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HOW VENUS' FLYTRAPS CATCH SPIDERS AND ANTS

By Stephen E. Williams¹

The Venus' flytrap is a plant which is often written about and seldom understood. The literature about the plant is almost as much of a paradox as the plant itself. Although *Dionaea muscipula*² was called "Fly Trap Sensitive" in the first letters reporting its existence, the Venus' flytrap catches few flies in its native habitat in the Carolinas. How the trap senses an insect and signals its cells to move has been known for over one hundred years. Yet this mechanism, based on easily reproducible experiments which have been performed in reputable scientific laboratories all over the world, is often treated as trifling speculation in popular and educational literature. The mechanism by which the trap closes is usually confidently stated to be driven by a turgor change. However, what little evidence there is indicates that it may be a very rapid growth response! Much is known about how *Dionaea* traps its prey. Unfortunately most of the information in the technical journals does not make it to the average college and high school biology textbooks, which typically devote two to three pages to attractive pictures of and misinformation about carnivorous plants.

Do flytraps trap flies? What "flytraps" trap in their native habitat has been the subject of at least three investigations. All three indicate that a wide range of animals is caught, the most common being ants [about 1/3], spiders [about 1/3], grasshoppers [about 1/10], and beetles [about 1/10]. About one to four percent of the animals tend to be flies and mosquitos. Subsequent investigations I have made at other times of the year tend to confirm this pattern as a general one. However, photos in books and educational films

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² The scientific name *Dionaea muscipula* means 'mouse-trap plant of Venus'. See the note by Dr. William Dress in this issue for more detail.

nearly always show the plants catching flies. Indeed the plants do catch flies in our college greenhouse so, perhaps the observation of cultivated *Dionaea* led to the plants' inappropriate name.

How do the prey animals get into the trap? Most prey animals must walk or hop into the trap since the majority of prey are incapable of flight. The bright red traps and statements in the scientific literature have led some authors to say that animals are lured in by the color, a scent, or a secretion from the small glands that ring the rim of the trap. This seems reasonable until the evidence upon which the statements are based is examined. I have never noticed a secretion on these glands or an odor from a trap which has not captured prey. If an attractant does exist it must be one that attracts such unrelated animals as spiders, grasshoppers and ants. What attracts carnivores, herbivores, and omnivores from different phyla? The very low rate of capture of insects in the field is also strong evidence against the hypothesis that there is an attractant [Table I]. Frank Lichtner and I observed 224 open traps for a period of 24 hrs. Of these 201

Table I. Prey capture by *Dionaea* observed during a 24 hr. period dominated by heavy rain and during a period with no rain in late June near Supply, NC.

	RAIN	NO RAIN
Total traps	224	224
Traps that could close	202	201
Captures	0	6
Closures without capture	15	4

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were observed to be capable of closing rapidly enough to capture an insect and yet only 6 traps did capture prey. If we assume that the four traps that were closed but did not capture prey were triggered by prey that got away, Then only 5% of the traps were triggered by prey during 24 hours of a warm summer day. At this rate a single trap might be triggered by prey an average of once every 20 days, and capture prey once every 40 days! If there is an attractant it is not a very effective one.

An insect or spider that enters a trap is likely to be just passing through or even resting in the trap. I have seen spiders resting in untriggered traps and ants and beetles passing through. All seemed as indifferent to the trap as they might be to any other twig or leaf. The one beetle I saw pass through tripped two hairs and was captured. The clumsy beetle, which was running when caught, is the only spontaneous capture in nature I know of that has been observed. I hope other readers will report their observations on plants in the field so that a more complete picture of prey capture can be obtained.

