From

SINNESORGANE IM PFLANZENREICH

by Gottlieb Haberlandt

Insectivores: *Dionaea muscipula*

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The tactile bristles on the upper sides of the leaf of *Dionaea muscipula* (Fig. b) were noted by Ellis, who first described the plants, named them, and also guessed that they trapped insects for food. However, he had not recognized their function. In the translation by Schreiber (1780), the passage reads as follows: "Although the small animal struggles to save its life, it cannot free itself because of three small upright spines located in the middle of the lobe between the glands, which frustrate all of its efforts." It would seem that Ellis believed that the insect is pierced by the "spines." Sydenham Edwards (1804) and Nuttal (1818) recognized the sensitivity of those small bristles to stimulation by contact. Edwards described his discovery, so very significant for the sensory physiology of the plants, as follows: "The small spines mentioned and figured by Ellis, are the only irritable points." Curtis (1834) and Lindley (1848) subsequently concurred. Meyen (1839), on the other hand, designated the upper side of the median nerve as the irritable part of the leaf.

The work of Oudemans, published in 1859, first pointed out an important step toward the solution of this question. Independently of those prevously mentioned, this researcher also established that the irritability is mainly centered in the si bristles (Fig. b). He investigated their anatomical structure further and found that the lower, more swollen part is separated from the footpiece by a definite construction (Fig. 10). But Oudemans is not only the discoverer of the "hinge" of the tactile bristles; he also determined the footpiece to be the most sensitive part of the entire bristle. However, he seems not to have understood the significance of the hinge.

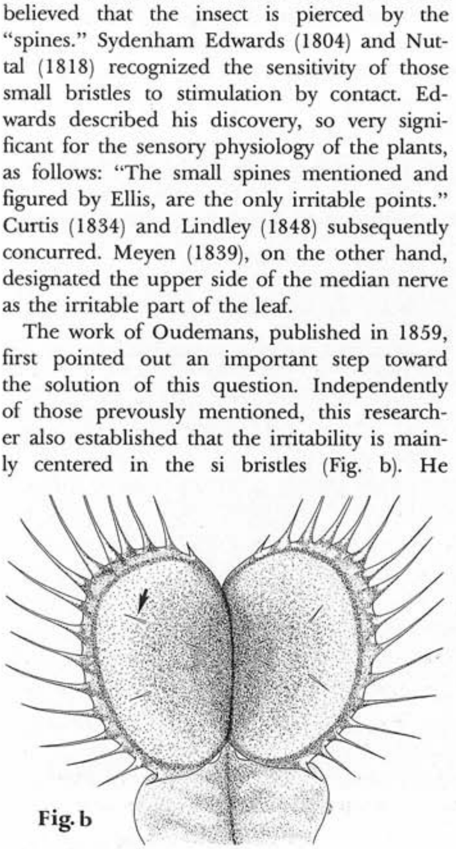

Fig. b

In contrast to this, what Charles Darwin (1876) said about the tactile bristles constituted a step backwards, because he believed that the bristles were sensitive to an instantaneous contact over their entire length. Thus he could not help but fail to understand the function of the hinge in the perception of stimuli. He believed that its sole purpose was to prevent the bristles from breaking off when the halves of the leaf closed.

The detailed work of H. Munk, published in the year 1876, was introduced by an anatomical examination of the *Dionaea* leaf, which F. Kurtz carried out. What this said about the anatomical structure of the tactile bristles is very incomplete. Kurtz entirely overlooked the hinge; therefore, his illustration of the base of the bristle is incorrect. Nevertheless, Munk arrives at the same view as Oudemans regarding the localization of the irritability, although he did not know Oudeman's work. "Pieces may be cut off from the point down to the base with fine, sharp scissors, without causing the motor response, until one approaches the button-shaped protrusion of the alar parenchyma: contact to this area immediately causes the leaf to close.* Also the upper portions of the hair itself are easily bent without causing the leaf to move. While any similar bending, any impulse, any pulling on the hair, which results in a distortion of the base causes the leaf

*Footnotes will appear at the end of the article, which will be continued in the June issue.

Dionaea (continued from page 9)

to close, whether the stimulus is applied on the point or lower down." Munk, like Darwin, did not believe the sensitivity was confined only to the tactile bristles. He believed that the motor response would also occur when strong pressure was applied on the epidermis of the upper side of the leaf. Therefore, his interpretation of the importance of the bristles was merely "that it is possible to stimulate portions of the sensitive parenchyma by means of a long, flexible lever arm." Had Kurtz correctly described the structure of the footpiece with its hinge, then Munk certainly would have recognized that this provides a much more specific adaption for the purpose of sensory perception.[2]

Almost simultaneously Batalin (1877), who knew Oudemans' work, arrived at the conclusion, which he offered only as a possibility, "that the upper part of the small hair up to the constriction is not at all irritable, and if it appears to be sensitive to contact, then it is because pressure is placed on the lower parts of the hair when it is bent, thereby causing stimulation."

