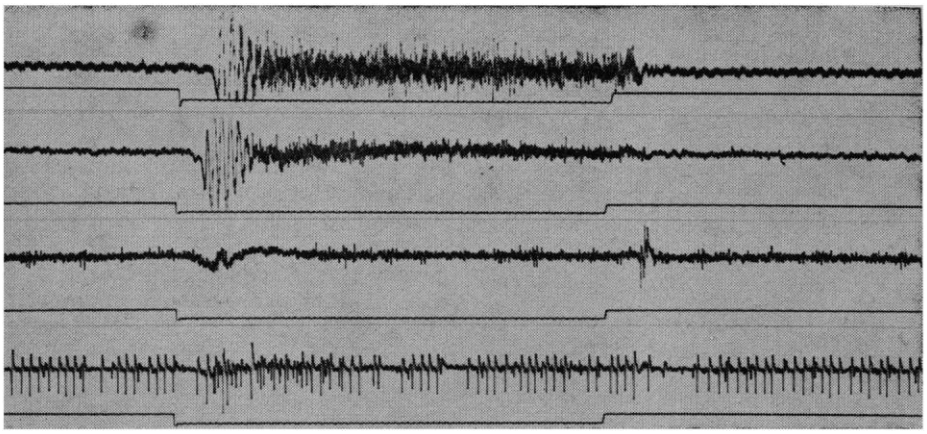

Fig. 1. Electrical activity of the retinal nerve and optic ganglion of the living squid. A glass-covered platinum 30-percent iridium microelectrode was applied directly to the surgically exposed nerve and ganglion. (Top trace) Electrode on nerve at point of emergence from retina; (2nd trace) electrode on surface of ganglion; (3rd trace) electrode penetrating ganglion; (bottom trace) electrode deep in ganglion. The bottom line of each trace shows the signal from the photoelectric cell; downward deflection indicates light on. Duration of stimulus, 0.51 second; amplifier coupling time constant, 0.001 second; amplitude of spikes in top record, approximately 500 μv.

the retinal nerve gave a discharge of impulses with a latency of about 0.05 second after the stimulating light was turned on. The frequency of impulses decreased within less than a second to a steady, maintained value and ceased abruptly after the stimulus was turned off. A damped train of slow oscillations appeared at the beginning of the discharge. These oscillations are of unknown origin and appear to be similar to those described by Fröhlich in the electroretinogram of *Eledone* (*3*), and by Wagner and Wolbarsht (*1*) in the octopus. They had many times the amplitude of the impulses from the nerve fibers, even though a millisecond coupling time constant was used in the amplifier to remove the slower components of the electroretinogram. No "off" discharges were found in the retinal nerve.

The discharge recorded from the surface of the optic ganglion (Fig. 1, second record) was identical to that recorded from the nerve and was presumably due to the fibers which cross the surface of the ganglion before entering it. Within the ganglion, both "on" and "off" discharges (third record) were obtained, similar to those found by Wilska and Hartline (*5*) in the optic lobe of *Limulus*. There was also a great deal of impulse activity within the ganglion, which was of spontaneous or undetermined origin (fourth record), though tactile responses were sometimes obtained. Obviously the two optic ganglia, which comprise the largest portion of the squid's central nervous system, are concerned with more than purely visual responses.

In these preliminary experiments (*6*) it was not possible to obtain quantitative information from single units, as has been done so successfully in *Limulus* and in the vertebrates. We only attempted to show that the retinal nerve of the squid discharges impulses in response to light and, in general, behaves as might be expected for the axon of a primary photoreceptor. We hope that others will be encouraged to make quantitative studies on the responses of the visual system and will solve the problem of keeping the microelectrode rigidly fixed with respect to the head, so that responses from single units can be recorded for an indefinite period. We also hope that our success in keeping the squid intact though immobilized for an indefinite period will encourage the study of the physiology of the circulation, the central nervous system, and the other sense organs of this intricate and highly organized animal.

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7 July 1960

Factors in Phoretic Association of a Mite and Fly

Abstract. Combined rearing of the mite *Myianoetus muscarum* (L.), and the fly *Muscina stabulans* (Fall.) has revealed adaptations of the hypopus to a series of fly factors. These adaptations favor the mite's dispersal. Hypopi are attracted to the pupa by a volatile substance and cluster on the anterior end, from which the fly emerges.

Anoetid mites share with some other mite families a distinctive stage in the life cycle, the deutonymph, which is highly adapted for dispersal by insects. The deutonymph, or hypopus, is an alternative stage interposed between protonymph and tritonymph. Conditions eliciting its appearance are as yet poorly understood, and may involve genetic factors besides physicochemical factors of its environment. Adaptations of the deutonymph include increased sclerotization, reduction in leg size, anal suckers, and rudimentary mouthparts (*1*). A marked degeneration of the digestive tract of *Histiostoma laboratorium* Hughes has also been observed (*2*, p. 122). The hypopus of *Myianoetus muscarum* (L.) was first noted on the housefly in 1735 (*3*). Berlese (*4*) reared the adult from hypopi found on *Muscina stabulans* (Fall.), and recently Cooreman (*5*) redescribed the species. We know of no work in which this or any other species in the family has been raised with fly larvae for the purpose of studying phoretic behavior. This report describes a series of orientations of the hypopus of *Myianoetus muscarum* which are behavioral counterparts of the anatomical adaptations noted above.

