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

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**Editor's note:**

*Professor Dr. Gottlieb Haberlandt of the University of Graz published* Sinnesorgane im Pflanzenreich: sur Perzeption mechanischer Reize *in 1901. A second edition with important additions including some major observations on the anatomy of* Dionaea *was published in 1906 by the Verlag von Wilhelm Engelmann in Leipzig, Germany. No English translatioon of this classic work exists. Some of Professor Haberlandt's observations are still the best information available on the subject, but because of the early date of the work and the lack of a translation they are often overlooked by the English speaking authors.*

*We plan now to present the first translation into English of Haberlandt's chapter on insectivorous plants from the second edition of* Sinnesorgane. *The following section on* Dionaea *and one on* Drosera *will follow. These portions of* Sinnesorgane *were translated by Carla R. Powell, a chemistry and German student at Lebanon Valley College. Dr. James W. Scott of the Lebanon Valley College Department of Foreign Languages supervised her work. Dr. Stephen E. Williams of the Lebanon Valley College Department of Biology read the text for technical accuracy and added annotations, some included within the text in square brackets, and the rest in the form of numbered endnotes to point out some current developments and to clarify the text. Dr. Yolande Heslop-Harrison of Aberystwyth, Wales, has contributed to the work with her useful comments.*

As Auge de Lassus (1861) first discovered, and as B. Stein (circa 1876) later rediscovered, the leaf blades of these aquatic plants belonging to the family Droseraceae are sensitive to contact. The edges of the leaf blade curve upward along the axis of the midrib; the portions adjacent to the midrib bulge outward, while the upper portions close to form a cavity in which small aquatic animals are caught and digested. Tactile bristles occur on the upper side of the midrib, but also on the adjoining parts of the leaf blade [fig. a]. These were discovered by Ferd. Cohn (1875), who very briefly described their anatomical structures as follows: "In addition, the inner surfaces bear long, colorless, articulated hairs consisting of double or single rows of cells, in which longer, internodal cells alternate with short nodal cells." Regarding their function he says the following: "The analogy with *Dionaea* suggests that those multicellular, articulated hairs which occur sparsely on the inner sides of the leaf blade, but in a thick beard over the midrib, receive a stimulus from contact with small aquatic animals, and transmit it out to the leaf surface."

Darwin (1875) also had little to say about the tactile bristles of *Aldrovanda.* According to him, they differ from the *Dionaea* tactile bristles in that they are colorless, and have "a middle, as well as a basal articulation." This is, however, incorrect. There is only one articulation [Plate VI, fig. 1]. It is Darwin's view that this articulation is important because it prevents the tactile bristles, in spite of their length, from being broken when the leaf blade closes.

The detailed structure of the tactile bristles was not discussed by Goebel (1891). He simply emphasized the thinness of the walls of the hinge cells. In the second edition of my *Physiologishen Pflanzenanatomie*[1] I have presented a more exact and illustrated description of the structure of these organs (pp. 480, 481). The following remarks repeat and enlarge upon these views.

Strictly speaking, the tactile bristles

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**ALDROVANDA** continued from p. 73.

occur, not on the midrib of the leaf, which is occupied by compact, patelliform glands [See the small gland at the base of the tactile hair; Plate VI, fig 1.], but rather toward both sides of the leaf. They do not form a thick beard, however, as Cohn indicates. I never counted more than 18 to 20 bristles along the midrib. They occur only sparingly on the surface of the part of the leaf blade which forms the bladder. They are more numerous on the edge of the leaf, where I counted 7 to 9 bristles on either side. In all then, a leaf exhibits no more than about 30 to 40 tactile bristles.

In their lower parts, the 0.45 to 0.6 mm long tactile bristles are composed of four, and in the upper parts of two rows of cells occurring side by side, which form 5 to 7 tiers (Plate VI, fig.1). The lowest tier is short-celled and forms a pedestal. Darwin erroneously considered it to be a basal hinge. But its outer walls are only slightly, if at all thinner than those of the tier above it (fig. 9). Neither does this footpiece exhibit the remarkable deviations in chemical and physical properties which are characteristic of the true "hinge" of the bristle. The bristle is inserted into the leaf surface at an angle. The colorless footpiece is separated from the chlorophyll-containing "epidermis" by very delicate, slightly bowed walls, which have numerous, though faint, fissure-shaped pits. Most cells of the footpiece contain some fine-grained starch.

