From
SINNESORGANE IM PFLANZENREICH
by Gottlieb Haberlandt
V. Insectivores: *Aldrovanda vesiculosa*

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Continued from September, 1981.

The radial walls of the hinge cells are likewise thin, and have numerous very small pits shaped like transverse fissures, which are only apparant on bristles treated with Javelle water. When treated with zinc chloride-iodine, these walls turn light violet, like those of the elongated cells.

All of the cells of the tactile bristles have a mature cytoplasmic tube with a more or less elongated nucleus pointed on both ends. In comparison, the protoplast of the hinge cells is even more strongly developed. The nuclei here are, as a rule, finely pointed only at the end facing the point of the bristle; the lower ends are rounded off (Plate VI, fig. 2).[3]

Because the hinge cells are undoubtedly the senstive elements, one may expect to find very fine pit channels with plasmodesmata in their lower transverse walls, through which the received stimulus is conducted downward. It is however, difficult to prove the existence of these plasmodesmata, because it is not easy to cause the transverse walls in question to swell sufficiently. After the fresh, intact leaves had been soaked in iodine-potassium iodine solution for 24 hours, they were pulled apart in water on the slides. The excess water was drawn off. Several drops of 50 percent sulfuric acid were added, and then after a few seconds, the slides were completely immersed in a glass dish filled with water. The rinsed leaf fragments together with the tactile bristles protruding over their edges were then treated for 24 hours with toluidine blue solution. After rinsing, glycerine may be added only with very great care, because the tactile bristles collapse easily.

The lower, as well as the upper transverse walls of the hinge cells have no pits. From their very thick periphery, they simply thin out toward the middle of the hinge. If treated in the previously described manner, most swell a great deal, some even swell too much. By contrast, if the soaking time is reduced, or if more dilute sulfuric acid is used, the swelling hardly occurs at all. Apparently it is difficult for the transverse walls to swell. When they do begin to swell however, swelling takes place so rapidly that the desired degree of swelling is easily exceeded. Nevertheless, it is possible now and then to obtain suitable preparations, in which the transverse walls are not too severely swollen. Then, using strong magnification, one can observe that the thin, unswollen portions of the transverse walls are penetrated by a few extremely delicate plasmodesmata. In a few cases in which the plasma filaments did appear clearly enough, I was not able to count more than three filaments (Plate VI, figs. 5-8).[4]

Touching the upper part of the hair does not cause it to bend evenly lengthwise. The sections above and below this hinge are stiff and resist bending because of their thickened outer walls. The hinge itself, with its thin and very flexible outer wall is easily bent. Touching the point of the bristle results in a distinct buckling of the hinge. One

Please see **ALDROVANDA** p. 92.

ALDROVANDA continued from p. 89.
can see this very clearly under the microscope. In this case, the cells or plasma membranes of the longitudinal wall are greatly stretched on the convex side, and they are highly compressed on the concave side. In the case of more severe buckling, the outer wall of the concave side turns inward, forming a transverse fold. (I have given an illustration of this in my *Physiol. Pflanzenanatomie*, 1896.) This results in extensive deformation of the protoplast of the hinge cells. The entire structure of the hair evidently is designed to concentrate the mechanical effect of any contract on one particular area on the hair. That this spot must be the sensitive part of the hair is the indisputable conclusion.[5]

Darwin assumed that the hinge had a purely mechanical significance: to protect the bristles from breaking when the leaves closed. But this is, at best, a secondary function, and would apply in any case, only to the peripheral tactile bristles. The tactile bristles located on both sides of the midrib are either not bent at all, or are only slightly bent when the leaves close. The bristles are at most 0.7 mm long, and the diameter of the bladder at its widest point is 1.2 to 1.7 mm. The distance from the midrib up to the closure is 1.2 to 1.5 mm. Indeed, if a closed leaf is made sufficiently transparent by extracting the chlorophyll with alcohol, one can see that the tactile bristles of the midrib in the bladder are completely straight. This is also true for those bristles which are located even nearer to the base or to the top of the leaf blade, where the bladder is considerably smaller.

