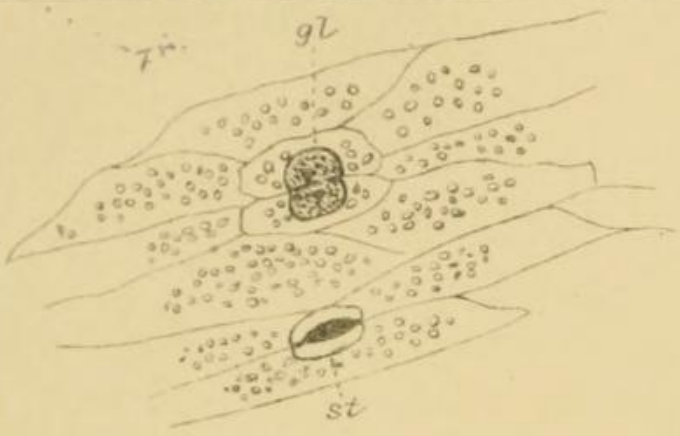

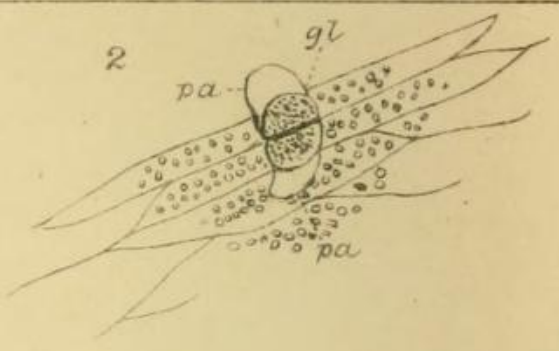

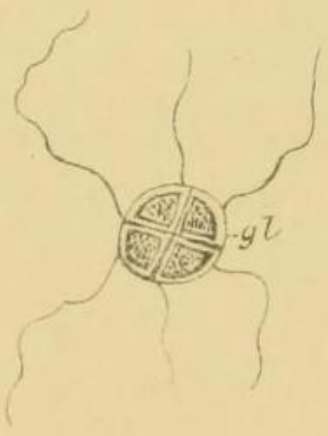

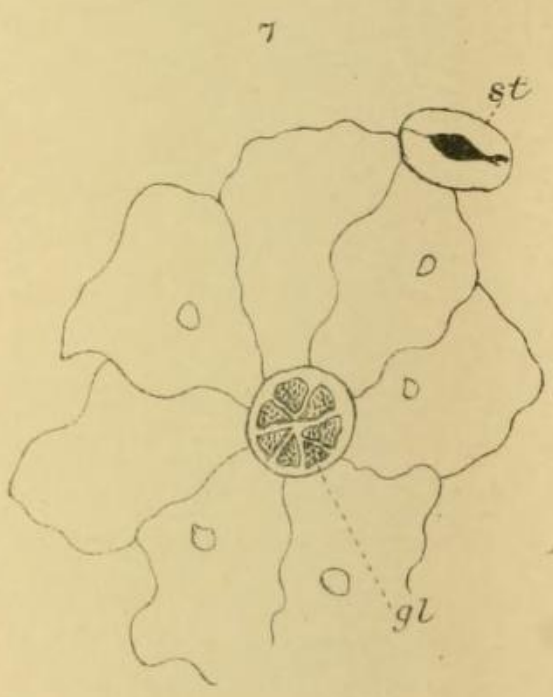

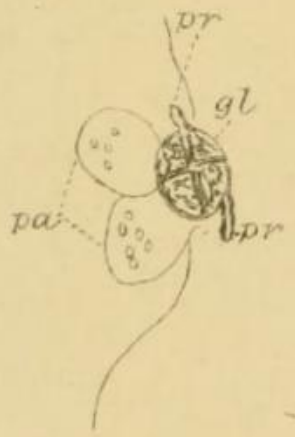

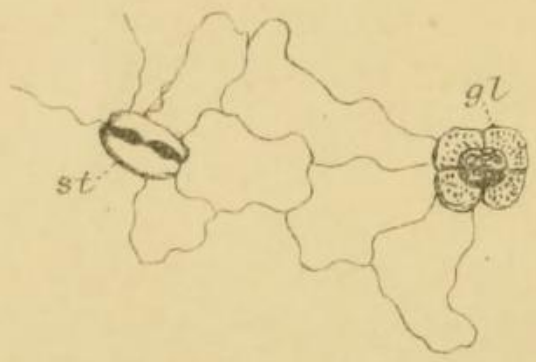

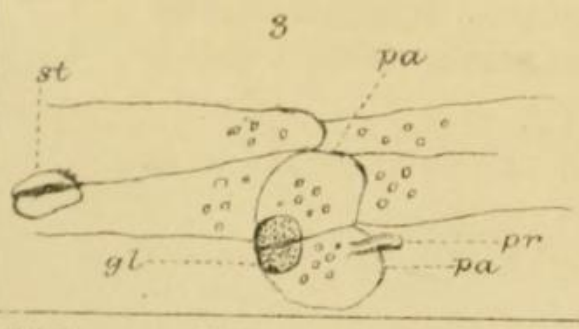

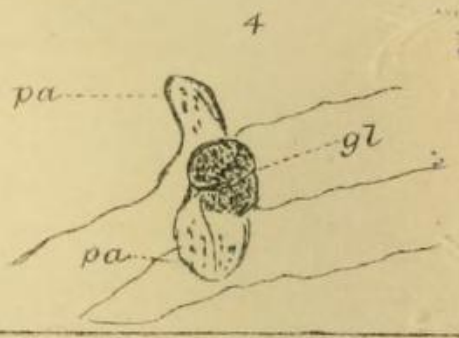

A.W. Bennett del. W. West & Co. lith.

THE

MONTHLY MICROSCOPICAL JOURNAL.

JANUARY 1, 1876.

I.—*The Absorptive Glands of Carnivorous Plants.*

By Alfred W. Bennett, M.A., B.Sc., F.L.S., Lecturer on Botany at St. Thomas's Hospital.

(*Read before the* Royal Microscopical Society, *December* 1, 1875.)

Plate CXXVI.

Those plants which possess the peculiar power of absorbing and digesting nitrogenous substances presented to their leaves, have from time to time engaged the attention of vegetable physiologists. Among the more important papers on the subject may be mentioned those by Grönland and Trécul, in the 'Annales des Sciences Naturelles' for 1855; Nitschke, in the 'Botanische Zeitung' for 1860–61; Warming, in the Proceedings of the 'Société d'Histoire Naturelle de Copenhague' for 1873; and, above all, Darwin's work on Insectivorous Plants, published during the present year. These publications deal chiefly with the insectivorous plants belonging to the genera *Drosera*, *Pinguicula*, *Dionæa*, and *Utricularia*; the "pitcher-plants," *Nepenthes*, *Sarracenia*, *Darlingtonia*, and *Cephalotus*, not having at present received so large a share of attention. As might naturally be expected at first, observation has been up to the present time chiefly directed to the remarkable phenomena connected with the capture and apparent digestion of the living animals which in the natural state are chiefly devoured by these plants; while but little investigation has been applied to the discovery of internal organs by the aid of which absorption is effected; and the assumed absence of any such organs has indeed been brought forward as an argument

EXPLANATION OF PLATE CXXVI.

Figs. 1–5.—*Drosera rotundifolia*: *gl*, absorptive gland in various stages of development; *pa*, cellular papillæ; *pr*, processes from papillæ; *st*, stoma.

„ 6–8.—*Pinguicula vulgaris*; *gl*, absorptive gland; *st*, stoma. Fig. 8 represents a lateral view of a gland projecting slightly above the surface.

Fig. 9.—*Callitriche verna*; *gl*, absorptive gland; *st*, stoma.