One to three tiers of elongated cells occur on the short-celled pedestal, whose outer walls are very thick, while the radial walls remain delicate. On top of this follows a remarkably short-celled tier, whose cells are only approximately twice as long as wide, and have thin outer walls. This tier represents the sensitive part, the hinge of the bristle. The upper tiers finally are long-celled, and have thickened outer walls—of course, the thickening here, is for the most part—not as strong as in the lower parts of the bristle, with the exception of the section bordering immediately on the hinge. The two top end cells usually separate slightly at the tip of the bristle.

The hinge has two cells, or sometimes four as a result of a cross-division (Plate VI, fig. 2). The adjoining elongated cells arch forward slightly on both sides toward the hinge cells. The thinness of the outer walls of the hinge is all the more noticeable because of the contrast with the walls of the elongated cells bordering directly on them, which are usually somewhat thicker than the rest. The hinge is restrained on both ends by a tough ring of wall material, which prevents excessive deformation of the cross-sectional form of the hinge when it is bent [See the thickened parts of the wall at the top and base of the cells in the center of Plate VI, fig. 2.]. The thin outer walls of the hinge cells are covered by a very delicate cuticle, which extends to cover the entire surface of the bristle in the same fashion. Only in the case of the elongated, rigid cells and the footpiece do the parietal layers under the cuticle consist of relatively pure cellulose. Here they stain a beautiful shade of violet with zinc chloride-iodine, without significant swelling. However, the delicate outer walls of the hinge cells swell tremendously and exhibit pulvinate thickening, but remain completely colorless (fig. 4). Such mucilaginous swelling of the outer wall occurs easily, in any case. One can frequently observe it on old leaves without the addition of reagent, particularly toward the end of the vegetative period. The swelling regularly occurs during treatment of the brisles with Javelle water[2] (fig. 3). The huge

Please see **ALDROVANDA** p. 83

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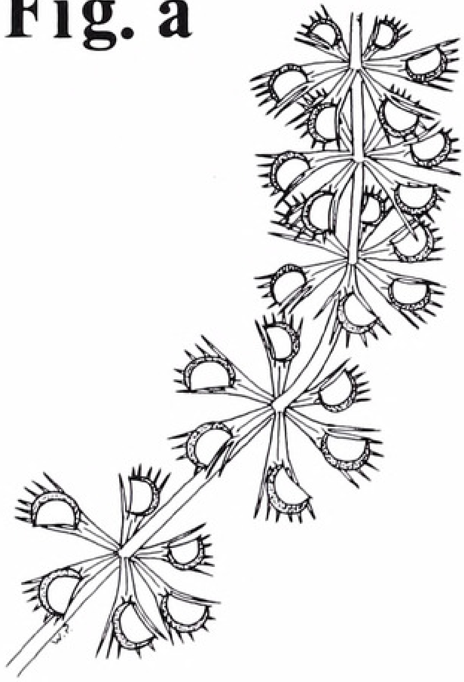
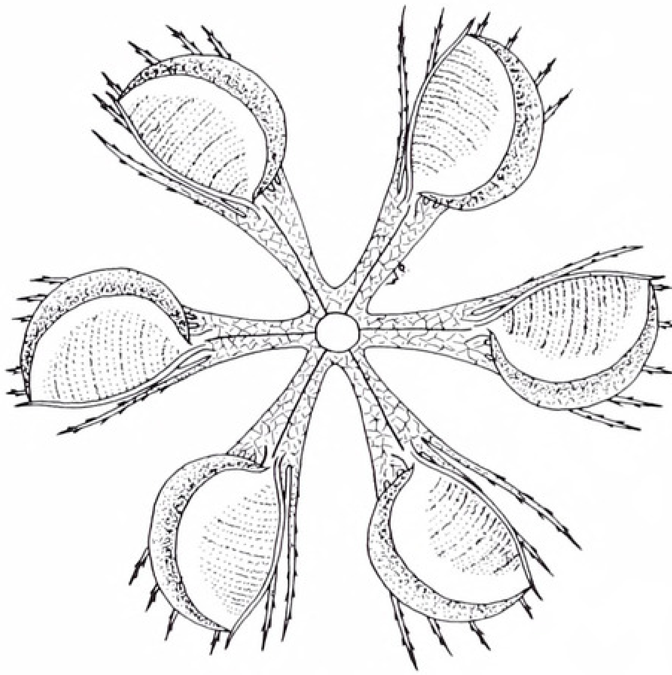
**NEPENTHES** continued from p. 75.

Jack, R. L. (1921) "Northmost Australia" 2 Vols. Simpkin, Marshall, Hamilton, Kent and Co., London.

Mueller, F. (1866) "Fragmenta Phytographiae Australiae" 5.