Do raindrops close traps? The observation was made by Darwin that "Drops of water, or a thin broken stream, falling from a height on the filaments, did not cause the blades to close". Anyone who has watered a bunch of *Dionaea* plants knows that in general this statement is true, although on occasion a trap will snap shut. Darwin concluded "No doubt as in the case of

Drosera, the plant is indifferent to the heaviest shower of rain". This has been picked up by many authors and drops of water have been treated as having mystic properties that will not result in the closure of traps. However, any stimulus that bends a trigger hair far enough to cause it to send its signal and does this twice within a few seconds will cause the trap to close—heavy rain included. Frank Lichtner and I observed 224 traps during heavy rain. In table I it can be seen that the insects, unlike the botanists, had enough sense to stay out of the rain since none were captured. [We also observed very little insect activity as compared to the dry period.] Despite this, there were 15 closures without capture, which were presumably caused by raindrops. The rain was extremely heavy and lasted all night and much of the morning. It is likely that drops which push a trigger hair far enough to cause it to send a signal are rare and that two within a few seconds are a very unlikely event. Perhaps the lack of closure of *Dionaea* in response to a single stimulus to a trigger hair is an adaptation which helps prevent traps from being closed by rain but traps are not "indifferent to the heaviest shower of rain." About 7.5% of the traps were closed during the rainy day we observed.

How are traps triggered to close? However it gets into a trap an insect must trip trigger hairs to cause it to close. Unless it is very hot, the insect must trip one hair more than once or two hairs in succession within a few seconds or the trap will not move. It is at this point that on understanding of the physiology of the trap helps us understand how capture occurs.

As long ago as 1873 Burdon-Sanderson demonstrated that pushing a trigger hair results in an electrical signal called an action potential which spreads over the surface of the trap at a rate of 10 to 20 cm a second. Since that time Burdon-Sanderson's experiments have been repeated in numerous laboratories around the world so that there is no question of their accuracy [FIG. 1]. Burdon-Sanderson and his colleague, Page, also first clearly demonstrated that more than one electrical signal is needed to cause trap closure. Their 1876 paper [which is the

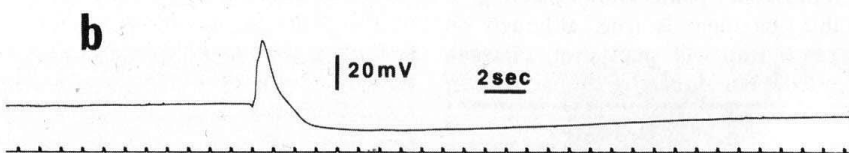
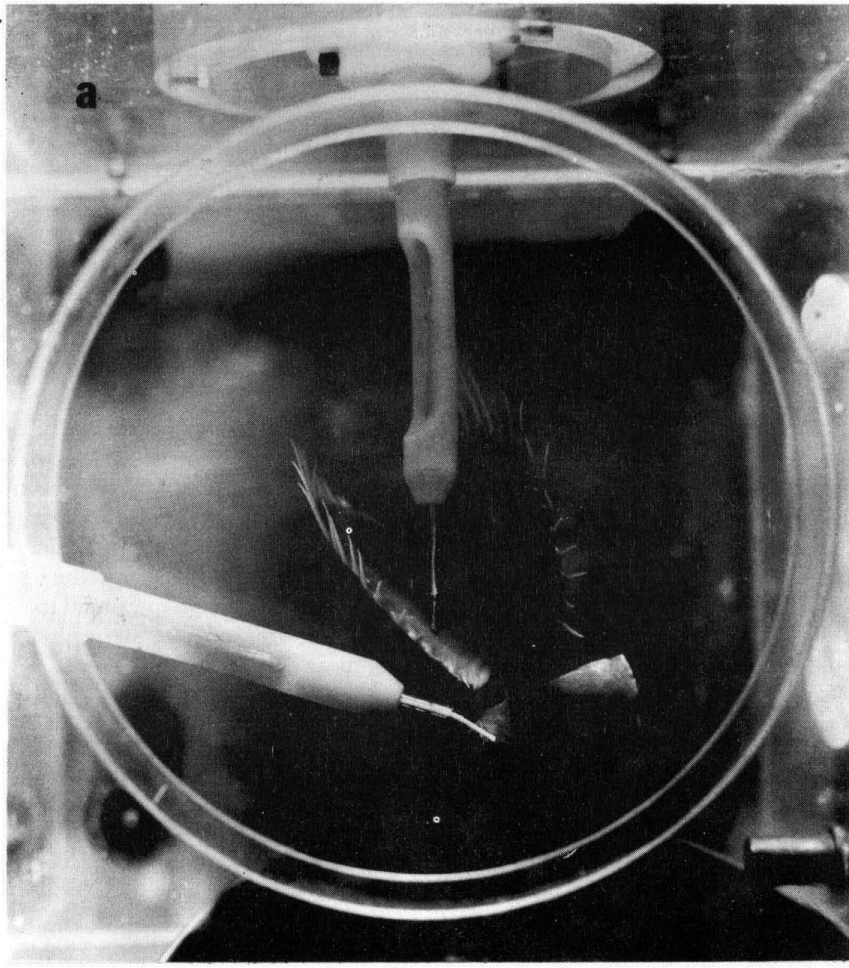
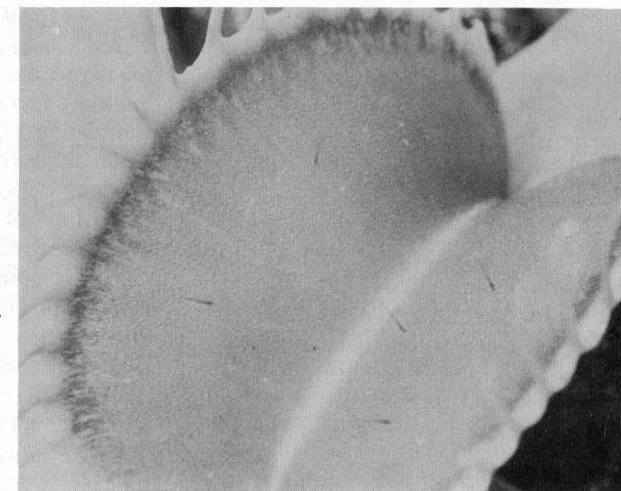