All from nature, and × 250 diam.

against the possibility of absorption by the leaves. In the case of *Dionæa*, Darwin gives a very brief description of minute glands of a reddish-purple colour which cover the upper side of the leaf, and which he states to have the power of absorption. But in order to find an adequate description of these bodies we must go back nearly thirty years, when Dr. Lindley gave accurate descriptions and figures of them in his 'Ladies' Botany,' published in 1834, and, in the following words, showed a wonderful insight into their probable function:—"From the cuticle of the upper surface of the leaf of *Dionæa* there spring at short intervals little red glands, which grow from minute green oval spaces, composed of two parallel green cells and resembling stomates. They are firm fleshy bodies resembling little convex buttons, and are composed of cells arranged in a circular manner round an axis consisting of two such cells stationed one on the top of the other. I presume that these glands are analogous to the curious hairs of Sundew, although we do not see that they are possessed of any irritability; but in the Sundew they arise from a general expansion of the cuticle and not from spurious stomates. We moreover find upon the surface a prodigious number of red glands, so minute as to be individually invisible to the naked eye, and giving a red tinge to the leaf. Such glands are found nowhere except upon the upper surface of the leaf in the neighbourhood of the delicate seat of irritability. It is not improbable that these glands are either in some way connected with the irritability, although it is not they through which the shock is first communicated to the leaf, or, as Mr. Curtis supposes, are intended to absorb the nutriment afforded to the leaf by the decay of the insects entrapped in it." Similar bodies are also known to exist in *Nepenthes;* and were likewise described by Dr. Lindley, in his 'Introduction to Botany,' edition 1848, as stomates of a peculiar construction in contact with an internal deep brownish-red gland.

My own observations have been entirely confined to the two most readily obtainable of our English carnivorous plants, *Drosera rotundifolia* and *Pinguicula vulgaris;* having paid considerable attention to the structure of the leaves in these two species during my summer holidays for the last three years. In the summer of 1873, while staying in Westmoreland, I first observed and drew certain bodies imbedded in the leaf of *Drosera* which it struck me must be connected with the processes of absorption and digestion, although I could find no record of them by any previous observer. Hearing shortly afterwards that Mr. Darwin was likely soon to bring before the public his store of long-accumulating investigations on these plants, I refrained from publishing my observations. When, however, Darwin's 'Insectivorous Plants' came out, in the spring of 1875, I found no record of the existence of these bodies, notwithstanding the otherwise full and accurate description of the structure

of the leaves in both genera.* I therefore sent to the 'Popular Science Review' for October in that year, a brief and somewhat inadequate description and figure, which I now propose to give somewhat more in detail, in the hope of throwing some additional light on the processes with which they are apparently connected.

If a careful section is made of the leaf of *Drosera rotundifolia*, there will be found a number of bodies which might at first sight be easily mistaken for stomata, but which are of essentially different structure. In Fig. 1, Pl. XXVI., one of these bodies is represented at *gl*. They are, in their first origin, not superficial, but appear to arise immediately beneath the cuticle chiefly, or perhaps exclusively of the upper surface; in one case I found one imbedded in the tissue immediately beneath a "tentacle" or glandular filament. They consist of two nearly hemispherical cells, filled with a yellowish-brown apparently protoplasmic substance, and form together a nearly spherical body, of which the longest diameter is about ·00075 ($\frac{3}{4000}$) inch. They are more nearly circular and somewhat smaller than the stomata, one of which (*st*) is shown in the drawing. In each of the hemispheres is a darker nucleus-like spot, and each is surrounded by a thin-walled cell containing chlorophyll-grains, much smaller than the ordinary cells of the mesophyll of the leaf, and which seems subsequently to disappear. From these hemispherical bodies are developed two papillæ, successive stages of which are shown by *pa* in Figs. 2–5, with thin transparent walls, and containing grains of chlorophyll. These papillæ sometimes rise above the surface of the leaf or of the filaments of the "tentacles." The hairs or papillæ which result from these glands have been described and figured by Meyen,† Trécul,‡ and Nitschke,§ and are referred to in Darwin's work, p. 8; but their origin from the glands does not appear to have been observed, and they are described as being entirely of an epidermal nature. In the gland drawn in Fig. 5, an indication is apparent of a quadripartite division; and there are also a couple of minute processes (*pr*), one from each hemisphere, which I have also observed in other instances springing either from the glands themselves or the cellular papillæ; one such process is again represented in Fig. 4. To the bodies now described I gave, in the article already referred to,‖ the provisional name of "ganglia," which term however I propose now to replace by "absorptive glands," in allusion to their supposed function, and in order to distinguish them from the secretive "glands," as they are termed by Darwin, which form the apices of the "tentacles."