Please see **ALDROVANDA** p. 93.

Endnotes
by Stephen E. Williams

1. An English translation of this work by M. Drummond has been published by MacMillan and Co., Ltd., London, in 1914 as G. Haberlandt, *Physiological Plant Anatomy.*
2. Javelle water is a solution of chlorinated potash. When freshly prepared, it contains about 2.5 percent active chlorine. *The Merck Index*, 8th Ed., Rahway, New Jersey (1968).
3. The histochemical and cytological work in the preceding three paragraphs is, to the best of my knowledge, the most thorough and up-to-date study of this subject. However, Lloyd (p. 200 and plate 19-Fig. 20) has added the important observation that there are four sensory cells and four elongated cells connected them to four basal cells. An electron microscopic investigation would be desirable.
4. Anyone who has worked with these tiny hairs can appreciate the magnitude of Haberlandt's accomplishment here. Plasmodesmata were observed by him in the sensory cells of *Dionaea.* Electron microscopic verification of his observations would be desirable.
5. It has since been demonstrated by Ashida (Mem. Coll. Sci. Kyoto Imp. Univ. Ser. B 9, 141-244, 1934) and Lloyd (Lloyd, pp. 200-201, Carnivorous Plants, 1942) that these hairs trigger the trap, that one stimulus suffices to close some young traps. Young, healthy traps sent to me by Joseph Mazrimas always closed with a single stimulus delivered to any sensory hair. The hairs bend at the hinge and, by analogy with *Dionaea,* the hinge cells should be the sensory elements; however, I know of no direct proof of this. Both Dr. Takao Sibaoka (in Skoog, *Plant Growth Substances 1979,* 462-469, 1980) and I (*Proc. Amer. Phil. Soc., 120,* 187-204, 1976) have independently confirmed that *Aldrovanda* trigger hairs initiate action potentials which spread through the lobes of the trap in a manner analogous to the action potentials of *Dionaea.* Dr. Sibaoka has a student who is presently doing further work on the physiology of this sensory mechanism so that the anatomical work of Professor Haberlandt should soon be supplemented with modern physiological information.

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ALDROVANDA continued from p. 92.

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GOLGI continued from p. 91.

In both cases, active Golgi were found to be located only in those gland cells located at the outer apical areas of the glands. Radioautography revealed intense labeling over the Golgi apparatus, with little incorporation occurring elsewhere. Additionally, the time necessary to achieve good label incorporation was drastically reduced in labeled glands, indicating a marked increase in radioprecursor utilization.

This investigation has resulted in a body of data which firmly establishes morphological criteria characteristic of the various developmental stages. In addition, several new techniques were developed to facilitate study of these glands. The finding of the selective activation of the Golgi apparatus only in the outer apicla digestive gland cells is most significant, and indicates a degree of specialization in this species not usually found in higher plants. These, and other findings, are discussed in the context of the universality of the secretory process which may be operative in all eukaryotic cells.

PINGUICULA continued from p. 90.

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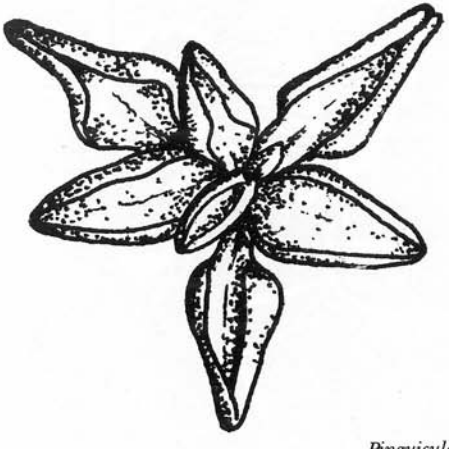

Pinguicula pumila
Drawing by Ron Fleming