be the local centres for the growth of epithelium, for the cells in their immediate neighbourhood were all small and seemed to radiate from the ostiole as from a centre, and the intercellular canals seemed to grow with them (see Fig. 7, also Fig. 4 from *S. rubra*.) There were also a few multifold buds. The first and second zones of this pitcher resemble those of *S. purpurea*. The third has short tubular trichomes and no glands, and the fourth has long tubular trichomes. This variation in the third zone is noteworthy. I found no evidence of secretion here, and when the pitcher was over-fed, whether by albumen or naturally by a too large fly, the decomposition spread to the parenchyma of the leaf and killed it.

[TO BE CONTINUED.]

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BIRMINGHAM ROYAL SOCIETY OF ARTISTS, ETC.

(Continued from Vol. II., page 297.)

SARRACENIÆ CONTINUED.

Sarracenia rubra closely resembles *S. flava* in all the above details, and the amount of fluid in both was always exceedingly small, only enough to moisten the hairy zone and sometimes not sufficient even for that.

S. flava maxima.—I found the zones here to correspond closely with those above detailed. At the base of this pitcher the development of the trichomes and their relations to the intercellular canals can be especially well seen. I have had no opportunity of examining a fresh lid of this magnificent pitcher.

S. Drummondii.—Unless this plant is in extremely good growth its leaves abort and do not grow pitchers. It can evidently make use of only very small insects, for anything larger than a house-fly kills the pitcher. Its first two zones correspond exactly with those already described, and its third, which is homologically its fourth, is destitute of glands, but studded with numerous trichomes. Below this is a very extensive continuation of this zone destitute of everything but epithelium. I have never found any fluid at all in its pitchers. The species is evidently an instance of imperfect or early development.

S. variolaris.—I selected this plant as representing Dr. Hooker's second group. I found the surfaces of the lid the same as in *S. rubra*. The first zone of the pitcher had no stomata and very few glands, and these were evidently not sub-epithelial, though the mammillary process of the cells was produced over them. The second zone had no glands or stomata, and the third had the usual tubular trichomes. I found one pitcher of *S. variolaris* filled with natural food, amongst which a little moisture had gathered. The source of this moisture is probably the air of the hot-house, for I found quite as large an amount gather in a narrow test tube containing a number of flies, placed under similar circumstances. I squeezed the fluid out of the flies from the pitcher, but it had no acid reaction.

Darlingtonia Californica.—I have had opportunities of examining pitchers from four plants, one of which was sent living from its native soil at Sacramento, and a description of a pitcher of this plant, which was fourteen centimetres long and two in greatest diameter, will answer my purpose best. The curious two-lobed organ hanging from the lip, stated by Dr. Hooker, on the authority of Professor Asa Gray, to be smeared with honey, is abundantly supplied with spiral vessels. Both surfaces are numerously supplied with stomata, and situated on or close to the twigs of spiral vessels are large epithelial cells containing brown protoplasm and a large, bright nucleus. (Fig. 10.) I think these are nectaries. The first zone of the pitcher was spiked as in *Sarracenia*, there was abundance of spiral tissue, but no brown cells, ostioles,

* The figures referred to in this paper will be found in the Plates Nos. VII. and VIII. in Vol. II.

stomata, or glands were found. There was only one other zone, which was covered with the tubular trichomes as in *Sarracenia*, and had also a few scattered stomata. This surface retained water when wetted, and it extended for ten centimetres from the base of the tube. I failed as completely to obtain any evidence of a process of true digestion in *Darlingtonia* as I did in *Sarracenia*. The lacunar spaces on the lip, having brown nuclei, are probably nectaries.

