by Hendler (*1*) are fitted much better by a hyperbolic function than by an exponential one. It seems thus that it depends on the counting arrangement, or possibly on the method of sample preparation, whether or not the apparent absorption coefficient, as obtained from the experimental data, is independent of the sample thickness.

It is obvious that α cannot be compared directly with the absorption coefficient of Beer's law because β-rays interact with matter in a way essentially different from electromagnetic waves. The absorption process of β-rays is a complex one, including, besides the energy losses by excitation and ionization of the absorber atoms, also scattering and backscattering, two processes which change the energy spectrum and its angular distribution (*7*).

It is therefore to be expected that it depends on the geometrical arrangement of the sample and counting device whether or not the self-absorption can be described by an exponential law with a constant α.

P. MASSINI

Philips Research Laboratories, N.V. Philips' Gloeilampenfabrieken, Eindhoven, Netherlands

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16 November 1960

Action Potential and Contraction of Dionaea muscipula (Venus Flytrap)

Abstract. Observation of the action potential and contraction of the leaf of *Dionaea muscipula* Ellis revealed several interesting phenomena. Two successive stimuli are generally necessary to cause contraction. The first and ineffective stimulus is associated with slow depolarization. The second stimulus has much more rapid depolarization and initiates contraction.

The excitatory and contractile processes of *Dionaea muscipula* Ellis are of interest to biologists because of certain similarities and certain differences from the same phenomena in mammalian organs. *Dionaea muscipula* belongs to a small group of plants of the carnivorous type which are capable of trapping insects and then digesting them. The feature of interest in this study is the leaf or flytrap which contracts upon stimulation of one of the inner sensitive hairs. This plant early attracted the attention of Darwin (*1*). A complete description and pertinent references may be found in Lloyd's classical monograph (*2*). Bourdon-Sanderson (*3*) as early as 1873 recorded its electromotive properties with a capillary electrometer. Relatively little attention seems to have been paid to it until Stuhlman (*4, 5*) recorded its action potential and characteristic of the contractile process in 1948–50 with modern methods. He showed the similarity of the *Dionaea's* action potential to that of mammalian nerve and reported on the variations to be expected from positioning of the electrodes, health and age of the plant, temperature and intensity of the stimulus. It was further shown that the action potential may run its course without producing closure of the flytrap. The present report is directed towards a further delineation of the excitatory and contractile processes.

Fresh adult healthy specimens (*6*) were obtained in early summer. They were kept in a suitable terrarium at 26°C under 12 hours of flourescent light daily. With only minor differences the method of recording the action potential was similar to that described by Stuhlman (*5*). The contraction was simultaneously recorded isometrically with a strain-gauge transducer and amplifier. Stimulation was simply done by a fine cat whisker touching one of the sensitive hairs of the inner leaf. Although the experiment was monitored with a dual-beam oscilloscope, recording was actually done with a Sanborn oscillograph. The events of excitation and contraction proved to be slow enough to be reliably recorded by this method. Only leaves with a diameter of 1.4 cm ±3 mm were used. The leaf opening usually measured 1 cm or more.

In over a hundred trials it was found that the leaf contracted upon the second stimulus. Occasionally contraction required three stimuli at 2-second intervals. Rarely did the leaf contract on the first stimulus. A typical experiment is shown in Fig. 1.

The noteworthy features are the similarity of the general contour of the action potential to that of mammalian tissues such as heart muscle (*7*). There is a rapid negative phase followed by a positve after-potential. Several minor after-oscillations may occur in some leaves. However, the item of note is that the first potential elicited showed comparatively a slower depolarization rate than the following one. This important difference is documented in Table 1, which shows the distinct shortening of the duration of the negative phase (0.13 second) of the second

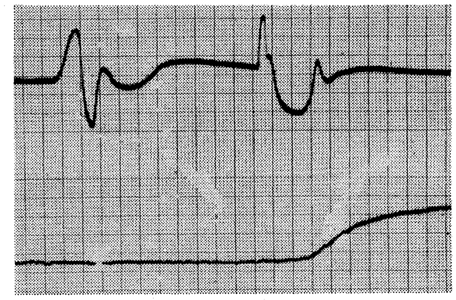

Fig. 1. Action potential and contraction of leaf of *Dionaea muscipula* Ellis. Top, action potential. Bottom, contraction. Abscissa scale (heavy lines) equals 0.2 second. Ordinate scale (heavy lines) equals 5 mv. Note that the first stimulus elicits a slow action potential which is not effective. The second action potential has much faster depolarization and causes contraction of the leaf.

action potential as compared to that of the first action potential (0.24). Apparently, for the excitatory process to initiate contraction, the rate of depolarization must attain a certain velocity.