Goebel (1891) drew the now obvious conclusion, that it is the hinge cells of the bristle which perceive the stimulation, since they undergo the most severe deformation when the bristle is bent. He was, however, unable to supply a more detailed explanation for this view, because the appropriate research material was not available to him at the time. Goebel was also the first who gave an essentially correct, although very brief, description of the more approximate structural relationships of the bristles, particularly of their hinges.

Macfarlane's (1892) work basically agrees with Goebel's conception of the function of the hinge. A few errors in reference to the histological structure of the bristle, especially the hinge, will be discussed later.

Finally, I have given a brief description of the structure of the bristles and the related experimental evidence (Haberlandt 1896). Contact to the stiff upper part of the bristle initially causes bending only at the constricted hinge point. On the convex side, the membrane fold is stretched, and on the concave side it becomes even narrower and deeper. In one particular case, the extension of hte hinge after bending amounted to 21 percent on the convex side. It is obvious that very severe deformations of the protoplasts occur in connection with this.

I will now proceed to my more recent investigations into the structure and function of the tactile bristles of *Dionaea*. In so doing, I will assume that the approximate morphological relationships of the leaf and the distribution of the bristles are known (Fig. b).

The tactile bristle, from the tip to the insertion, has four parts (Plate VI, Fig. 10); these are:

1. The stiff, roughly 1 mm long, sharply tapering endpiece, which represents the mechanically active part of the entire apparatus, the lever arm which functions as a stimulator. It consists of living, elongated, prosenchymatous cells, whose walls are only moderately thickened and are neither lignified nor cuticularized (one cannot really call these cells, as Goebel did, "thick walled." Goebel himself (1891) illustrates them as rather thin-walled, by the way, see his Fig. 12). When treated with zinc chloride-iodine[3], they take on a muddy greenish-blue color. The cuticle is delicate, and very finely striated lengthwise at the point of the bristle. Because the pointed apical cells often split apart, the tips of the bristles become, as Darwin noted, bi- or tripartite. Often the basal cells are very short.

2. Bordering on this is a tissue layer consisting of crosswise lamellar cells which contain 2-3 cell layers in the middle, and 3-4 at the edges, where the epidermis forms part of the structure. All of the cells contain living protoplasts. According to Goebel, their walls are suberized. Although I have found only the walls of the middle cell layer to be suberized, on thin microtome sections these suberized walls appear as a pair of sharp, dark brown lines, which traverse the bristle at the aforementioned place (Plate VI, Fig. 10k)[4]. The lateral walls also exhibit this quality. It is quite possible, under different growing conditions than those enjoyed by the plants I examined, that the cell layer in question is suberized all the way through. What this "suberization" has to do with the function of the tactile bristles remains uncertain.[5]. In any case, it does not prevent water and soluble nutrients from being supplied to the terminal piece of the bristle above it. The cells of the terminal piece are, after all, alive.

(Continued on page 21)

*See plates pages 21-22.

Dionaea (continued from page 12)

3. The irritable hinge of the bristle is externally characterized primarily by a severe constriction running all around it (Plate VI, Fig. 10g). It consists of a ring of peculiarly transformed epidermal cells and a central cell bundle (Plate VII, Fig. 2). The epidermal cells, which obviously function as the sensory cells, possess a radial-laminar, or more precisely, a wedge-shaped form, because their width naturally decreases from the outside toward the inside. Their length, on the other hand, increases considerably from outside to inside, such that their outline at the median longitudinal section resembles a trapezoid.

These sensory cells contain a strongly developed, heavily reticulated protoplast with a centrally located, rounded nucleus, which is somewhat larger than the nuclei of the remaining cells of the bristle and of the mesophyll.

As Goebel previously noted, the outer walls of the hinge and sensory cells are very thick, and thin out only at the base of the hinge furrow (Plate VI, Fig. 10 and Plate VII, Fig. 1). They are covered by a strongly developed cuticle, which is also described in the illustration by Goebel. Macfarlane, on the other hand, mistakenly argues that the cuticle over the "irritable joint" is completely absent, or at least extremely delicate[6]. In the surface view the outer walls of the sensory cells are very finely and closely perforated (Plate VI, Fig. 11). Macfarlane considers these spots to be pores, and leaves the question open as to whether they are completely open, or are sealed by a fine membrane. Of course, he is inclined toward the latter hypothesis, because he is of the opinion that the water eliminated during a motor response escapes through these supposed pores. He has not succeeded in directly observing such a discharge of water, however. What Macfarlane now considers to be pores are none other than very small nodules, or small tooth-shaped thickenings on the inner side of the cuticle, which protrude into the adjacent cell wall layers. This can easily be observed on longitudinal and surface sections. When examining such sections, one focuses on the edge of the hinge furrow, such that one can see the optical cross-section of the cuticle. Here, the delicate denticulation of the inner side of the cuticle is very clearly perceptible with sufficiently strong magnification[7]. After The addition of zinc chloride-iodine[3], the small points appear as more darkly colored spots on the yellowish-brown cuticle. Upon swelling and disintegration of the hinge cells with sulfuric acid, the cuticle is preserved together with its nodule-shaped sculpture. The even, dense perforation of the cuticle extends only up to the epidermal cells adjoining on both sides. Those adjoining on the upper side exhibit only sparse perforation when seen from the surface; those adjoining the underside, i.e., the uppermost epidermal cells of the base, exhibit somewhat larger cuticular denticulation, as do those which may be observed over the radial walls of the epidermis right up to the base of the pedestal. They also occur over the radial walls of the hinge cells themselves. The extensive fine meshing of the cuticle with the underlying wall layers of the hinge cells probably is for the purpose of increasing the tightness of the connection, and for preventing the connection between the cuticle and the underlying cell wall layer loosening or releasing due to the severe stretching to which the outer walls of the hinge cells are exposed when the bristle is bent.