# Fig. a





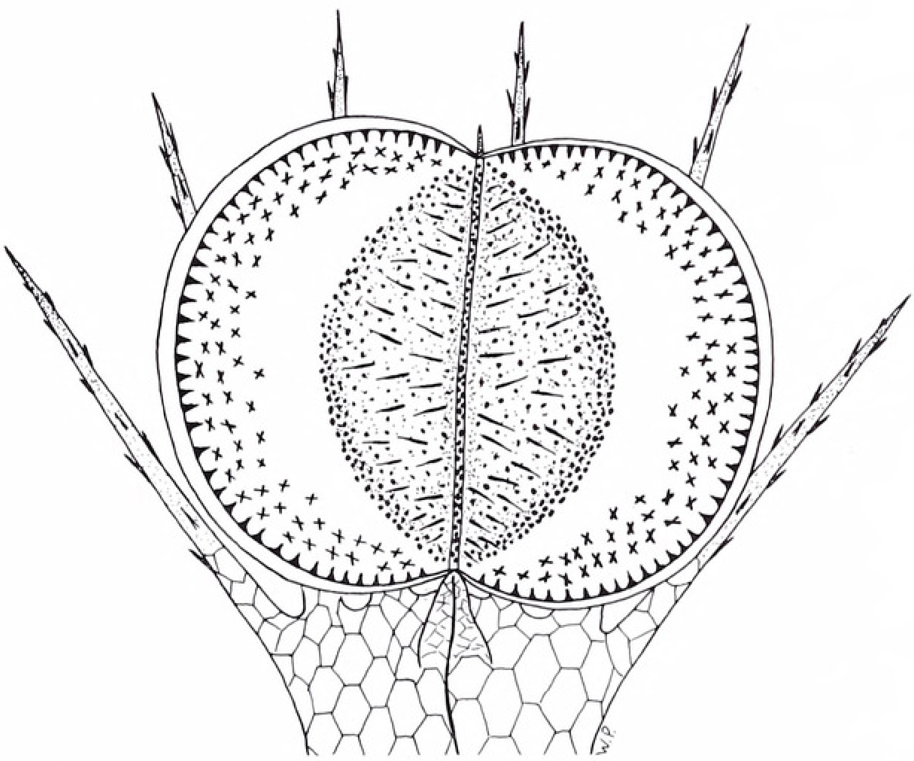
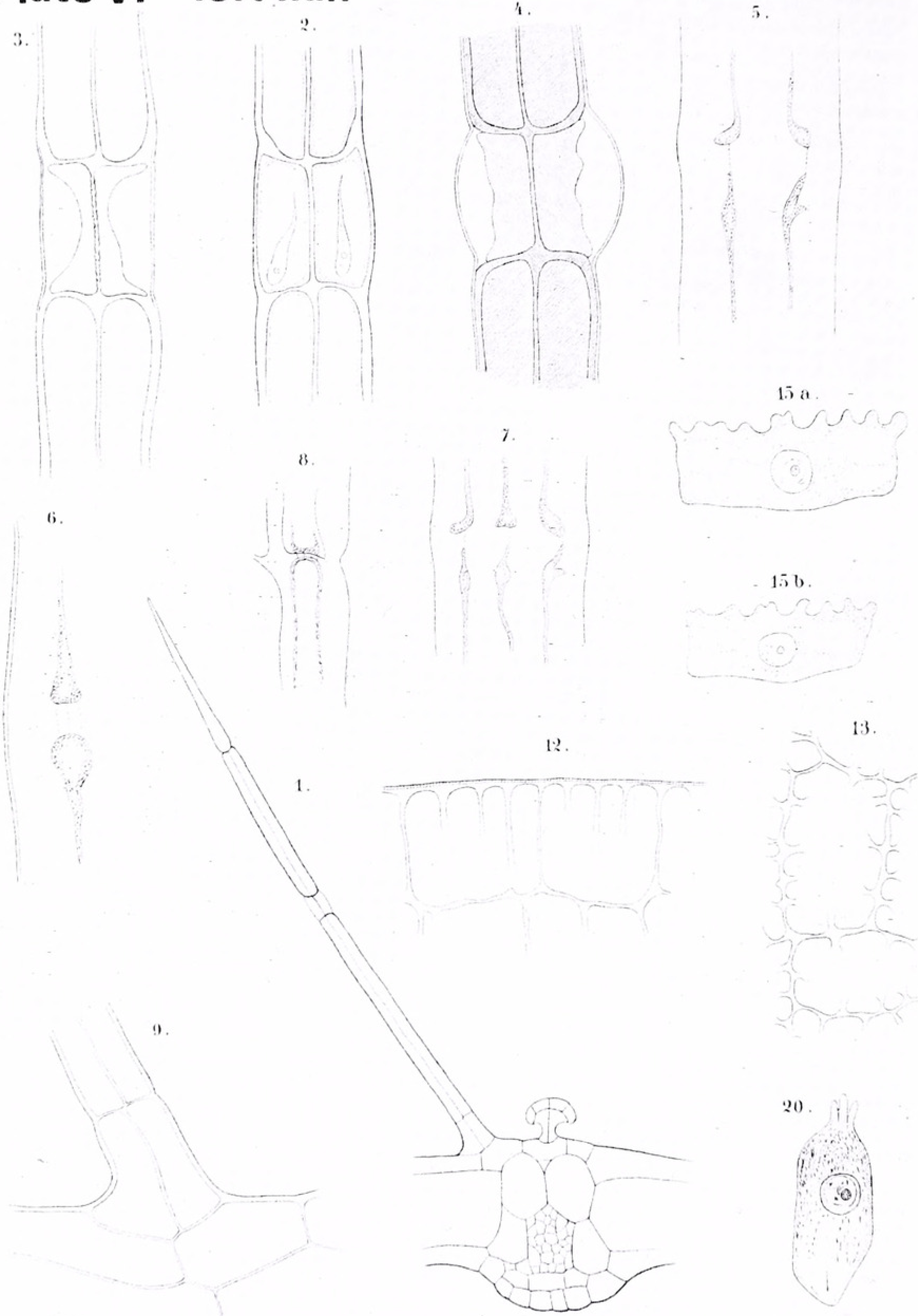