From Table 1 it may also be ascertained that the positive after-potential does not show the distinct changes upon repeated stimulation as the negative phase. Not infrequently, leaves which failed to develop more rapid deplorization upon repeated stimulation also failed to contract. However, this observation was not constant, for some leaves showing characteristic action potential changes also failed to contract. Other factors which influenced the contractile process were obviously also critically important.

In the 31 leaves it was possible to determine that the mean delay between the second or effective stimulus and the onset of contraction was on the average 0.6 second (standard error, ±0.05). The time which elapsed between the onset of contraction and the development of initial tension was 1.07 seconds (average standard error, ±0.14). The attainment of maximum tension took an additional 6 to 7 seconds. By

Table 1. Comparison of the first action potential (ineffective) and second action potential (effective) of two stimuli on 31 separate leaves of *Dionaea muscipula* Ellis. Figures in the first lines under each phase are means; figures in the second lines are standard errors.

Action potential			
First		Second	
Amplitude (mv)	Duration (msec)	Amplitude (mv)	Duration (msec)
Negative phase			
11.2	0.24	14.6	0.13
±0.8	±0.1	±0.7	±0.02
Positive phase			
10.4	0.76	8.4	0.65
±0.8	±0.1	±0.9	±0.07

calibration of the strain-gauge transducer it was possible to calculate that the average force of contraction was 6.74 dy.

The ease of observation of *Dionaea muscipula* Ellis and its general availability make it a suitable object of further study of the excitation process. It should be studied with a view toward the relationship between permeability and transfer of intracellular ions with respect to its action potential.

JOSEPH R. DI PALMA
ROBERT MOHL
WILLIAM BEST, JR.

Cardiovascular Institute, Hahnemann Medical College, Philadelphia, Pennsylvania

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29 November 1960

Phylogeny of Priapulida

Abstract. The systematic position of the small invertebrate group, Priapulida, is uncertain. In more recent publications they are classified usually as pseudocoelomates in the division Aschelminthes. A histological investigation of *Priapulus caudatus*, a widely distributed species, reveals the body cavity to be a coelom, its lining a peritoneum. These features, and others, indicate the priapulids to be coelomates rather than pseudocoelomates. Unique morphology perhaps qualifies the group for the status of phylum.

In all members of the small invertebrate group Priapulida, certain basic organ systems are lacking, and other unusual structures are found. As a result, the systematic position of the group has been perhaps as uncertain as that of any group in the animal kingdom.

In the latest study of priapulid affinities, Lang (*1*) supports the popular view that the Priapulida are pseudocoelomates in the division Aschelminthes. In her treatises, *The Invertebrates*, Hyman (*2*) also places the priapulids in this position, and in a later volume (*3*) cites Lang's paper as additional evidence for inclusion of the Priapulida in the Aschelminthes.

Lang has listed numerous reasons to support his systematic conclusions. They are based in part upon his own histological investigations and in part upon those of others. He believes the more important reasons are:

(i) The dermomuscular tube of the Priapulida agrees histologically and topographically with those of the two pseudocoelomate groups, the Acanthocephala and the Kinorhyncha (Echinodera). (ii) In the Priapulida a very thin, structureless membrane, devoid of nuclei, lines the spacious body cavity. The same kind of membrane, positioned like a mesentery, holds the urogenital complex to the body wall. The membrane is structurally not a peritoneum, and thus the body cavity is a pseudocoelom. (iii) The excretory organs of priapulids, as well as of most pseudocoelomates, are protonephridia. Such organs are primitive; therefore, the body cavity they service is a pseudocoele. (iv) The proboscis apparatus is homologous in the Acanthocephala and Priapulida. (v) Kinorhynchid and priapulid nervous systems bear a striking similarity. (vi) The priapulid stereogastrula larva, first described by Lang (*1*), greatly resembles the acanthocephalan larva, and the earliest known kinorhynchid larva.