Cephalotus follicularis.—The amount of material at my command for experiment in this case was limited, but what results I did obtain were so decided that I think my conclusions are well founded. The plants examined were all grown in this country. The pitchers of *Cephalotus* seem to rest their base on the ground, and have three ridges or wings, the outer two of which are fringed, and afford excellent guides into the pitchers for insects creeping off the ground. The lid completely covers the mouth, and in all the specimens which I have examined it is very slightly raised from the lip, this arrangement, with the fluted structure of the lip, allowing the passage of only small insects. The pitchers averaged about 25mm. in depth and fifteen in greatest diameter, the development of erythrochrome being principally on the under surface of the lid. On the unaltered leaves there is abundant erythrochrome on the under surface and numerous stomata. Besides these there are papillary prominences with deep crypt-like cavities. In a young leaf the occurrence of transition forms between these craters and the stomata make it certain that they are developed from the latter, and ought, therefore, to be regarded as additional respiratory organs. We might call them tracheoles, for stomata are sometimes visible within them. On the upper surface of the unaltered leaf the epithelium is of the sinuous kind, and there are stomata sparsely distributed and multifid buds nearly sunk under the epithelial surface. These buds are about .05mm. in diameter, round, the cells being seen in many cases to have their protoplasm divided into processes or even into distinct cells. On section of the leaf they can be recognised by their brown colour, and can be seen to be only modifications of ordinary epithelium, and that in their most complete form they occupy a nest in the parenchyma, whilst the stomata occupy the top of small papillary eminences. On the under surface of the leaf they are also found, but there they are much less numerous than on the upper surface, and the reverse is the case with the stomata. This is one of many reasons which make me regard the upper surface of the unaltered leaf as the representative of the inner surface of the pitcher. On the outer surface of the pitcher stomata and buds are numerous, especially the former; but inside the pitcher there are no stomata, and the buds can be seen enlarging into glands of great size and importance. In a very young pitcher which I examined I really could not tell, in a section, except for the curve, which was external and which internal surface, for on both the buds were the same. But in the mature pitcher the protoplasm in the buds is divided, and large compound glands are to be found situated in cavities of the parenchyma, which are lined by epithelium. Of these glands only the upper part is presented above the surface, so that the appearances on

section very much resemble those of the solitary glands of intestine. They vary in size, even in the mature pitcher, from that of the multifid bud on the outside (.05 mm.) to a size which rivals that of the largest glands in *Nepenthes*, (.275 mm.) and are then quite visible to the naked eye. These largest glands are situated on two eminences, composed of a thickening of the parenchyma, situated obliquely, near the bottom of the pitcher, and symmetrically, one on either side. These glandular bodies are crescentiform, and measure about 11mm. by 3. The smaller glands are distributed very irregularly over the surface of the pitcher, but each gland, whatever its size, seems to have a close relation to a twig of spiral tissue with which the pitcher is very liberally supplied. The glands are composed of polygonal cells, between which run intercellular canals. I have never been able to trace any direct connection between the glands and the spiral tissue. On the inner surface of the lid the cells are spiked and point inwards, and the multifid buds exist just as in the *Sarracenia*. In a completely formed pitcher, which still had the lid adherent to the lip, I found a few drops of clear and slightly viscid fluid, perfectly neutral, and containing two substances, to which I have given the names of *Droserin* and *Azerin*, described elsewhere, together with traces of chloride of potash and soda. In two pitchers I found insects bathed in fluid, with a strongly acid reaction, and this fluid digested shreds of albumen exactly as I found the fluid of *Nepenthes* pitchers did. I conclude, therefore, that a true digestion of its victims is carried on by the *Cephalotus* pitcher.

NEPENTHES.

In this family I have been able to examine a large number of pitchers from the following varieties:—*N. distillatoria*, *ampullacea*, *ampullacea vittata*, *hybrida*, *hybrida maculata*, *lanata*, *Rafflesiana*, *phyllamphora*, *gracilis*, *levis*, *Hookeri*, *Sedeni*, *Khasyoma*, and *sanguinea*.

I have made a large number of observations on their gland structure and its functions, but they may be all liable to correction, as I have not yet had an opportunity of examining native-grown pitchers. The discrepancies which I have met with are very few, and being confined entirely to minor details of the quality and action of the secretion of the pitchers, I do not attach much importance to them. Still I feel certain that these interesting structures must be studied each in its native place before our knowledge of them is complete.

The form of the pitchers is too well known to need description. On their outer surfaces two ridges occur very constantly, which, in some varieties (*Rafflesiana* and *Veitchii*) reach to a large size, and are deeply fringed at the margins. They extend from the base of the pitcher in an angle from the stalk up to the lip, and include a space which I propose to call the *platform*. In such pitchers as have these wings there is a constant tendency for the stalk of the pitcher to rest in contact with the platform, and I have watched plants and seen that this is of essential service to them in procuring insect food.