Fig. 1. A method of recording the electrical signal or action potential from a *Dionaea* leaf. a[Cotton wicks soaked in 0.1M KCl solution are positioned on the leaf. These are connected by silver-silver chloride electrodes to a high impedance preamplifier which is in turn connected to a high speed chart recorder. One wick is placed on the surface of the leaf at the spot where the electrical event to be recorded will occur and the other wick, the reference, is placed on a site where we do not expect to see any changes; in this instance on the petiole of the leaf. The moving recorder chart shows how the difference in electric potential at these two spots changes with time. b] A recorder chart recorded from electrodes positioned like those above [negative is up]. The surface of the leaf suddenly becomes more negative after the trigger hair is stimulated, producing the "spike." Later the surface of the trap is more positive than it previously was during the "afterpotential." The photograph 'a' above is by Steven F. Vozzo, a student at Lebanon Valley College. The recording in 'b' is from Williams [1966] and is reproduced with the permission of the American Philosophical Society.



Close-up of trap of *Dionaea*. Trigger hairs are visible.

Photo by
Steve Smith

best research ever done on *Dionaea* physiology] was somehow overlooked by Lloyd and thus tends to be ignored by those who depend on his book as a guide to the older literature.

When a trigger hair is pushed it will either be pushed far enough to trigger an electrical signal or it will not. If it is pushed far enough a signal will spread out over the surface of the trap, radiating from the trigger hair like a wave radiated from a stone cast in a pond. For a fraction of a second [the refractory period] a second signal cannot be initiated by pushing this same hair. After this period a second signal can be initiated. The electrical signals are produced in cells on the surface of the trap as they spread. Each cell also has a refractory period so it cannot produce a signal for a short time after the previous signal was produced. As a result of this, if two hairs are pushed at once each will produce a signal that radiates from its base but, unlike two waves on a pond which will cross each other, these waves stop where they meet since they cannot pass the cells which are in their refractory period. Thus when two hairs are stimulated simultaneously, each cell in the trap sees only one signal even though two hairs were pushed.

The cells that cause the movement are apparently the cells on the trap surface [epidermal cells] and the movement occurs out in the lobes, not at a "hinge" at the midrib as it is often stated. The response to a

single signal is too small to be observed. Thus traps fail to move in response to a single stimulus [except at high temperatures] but they respond vigorously to two or more a few seconds apart. Somehow these cells sum the effects of the electrical signals they have generated. Each signal enhances the responsiveness to those that follow it so that the trap responds more vigorously to a series of signals than to just two. The influence of a particular signal on the response to a subsequent signal fades with time or decays and thus a signal given 20 seconds before a second stimulus will cause a far less vigorous response than one given two seconds before.