Fig. a. *Aldrovanda vesiculosa.* Upper left—a portion of a stem near its upper end illustrating the positioning of whorls of leaves. Upper right—an enlarged view of a single whorl of leaves illustrating the position of undisturbed traps on its surface. Lower center—a blade of a single leaf illustrating the various surface features of the interior of the trap. The left lobe (*free side lobe*) of the trap is illustrated in an unnaturally wide open position in order to allow a better view. The width of the trap illustrated here would be about 4 mm when measured at the point of its greatest breadth. The *tactile bristles* mentioned by Haberlandt occur in the central part of the leaf where they appear as lines. The *patelliform glands* which are also in this region appear as dots. Both of these structures are illustrated by Haberlandt in Plate VI-Fig. 1. The cross-shaped glands called *cruciform glands* and the small teeth on the edges of the lobes called *marginal spines* were not illustrated by Haberlandt in this book which deals only with sensory structures. These drawings are by Mr. Wayne Perry of Palmyra, PA and were not a part of Haberlandt's work. Detailed descriptions of the leaf structure can be found in Lloyd *Carnivorous Plants,* 1942.

# Plate VI left half




See explanation on opposite page.

## PLATE VI – Explanation of Illustrations

Figs. 1-9: *Aldrovanda vesiculosa.*

Fig. 1. Cross-section through the midrib of the leaf with a tactile bristle. X140.

Fig. 2. Sensitive hinge of a live tactile bristle. X480.

Fig. 3. The same after treatment with Javelle water; the delicate outer walls of the hinge cells are greatly swollen.

Fig. 4. The same after treatment with $ZnCl_2$-$I_2$ solution. The varying intensity of the violet coloring is indicated by the varying gray tints. The swollen outer walls of the hinge cells remain colorless.

Figs. 5-7. Plasmodesmata between the hinge cells and the mechanical cells of the tactile bristle bordering on the base. After treatment with $I_2$-KI solution and dilute sulfuric acid and staining with toluidine blue. X approx. 1200.

Fig. 8. The same with much less swelling of the transverse wall.

Fig. 9. The base of the tactile bristle. X530.

Figs. 12 and 13: *Drosophyllum lusitanicum.*

Fig. 12. Cross-section through two cells of the epidermal glandular layer of a stalked gland. The cuticle has fine pores. After treatment with Javelle water. X approx. 600.

Fig. 13. Surface view of two cells of the epidermal glandular layer. After treatment with Javelle water.

Fig. 15: *Drosera rotundifolia.*

Figs. 15a and b. Isolated protoplasts of the lateral glandular cells of a parietal tentacle as seen from the side. On the upper side a row of plasma appendages which project into the peripheral pits. After swelling of the membrane with dilute sulfuric acid. X approx. 900.

Fig. 20: *Drosera longifolia.*

Fig. 20. Isolated protoplast of an apical glandular cell. After treatment with dilute sulfuric acid and staining with toluidine blue. X approx. 1000.