This particular kind of nutrition seems to be most necessary for the plants during their youth, for as those which have winged pitchers grow old they tend to produce pitchers without wings, with other changes in their structure, and with very much impaired digestive powers.

Thus the pitchers of *N. Rafflesiana* in a young plant are flask-shaped, the largest diameter being near the bottom, the wings are

very wide, and the stalk touches the platform. The pitchers of an old plant, however, have only very slight ridges to represent the wings, they are prolonged into conical funnels, and are bent on the stalk in the direction opposite to that of the young pitchers, whilst the stalk does not approach the side of the pitcher. Their structure is likewise altered in that the pitchers of the young plant are soft and easily withered, whilst those of the old are hard and coriaceous, and are scarcely altered either in colour or shape by prolonged drying. Digestive powers in the latter can hardly be said to exist, and the pitchers seem to have degenerated into mere receptacles of water.

On this most interesting point I have the following information from Messrs. Veitch, the well-known growers of pitcher plants:—“Flowers and pitchers are never borne on the same plant at the same time, the production of the latter always preceding that of the former, and when the plant is in a condition to produce flowers the pitchers become abortive and cease to be formed. The leaves of seedlings and young plants form their pitcher appendages from the very first. In young plants the winged side of the pitcher is turned towards the petiole, the lamina or lid being of course opened on the opposite side. As the plants increase in age and strength, the newly formed pitchers are elongated, and finally become curved something like the horn of an ox; their position with reference to the petiole being then changed, the winged side being turned away from it. During these gradual changes the wings cease to be developed. When the plants are several feet high, and are in a condition to bear flowers, the pitchers cease to be formed.”

It is clear, therefore, that the pitchers and their digestive processes are useful for the development of the reproductive function of the plant. This is also shown by the fact, stated to me by growers, that if it is wished that a plant of *Sarracenia* should continue to grow pitchers, its flower must be nipped off before it is impregnated.

These changes take place in the pitchers of other varieties of *Nepenthes* apparently sometimes independently of age, but rather in consequence of an abundance of food and its being easily obtained. Thus the pitchers of *N. gracilis* and *N. distillatoria* are quite wingless, but have always very active digestion. The real significance of these changes can be determined only by a study of the plants under their natural conditions, and when this has been done I have little doubt that they will afford very striking illustrations of the modification of structure by the influence of surrounding circumstances. Another noteworthy matter in the general structure of the pitchers is the lid. Sometimes it covers the mouth completely, as in *N. distillatoria*, *N. phyllamphora*, *N. Khasyoma*, &c. In other cases, it either stands erect, as in *N. Rafflesiana*, or covers the mouth very imperfectly. When it covers the mouth the pitcher is nearly always bottle-shaped, having a very distinct constriction about its middle, which marks the abrupt cessation of the secreting surface. In such cases the amount of secretion is always small, but its action is very powerful, and the lid covering the pitcher is evidently for the purpose of excluding rain. Mr. Albert Ratcliffe, a very successful grower and a minute observer, informs me that the lid of *N. distillatoria* closes over the mouth towards evening. This may be to prevent the ingress of nocturnal insects too large for its digestive powers. When the lid is erect, the glandular surface comes up close to the lip of the pitcher, the secretion is large in quantity and slow in action, and the addition of rain-water does not seem of much consequence. This is well seen in *N. Rafflesiana* and in *N. ampullacea vittata*. These differences are sure to be dependent upon some conditions peculiar to the native habitat of the plant, or to the food of which it partakes.

(To be continued.)

It has been observed that snail shells of the same species differ in brilliancy of pattern from various causes. The lesser or greater supply of lime, the more or less prevalence of succulent vegetation, and ample or deficient sunlight decidedly affect the shells. Confine handsomely-marked snails in a Wardian case with little sunlight, and the colours will exhibit a falling off in a short time. As an abnormal instance of absence of colour, Mr. Mann, the lepidoptera collector, of Clifton, had, a few years ago, white shells of *H. aspersa*, which he found in one spot near the Downs. It would be interesting if some Bristol correspondent would take notes respecting this variety. If the snail shells—empty shells, of course—are dipped in boiling water the outer scarf skin will come away, and leave them more bright in colour than before. This epidermis is put on (like a light overcoat) at the approach of winter in increased thickness, probably to preserve the shell during the long hybernation.