I have recently completed a histological study of *Priapulus caudatus*, one of the more widely distributed species, and have found considerable evidence indicating that the Priapulida belong with coelomates, rather than with the pseudocoelomates. The most important evidence follows:

(i) The dermomuscular tubes of both the Acanthocephala and Kinorhyncha (as well as of other pseudocoelomates) consist of syncytial tissues that exhibit relative nuclear constancy (*2*). The dermomuscular tube of *Priapulus caudatus*, however, consists of distinct tissue layers composed of discrete cells apparently of unfixed number. (ii) The membrane that lines the body cavity covers the numerous "coelomic" retractor muscles that extend between the body wall and the pharynx and covers the digestive tract and holds it to a pair of longitudinal spindle muscles. These muscles are dorsal and ventral to the gut and are free in the body cavity, except for their ends, which are attached to the pharynx and rectum. The membrane is always cytoplasmic with distinct enclosed nuclei (Fig. 1). As such it is structurally a peritoneum. (iii) Protonephridia, as found in the pseudocoelomates, are syncytial and lack nuclei in their flame bulbs, while the solenocytes of the Priapulida consists of discrete cells. (iv) The proboscis apparatus of the Acanthocephala is neither structurally nor functionally similar to the proboscis apparatus of *Priapulus caudatus*. (v) The nervous system of *Priapulus caudatus* has its main elements (circumpharyngeal nerve ring and ventral nerve cord) entirely within the body wall, in close contact with the epidermis, but distinct from it. In this way, and in others, it differs significantly from that of the Kinorhyncha. (vi) The first larval stage of both the Acanthocephala and Kinorhyncha shows extreme differences from the simple unciliated stereogastrula of *Priapulus caudatus*.

From histological examination, I have called the body cavity a coelom and its lining a peritoneum. Precise knowledge of the origin of the cavity and its lining will doubtless be revealed when embryological studies, still lacking, shall have been made. Solenocytic protonephridia are the most common form of excretory organs within the Pseudocoelomata, but they are not confined to these groups. Solenocytes are found in larval and in some adult archiannelids, polychaete worms, cephalochordates, and other true coelomates.

The presence, in these higher Meta-

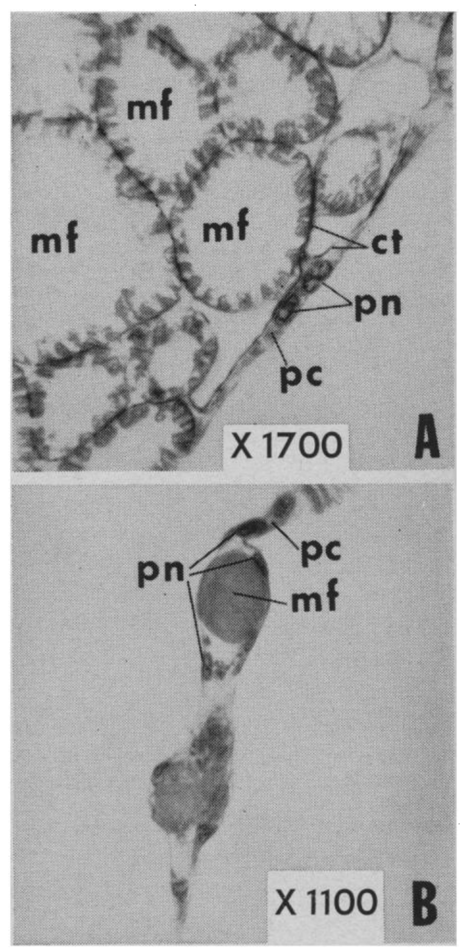

Fig. 1. (*A*) Cross section of a portion of a retractor muscle that extends between the body wall and the pharynx. Because of shrinkage the cytoplasm of the muscle fibers occupies only the peripheral portion (about × 1700). (*B*) Cross section of a portion of the mesentery between the digestive tract and a spindle muscle (about × 1100). *ct*, connective tissue; *mf*, muscle fiber; *pc*, peritoneal cytoplasm; *pn*, peritoneal nucleus.