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**EXCLUSIVE** continued from p. 68.
*Hydnophytum* is also an epiphyte, it is quite likely that it materially benefits from its insect meals. Ironically, *Nepenthes bicalcarata* is also an ant-plant as its pitcher-supporting tendrils are hollow and provide shelter for the ants which burrow into them.)

### Discussion & conclusions

The likelihood of discovering carnivory amongst many more plant species than currently recognised looks very promising. Although this article has only made brief mention of sticky and pitcher traps, there are many other promising candidates with other types of traps worth considering, many of which were included in Lloyd's introductory chapter in his book (Lloyd, 1942).

Yet since the publication of Lloyd's book, only *one* new genus, *Triphyophyllum*, has been officially added to the list of plant carnivores (Green, Green and Heslop-Harrison, 1979). Why has so little progress been made on this front?

One of the reasons is probably the uncertainty of what *exactly* a carnivorous plant is. The main criteria may be as follows (although there is at least one exception to every point):

1. Attracts animals to a trap.
2. Traps and kills the animal victims.
3. Secretes a digestive juice onto the prey.
4. Absorbs the products of digestion into the plant.
5. The plant derives material benefit from its animal nutrition.

Another reason for not investigating more species is that proving carnivory, as outlined in the above criteria, requires considerable time, facilities, and money. For example, absorption of digestion

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Dow Airen (12 Ross St.; Yeppoon; Qld 4703; Australia). [T] only *N. pervillei* seedlings of ca. 40-75 mm diam. for other *Nepenthes* except *N. alata, ampullaria, gracilis, gracilima, hirsuta, kampotiana, mirabilis, rafflesiana, thorelli, veitchii, ventricosa, × bossiense, × coccinea, × dormanniana, × dyeriana, × hookeriana, × wrigleyana, × ventrata.*

Ron Galiardo (1216 Cooper Dr.; Ralieigh, NC 27607). [B] *Heliamphora* spps., *Byblis gigantea* (plants), *Drosera gigantea, D. schizandra, D. auriculata, D. peltata, D. capensis* crestate, *D. prolifera, D. whittakeri, D. × hybrida, D. drummondii, D. petiolaris, D. linearis, D. anglica, D. platypoda, Cephalotus, Nepenthes rafflesiana, N. ampullaria, N. alata* large plants, *Polypompholyx, Sarracenia oreophila, S. rubra jonesii,* large *Darlingtonia.*

Marabini Johannes (St.-George-Str. 62; D-8552 Hochstadt/A; West Germany). [WT] *Heliamphora tatei, H. tyleri, Nepenthes clipeata, N. hirsuta, N. inermis, N. peniculata, N. rajah, N. edwardsiana, N. vieillardii, N. tobaica, N. truncata, N. veitchii.* [T] ca. 100 CP species available.

**ALDROVANDA** continued from p. 76.
mucous swellings bulge either inward toward the cell lumen, or toward the outside. If they bulge outward, the cuticle is stretched so tightly that it is often separated from adjacent parts of the elongated cells. This chemical transformation is accompanied by great flexibility and elasticity of the outer walls of the hinge. They are extraordinarily easily crumpled; their cuticle has a strong tendency to collapse in transverse folds.

(to be continued)

## Literature Review
continued

thus gives them some of the real spirit of scientific investigation while it teaches them a good deal of botany. It is an empirical or "hands on" approach which is the best way to teach science and the only way to do science.

On the negative side I have only a few comments. First I hope that any future printings will have page numbers. Some parts of the book may be referred to in the future by others, particularly the parts on growing plants and the lack of page numbers will make this difficult. Secondly, not all of the experiments have an emphasis which leads people to understand the plant as it functions in nature and I think the role of chemical stimuli in inducing and maintaining narrowing is understated, but these are minor points because the book is presented as a series of experiments. The results for the work that was done are there and the young reader can hopefully do more experiments of his own. It is more important to get young people asking questions and doing experiments than it is for them to gain a sophisticated understanding of the Venus' flytrap. (Stephen E. Williams, Dept. of Biology, Lebanon Valley College, Annville, PA 17003)

Zachariah, K. 1981. Chemotropism by isolated ring traps of *Dactylella doedycoides*. Protoplasma 106:173-182.

New work with carnivorous fungi continues apace! In this work, the author placed uninflated ring traps of the above fungus species on agar near dead or moribund nematodes. Some rings were then induced to inflate with chlorobutanol. All rings produced hyphae which grew towards the prey, eventually differentiating into feeding hyphae which digested the carcass. More very useful references at the end of paper. (DES)