This paper will have no sympathy from some reader who has suffered from an excessive immigration of snails into his garden, and he will not concur in the estimate, given at the outset, of the snail's utility; but if the birds provided to keep the species in check—the blackbird and thrush—were not scared away or killed off with such persistence, snails would only be seen in moderate quantities, and would pursue their functions, usefully and not destructively.

Time was when the rustic maiden in English rural parts read her fortune in the movements of a snail. It is thus poetized by Gay:—

“Last May-day I searched to find a snail
That might my lover's name reveal.”

She placed it on “the milk-white embers spread;” when

“Slow crawls the snail; and, if I right can spell,
In the soft ashes marked a curious L.
Oh! may this wondrous omen lucky prove,
For L is found in Lubberkin and love.”

W. B. STRUGNELL, Cheltenham.

NOTES ON THE STRUCTURES OF PITCHER PLANTS.

BY LAWSON TAIT, F.R.C.S., PROFESSOR OF ANATOMY TO THE
BIRMINGHAM ROYAL SOCIETY OF ARTISTS, ETC.

(Continued from page 8.)

On the outside of all *Nepenthes* pitchers multifids and their buds are seen in great numbers, and they are always most numerous and largest at those parts of the pitchers where rain water would be most likely to lodge. They are also best marked in the young condition of the plant in such an instance as *N. Rafflesiana*.

In the subepithelial parenchyma a number of cells may be seen to send up slender processes to be in contact with the insertion of the multifids. Bubbles of air may, in rare instances, be seen breaking the

column of fluid contained in the multifids, just as in the tubular trichomes of *Sarracenia*. This is probably the result of injury.

Stomata are not very numerous on the outsides of any kind of pitcher which I have examined, and they are not found at all on the inner surfaces. Numerous multifids and buds exist on the upper surfaces of the lids of all pitchers and on the under surfaces of such lids as do not cover the mouth. On such lids as do cover the mouths of the pitchers, as in *N. distillatoria*, they exist only as buds, and usually are not numerous, but they are also found inside the pitcher on a short zone immediately above the true glands. This, together with other reasons already given, leads me to believe that these structures are for the absorption of water and substances dissolved in it. It may be here just noted that these multifids exist in great abundance on the backs of the lobes of the *Dionæa*, and that when the trap is closed, they afford a spongy surface on which water remains for a long time, and its absorption there I think must be of great use to the plant when the trap is closed and the process of digestion is going on. On all the surfaces mentioned these buds are seen occasionally to be sunk beneath the epithelial surface, and to present the peculiar appearances already described in *Cephalotus*. This appearance in *Nepenthes* has been described by Lindley as a special kind of stoma, but he admits that they do not open into cavities of the parenchyma as is the case with the latter. (Introduction to Botany, Vol. I., p. 142.)

On the under surface of the lids of most pitchers are to be seen glands identical in structure with those to be immediately described as occurring on the inner surface of the pitcher. Dr. Hooker believes these to be honey glands, but I differ from that eminent authority for the following reasons:—That they are identical in structure with the true digestive glands, and that they are better marked in the pitchers where the lids cover the mouth completely than in those which do not; that in many such, as in *N. distillatoria*, they are hooded in exactly the same way as the glands of the pitcher; that when the gland is excited by food I have been able to detect acid secretion collected in the hoods of the lid glands of *N. distillatoria*; that nectaries are usually very inconspicuous, and only a small spot of tissue which, without being transformed, produces the nectar. (Sachs.)

Spiral tissue abounds in every part of the parenchyma of *Nepenthes*' pitchers. The most important structures in *Nepenthes*' pitchers are the round or oval glands found regularly distributed over a greater or less extent of the inner surface. These glands are sometimes to be found throughout the whole extent of a pitcher, as in *N. Rafflesiana*; but in many kinds they are limited to the lower part. When this is the case there are always two clearly defined zones, the upper of which resists wetting, and throws off water, while the lower readily retains it. On this upper surface the epithelium is irregularly polygonal in some pitchers, but in the majority it is of the sinuous kind and interspersed with regularly distributed crescentic markings of very small size, ($\cdot 03$ mm. in length by $\cdot 01$ in breadth,) which are arranged with the concavities