If an insect is to be captured or raindrops are to cause closure, two or more stimuli must be delivered to the trigger hairs at a frequency low enough to avoid the refractory period [they cannot be simultaneous or nearly simultaneous] but high enough so that the effect of one will not decay before the next signal occurs.

Each stimulus will result in an electrical signal even in a closed trap and the trap will respond to these by closing tighter and tighter. The more a prey animal struggles the more tightly the trap closes. The prey is not crushed by the lobes nor do any prey animals I have watched excrete anything as has been suggested by some authors. The prey is trapped in a pocket in the trap with
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HOW VFT CATCH...

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the trigger hairs where it is free to stimulate them and literally seal its doom. Continued stimulation of trigger hairs by an insect, nylon bristles or anything else for a number of hours will cause secretion of a fluid with an acid pH of about 2. This fluid kills the insect shortly after secretion begins.

At this point the stimulation of trigger hairs stops and the decomposition of the insect begins. Insect hemolymph [a fancy name for blood] leaks from the prey. This fluid is high in sodium ion [salt] and amino acids. Frank Lichtner and I have shown that traps are stimulated to close by these substances. Release of more amino acids and perhaps ammonium ion would occur once the prey's muscles begin to decompose. This chemical stimulation serves to keep the trap closed until digestion is complete.

Darwin tested a number of proteinaceous substance such as meat and egg white on *Dionaea* and claimed they stimulated closure. Most of the substances he tested would not have been salt free. Salt free egg albumin does not stimulate closure so it appears that salt in proteins and breakdown products from proteins such as ammonium ion and amino acids stimulate closure but that proteins themselves may be ineffective.

How the chemical stimuli act on the trap is not clear but a good guess would be that they are taken up by the digestive glands and cause the production of a plant hormone. Electrical signals are not produced once the insect stops struggling so the continued action on the trap must be due to stimulation by chemicals. When there are no more mechanical or chemical stimuli the trap reopens and awaits its next capture.

(to be continued)

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(Continued from September)

How does a trap move? Most authors, myself included, have preferred to think of this very rapid movement as being due to a rapid loss of water from various cells in the trap. Ashida proposed a model of trap movement based on this idea which is very attractive. He proposed that a loss of water from the cells on the inner surface of the leaf would allow cells on the outer surface of the leaf to expand and the lobes would then curve inward. Unfortunately there is no evidence that his ideas are correct and evidence from experiments by Brown [Table II] indicate that this is not likely to be the case. Although it is based on an inadequate number of samples and the methods are a bit crude, Brown's experiments indicate that closure results from a very rapid growth of the cells on the outer surface of the trap. A sudden release of a factor that causes the cell walls of this surface to loosen is not out of the question, while a reopening process due to

growth is quite reasonable. Our laboratory is presently working on this problem—the answer to which may have importance to understanding the nature of plant growth in general. Presently, however, the best answer to the question of how a *Dionaea* trap moves is: "It is not known".

We are left with a picture of an ant or spider walking inadvertently into a trap, tripping two hairs at an interval of a few seconds and finding itself trapped in a pocket with the triggerhairs. It stimulates these as it struggles and thereby tightens the trap around itself and initiates the secretion of digestive fluid which kills it. As the digestive fluids decompose the prey, salts and amino acids are released. These stimulate the trap to remain closed and perhaps also stimulate more secretion. When no more breakdown products exist to stimulate trap closure it reopens. When all of these actions are put together we see behavior which is as complex as that of some primitive animals. I cast my vote with Darwin, *Dionaea* is "the most wonderful plant in the world."

References: Except for the original data presented in Table I the author and others have reviewed these subjects in the following articles, each of which gives complete references.

Burdon-Sanderson, J.S. and Page, J.F.M., 1876. On the mechanical effects and on the electrical disturbance consequent on the excitation of the leaf of *Dionaea muscipula*. Proc. R. Soc. 25:411-434.