(To be continued)

SPECIAL ANNOUNCEMENT

There have been some problems with people requesting missing issues several times. The following policy will now be observed with respect to missing issues.

1. After two requests for the same issue, any further requests for that issue must be accompanied by a $2.00 per issue and mailing charge.
2. No requests for a missing issue can be honored after six months past the date of issue.

Coming in June issue:

"A Photographic Primer of Variants of *Sarracenia rubra* Walt."
by Donald E. Schnell

PLATE VII LEFT SIDE

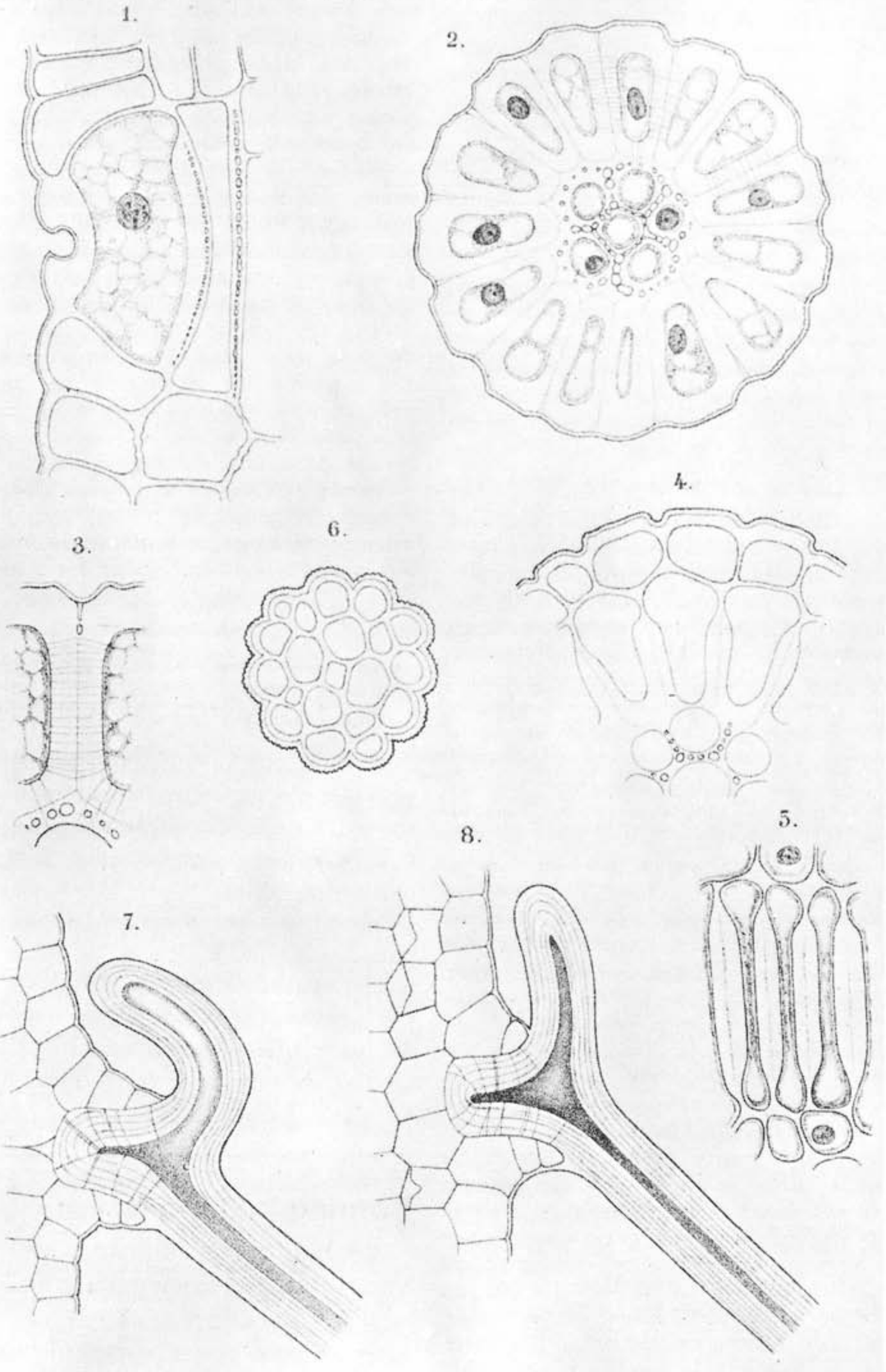

PLATE VI RIGHT SIDE