downwards, and in the same position as the hoods of the glands lower down. Occasionally at a little distance below one of these markings an epithelial cell can be seen enlarged, and with an increase of protoplasm, sometimes even having a semblance of segmentation, which makes it appear as if it were making an effort to become a gland. The crescentic markings on section can be seen to be formed by the doubling of one epithelial cell under another, so that beyond doubt they are rudimentary hoods. These hoods, as will be afterwards seen, have a very important purpose, but even in this rudimentary condition they would prove serviceable by affording an increase of absorbent surface, just as the *valvulæ conniventes* do in the intestine. These latter structures are found in quite as rudimentary a state in the intestine, as those by which the perfect hoods are represented in the upper surface of the *Nepenthes*' pitcher.

The line of commencement of the glands (in a pitcher where there is a non-glandular surface) is quite abrupt, and corresponds with the ampullary enlargement generally seen outside. From this point the glands are found distributed with great regularity, and increasing in size towards the bottom of the pitchers, where, on the lower or greater curvature, the largest are always found, that spot being, of course, the position in which the gland function will most frequently be called into action. These glands resemble in structure very closely those seen in *Drosera* and *Dionæa*, though, of course, their details differ somewhat. They are sessile, and are placed in depressions of the parenchyma, lined with epithelium, which, at the top of the pit, is produced into a double fold of modified epithelium, between the cells of which run intercellular spaces, and each gland is placed on a twig of spiral tissue, in this arrangement being identical with the glands of *Drosera*. It requires favourable sections to display this fact, and it gave me much trouble to make myself certain of it. The cells of the outer layer of the epithelium of the gland are regularly columnar, and do not seem to be nucleated, except in virgin pitchers. (Fig. 11.) When crushed between the cover and the slide they do not seem to have fluid contents, but spread out as if they had a putty-like consistency. The inner cells are larger, more irregular, and have coloured nuclei. In a few cases I have seen appearances as if the intercellular canals had direct communication with the spiral tissue; but the possibility of this being an optical illusion is so considerable, that I could not venture to assert it as a conclusion. There is, however, as great probability that such connection does exist as there is in the view of the origin of the hepatic ducts advanced by Chrzonczszewsky and others. Examination by high immersion powers have convinced me that these intercellular canals are really walled, and that they contain streams of colourless protoplasm, which is in a state of slow movement. These glands vary very greatly in size in different varieties of *Nepenthes*, the largest which I have seen being at the bottom of a mature pitcher of *N. distillatoria*, which measured $\cdot375$ mm. by $\cdot2$, whilst the smallest were at the top of a virgin pitcher of *N. Rajsthesiana*, measuring only $\cdot045$ mm. (Fig. 12.) The rule of their

progressive increase towards the bottom of the pitcher is quite uniform, and with their increase in size they have a varying relation to the hood. Thus in a mature but unopened pitcher of *N. Rafflesiana* I made a set of careful measurements of the glands and their hoods over the whole surface, the results of which are embodied in the following table:—

MEASUREMENTS OF THE GLANDS OF A MATURE BUT UNOPENED PITCHER OF
NEPENTHES RAFFLESIANA.

Millimetres from the top of the Pitcher.	Size in largest diameter.	Depth of Hood.	Dist. from lip to lip of Hoods.	From centre to centre of Glands.		
I.	0	·045	·03	·1	·1	Round glands, wholly covered by the hood. Average size of glands, ·053. Average depth of hoods, ·056. Estimated number of glands to one sq. mm., 73 Proportion of gland surface to the whole area, ·09225.
	5	·045	·04	·1	·1	
	10	·05	·06	·11	·1	
	15	·055	·05	·11	·11	
	20	·065	·055	·11	·125	
	25	·065	·065	·15	·125	
30	·07	·09	·16	·13	Here the glands become oval.	
II.	35	·135	·09	·18	·18	Glands covered by hoods in proportions varying from $\frac{2}{3}$ at the top, to $\frac{1}{3}$ at the bottom of the zone. Average size of glands, ·163. Average depth of hoods, ·056. Estimated number of glands per sq. mm., 25. Proportion of gland surface to whole area, ·3.
	40	·135	·11	·19	·18	
	45	·165	·11	·2	·21	
	50	·165	·075	·185	·21	
	55	·19	·075	·175	·175	
	60	·19	·075	·175	·175	
III.	65	·19	·05	·175	·175	Hoods cover less than $\frac{1}{2}$ of the glands. Average size of glands, ·2. Average depth of hoods, ·04. (At this point hoods are entirely above the glands.) Estimated number of glands per sq. mm., ·36. Proportion of gland surface to whole area, ·84.
	70	·2	·04	·175	·175	
	75	·2	·035	·175	·175	
	80	·21	·035	·175	·175	
	85	·2	·035	·175	·175	
	90	·2	·035	·175	·175	