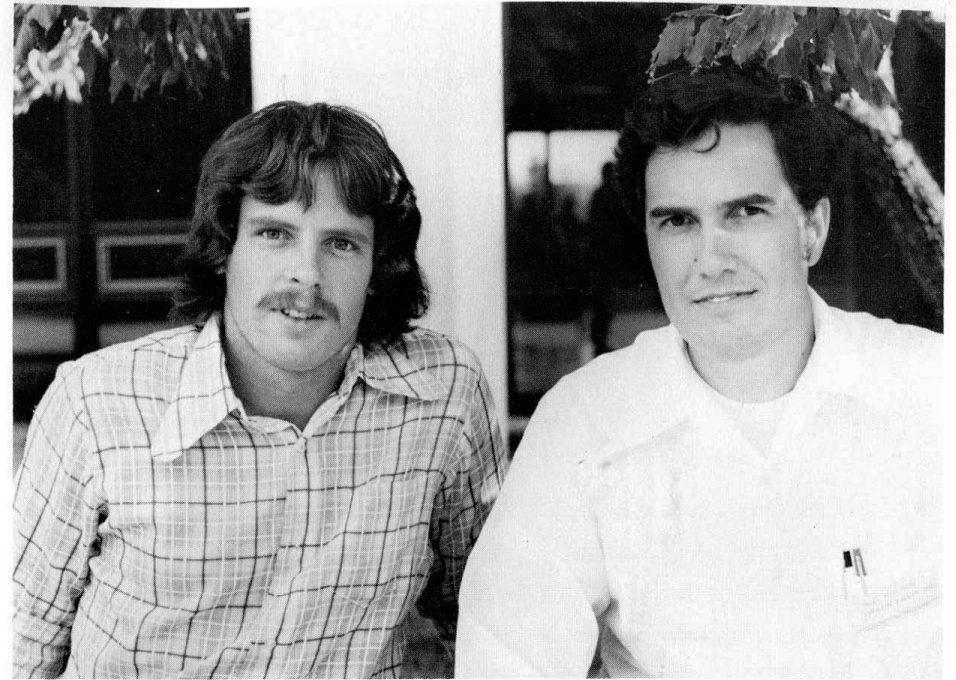
Lichtner, F.T. and Williams, S.E., 1977. Prey capture and factors controlling (Please see WILLIAMS p. 100)

TABLE II. PERCENT INCREASE IN LENGTH OF ABAXIAL AND ADAXIAL SIDES OF *DIONAEA* TRAP LOBES DURING CLOSURE AND RECOVERY VERSUS THE INCREASE IN LENGTH OF UNSTIMULATED CONTROLS. ^a

	<i>DIONAEA</i>			
	ABAXIAL		ADAXIAL	
CLOSING	8.4	(5) ^b	-1.0	(2)
RECOVERY	0.8	(3)	9.4	(2)
GROWTH OF CONTROL DURING ½ DAY	0.5	(3)		

^a Data from W.H. Brown, Amer. J. Bot. 3,69-90 (1916).

^b The number of replications is given in parenthesis.



Frank Lichtner [left] and Steve Williams [right] collaborated on a study of the stimuli which control trap narrowing in *Dionaea* [Lichtner and Williams, Amer. J. Bot. 64:881-886, 1977]. This study also includes an analysis of the insects *Dionaea* captures in the field. Where they grow in North Carolina they are not "flytraps"; they are ant and spider traps! Frank did this work as student independent study project at Lebanon Valley College where Steve Williams is a professor. Frank has just completed his doctoral work at Cornell and is now an assistant professor at the University of California at Davis. Although his graduate research has been done on soybeans Frank has done some additional work on *Dionaea*. Steve Williams is continuing his research with the carnivorous plants at Lebanon Valley College where he has directed a number of students in research projects involving the physiology of carnivorous plants. He first began doing research on them in 1966 as the subject of his doctoral dissertation at Washington University and he continued his research at Cornell University where he did his post-doctoral work before going to Lebanon Valley. His major contribution to the understanding of carnivorous plants is his work, done with Barbara Pickard, which demonstrated that rapid *Drosera* tentacle movements are controlled by electrical signals, called action potentials, similar to those in *Dionaea* [and in animal nerves].

WILLIAMS - continued from p. 91
trap narrowing in *Dionaea* (Droseraceae). Amer. J. Bot. 64:881-886.