* I have since had the pleasure of showing my preparations to Mr. Darwin who tells me that these bodies have not hitherto engaged his attention.

† 'Die Secretions-Organe der Pflanzen,' 1837.

‡ 'Annales des Sciences Naturelles, Botanique,' 4 series, vol. iii. p. 308.

§ 'Botanische Zeitung,' 1861, p. 235.

‖ 'Popular Science Review,' 1875, p. 358.

The leaf of *Pinguicula* possesses similar bodies, but somewhat different in structure. Fig. 6, *gl* represents their ordinary form. They are considerably larger than in *Drosera*, nearly circular (but apparently flat rather than spherical), and about ·0014 inch in diameter, divided into four quarters, filled with a similar yellowish-brown protoplasmic substance, and each of the quarters distinctly enclosed (in the young state of the gland) in a transparent cell-wall. A circular transparent wall encloses the whole; but there are no enveloping cells similar to those delineated in Fig. 1; nor have I ever observed any papillæ or other processes proceeding from them. They sometimes, however, form slight elevations above the surface, as seen in Fig. 8. At a later period, as shown in Fig. 7, the number of divisions increases, sometimes amounting to as many as eight, and the separating walls of cellulose nearly or quite disappear. A stoma is here again represented, to show the comparative size.

Before commencing my investigations of *Drosera*, my attention had been directed to the occurrence of bodies of a similar nature in a corresponding position in the floating leaves of a common little water-plant, *Callitriche verna*, i. e. beneath the cuticle of the upper surface.* These bodies were described as long ago as 1850,† by the late Dr. Lankester, who, however, ascribed no special function to them. The glands themselves are more minute even than in *Drosera*, about ·0005 inch in diameter, nearly spherical, and distinctly quadripartite, each division being again filled with a yellowish-brown substance. These are surrounded by a circular border or cell-wall of cellulose, also divided into four, and less opaquely filled up with a similar substance They are entirely concealed beneath the surface, and do not appear to develop into papillæ. One is represented at Fig. 9, together with a stoma. From the extreme similarity of these bodies to those already described in *Drosera* and *Pinguicula*, the idea suggests itself whether *Callitriche* is not also carnivorous.

The question now arises, What is the purpose of these organs, which present so similar a structure in the plants now described? Is it connected with the absorption and digestion of nitrogenous food presented to the leaves? A direct answer to this question is attended with almost insurmountable difficulties. Unlike the secretive glands of *Drosera* and *Pinguicula*, they are buried in the tissue of the leaf, and it is impossible to place them under the microscope without altogether destroying the surrounding tissue. It is certainly remarkable that bodies more or less analogous to these are present in every plant which has been, down to the present time,

* I had formerly, but erroneously (*l. c.*, p. 358, footnote), supposed the "rosulate" appearance of the leaves to be due to these bodies.

† 'Proc. Linn. Soc.,' ii., 1848–55, pp. 94, 95.

certainly included under the category of carnivorous. I have already alluded to their existence in *Nepenthes* and *Dionæa*. The bodies described by Darwin under the name of "quadrifids" in the bladders of *Utricularia* bear a strong resemblance to the absorptive glands of *Drosera* after the development of the papillæ; and the drawing, Fig. 30, at p. 448, of the similar bodies in *Genlisea*, a Brazilian plant nearly allied to *Utricularia*, exhibits a still more striking resemblance. No less remarkable is their absence from all plants which do not possess this power; the only exception to this, as far as I am aware, being in the case of *Callitriche*. I have closely examined the leaves of the British plant supposed to have the nearest affinity to *Drosera*, *Parnassia palustris*, without detecting the least trace of them. It is to be hoped that future researches will throw more light on these interesting objects.