The measurements in the last two columns are only relative and not absolute.

The epithelial cells and the intercellular canals have a corresponding increase in their size.

It will be seen from this table that the increase in size of the glands from the lip of the pitcher downwards is gradual up to a certain point, about a third of the way down. This zone clearly may be taken to represent the non-glandular surface of pitchers whose lids cover their aperture. We may also conclude that at one time the lid of *N. Rafflesiana* covered its mouth, but that some advantage being derived (probably that of a subsidiary insect trap, which it may readily be) from the modification of the lid now seen, the disadvantage of the admission of rain-water had to be made up for by an increase of the gland surface. This appears to me to make it certain that the minute crescentic markings already described on the non-glandular surface of *N. phyllamphora* are not retrogressions, but structures only needing the necessity for development which *N. Rafflesiana* has incurred. As all *Nepenthes*' pitchers have the lids of their pitchers originally over their mouths, it is again in evidence that the arrangements of *N. Rafflesiana* are an advance, and this is borne out by the whole appearance and character of the plant, for it is said even to

digest small vertebrata in its native haunts. The size of the glands, their number, and relative area are all less in this zone than in those below, because its digestive power would be less frequently called into action than would be that of the others.

The complete covering of the glands in this zone may be of advantage in protecting them and their secretion from accident and the depredation of insects, for the glands here are much more likely to be uncovered by water than those further down. I think it also very likely that these hoods store up the digestive principles of the pitcher until they are required or until it is washed out by the contact of water, it being retained in their cavities by capillary attraction.

In the second zone the glands gradually alter from a round shape to an oval one, increasing at the same time in size as they are viewed from above downwards, and they become less covered by the hoods. The relative gland area is also greatly increased. The greatest amount of work would necessarily fall on the third zone, so we have here the glands at their maximum, and almost uncovered by the hoods, which still remain in existence, however. The glands are so large and so close that the bulk of the surface is occupied by them.

The epithelial surface of the pitcher (*N. Rafflesiana*) is composed of irregularly polygonal cells, which, in the young pitcher, are regularly nucleated. Between these run continuous interspaces, forming a perfect network over the whole surface.

On the surface of the hoods the cells are elongated, and the spaces run up between them, at right angles, to the lip of the hood, where a canal seems to run, into which they all enter. These intercellular spaces are truly walled on the upper surface, whether they may be or not on their surfaces next the cells; for, in a mature pitcher, recently fed and perfectly fresh, I am quite satisfied they are slightly raised above the cellular surface. In a virgin pitcher they are scarcely perceptible, whilst in a mature pitcher they are large and distinct, and especially large in the lowest zone.

Further, I have on several occasions compared two pitchers as nearly alike as possible from the same plant, one of which I had fed, and the other I had starved, and I have been satisfied that in the fed pitcher the intercellular spaces were larger than those in the one which had not been fed. The stream of protoplasm in these canals can be occasionally seen broken, and in such a state the reality of their canalicular structure can be demonstrated. In one observation which I made on a fragment of a mature pitcher of *N. distillatoria* which had never been fed, I placed over it a drop of fluid taken from the results of the digestion of albumen in another pitcher. I then saw the canals present slight dilatations here and there, and I was satisfied that some of them underwent general increase in calibre. But in several repetitions of this observation I did not obtain convincing results, probably because it was getting late in the season and the pitchers were inactive.

In old pitchers the superficial canals sometimes seem to communicate with a deeper set.

Silver and gold staining did not help me in the investigation of these structures. From what I have seen I am inclined to regard these canals as absorbent vessels.