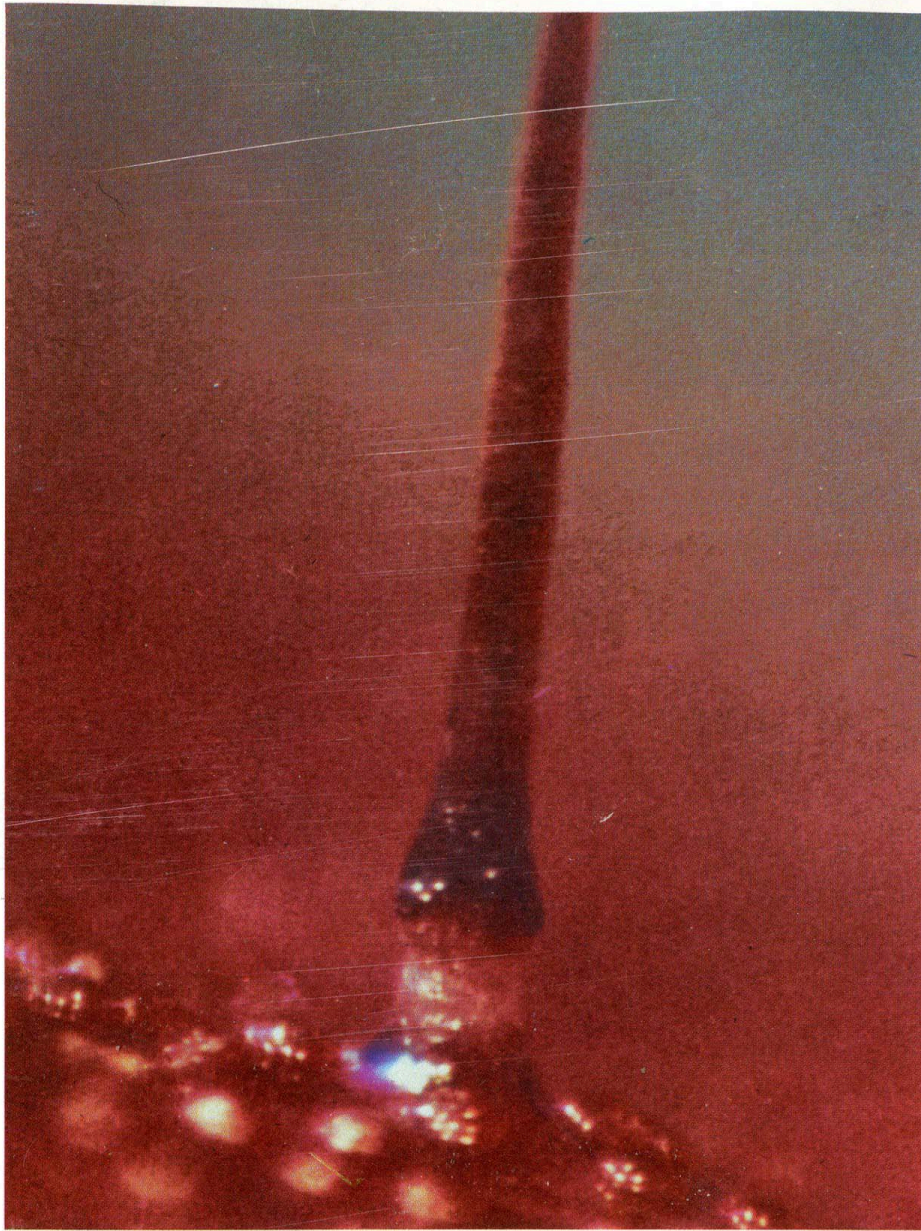
Williams, S.E., 1976. Comparative sensory physiology of the Droseraceae—the evolution of a plant sensory system. Proc. Amer. Philos. Soc. 120:187-204.

Williams, S.E. and Pickard, B.G. In press. The role of action potentials in the control of capture movements of *Drosera* and *Dionaea*. In: Galston, A.W. Plant Movements. Springer Verlag. Berlin, Heidelberg, NY.

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Where the podium and the lever meet is a lighter colored flexible area where the hair can be bent. It is in this area that the sensory cells have recently been demonstrated to be located by R.M. Benolken and S.L. Jacobson. These initiate the electric current that triggers the impulses which sweep over the surface of the whole trap. The smaller red knobs are digestive glands which are thought to secrete the enzymes that digest the insect.

Photo by Stephen Williams