Trapped flies bearing hypopi were placed in a fly cage and maintained on lump sugar and water. Maggots and mites were reared at 24°C on meat covered with moist sawdust. Oviposition and pupation of the fly also occurred in this medium, as well as the complete mite life cycle. As a prelude to pupation, the prepupa usually faces downward, and in this position begins to construct a cocoon of cemented sawdust. Presumably, salivary secretions constitute the cement, since the salivary glands are greatly distended in the prepupa, whereas in actively feeding maggots and newly formed pupae they are much smaller (*6*). The prepupa then inverts, completes the top of its cocoon, and pupates soon after. Inversion of the jar elicits immediate reorientation of prepupae. Noteworthy is the normal sequence of positive and negative geotropisms which occurs within the space of a few hours.

Clusters of hypopi which may contain thousands of mites are often found

Table 1. Summary of data on the attraction of hypopi to a volatile substance produced by pupae of *Muscina stabulans.*

Groups*	Number of observations	Average number of hypopi (±S.E.*)	Range
Exposed to light			
A. Tubes with pupae	33	30.2±5.2	10–150
B. Tubes without pupae (control)	25	3.5±0.5	0–8
Exposed to dark			
C. Tubes with pupae	19	18.8±3.4	7–64
D. Tubes without pupae (control)	16	1.3±0.4	0–5

* Significance: between groups A and B, $p < 0.001$; between groups C and D, $p < 0.001$; between groups A and C, $p > 0.1$.

within the cocoons and on the pupal case. The cocoons are mite-tight but for a few interstices through which mites can enter. Hypopi are not attracted to the prepupa within its cocoon. Less than an hour after pupation, however, they begin to cluster on the anterior end of the pupa. In moderately heavy aggregations, mites pile up three or four deep on the anterior third of the pupa (Fig. 1), while in occasional very heavy infestations they may cover the entire pupa. Those in contact with the puparium are quiescent; the others are more active and mobile. No other stage of the mite is attracted to the pupa, nor is the hypopus attracted to the food which attracts the other stages. It was the regular occurrence of these aggregates on pupae which led us to test for the presence of an attractant.

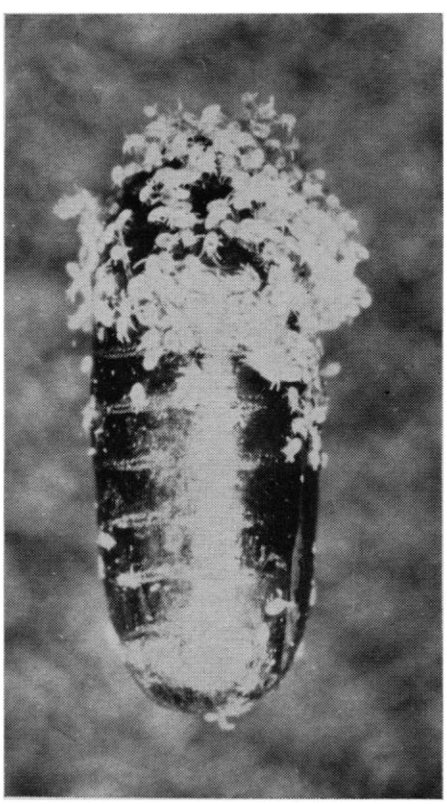

Fig. 1. Pupa of *Muscina stabulans* with hypopi typically aggregated at cephalic end.

Pupae were washed free of mites in cold running tap water, dried on paper toweling, and placed around the periphery of a piece of dry filter paper cut to fit the bottom of a 15-cm petri dish. Hypopi were taken from the medium and deposited at the center of the paper. The dish was covered and kept at 22° C and 20 percent relative humidity. The following observations are based on this method. The attractivity of individual pupae varies, but usually, after 1½ hours, about 30 to 50 hypopi collect on the anterior end of the pupa; about one-fifth as many are found on the rest of the pupa. The following factors had no effect on the polarity of attraction: age of pupae, plane of orientation, and direction or absence of light.

Pupae of several fly species maintained in our laboratory were similarly treated and placed in alternating sequence around the petri dish. Pupae of *Stomoxys calcitrans* (*7*), *Musca domestica,* and *Lucilia sericata* were attractive, and those of *Fannia canicularis* and *Drosophila melanogaster* were not. These results are confirmed by our observations of mite and fly associations in the laboratory media. Pupae of *Muscina stabulans* which were killed with cyanide gas or washed in acetone and then thoroughly air dried retained their attractivity. Those which were boiled in water or acetone for 15 minutes, rinsed several times, and thoroughly air dried had no attraction.

The volatility of the attractant was established in the following way. Plastic tubes, with an inside diameter of 7 mm, were diagonally cut at each end so that the side view had the form of a trapezoid. This provided sloping ends and maximum and minimum tube lengths of 28 mm and 8 mm, respectively. Eight pupae of *M. stabulans* were washed free of mites, dried, and placed in a tube. The tube was closed at each end with a piece of filter paper affixed with paraffin. Controls contained no pupae but were otherwise the same. Three controls and three tubes with pupae were placed alternately in the petri dish setup described above. With the aid of a dissecting microscope, hourly counts were made of mites on each end of the tube. After each count, the mites were brushed from the ends of the tubes and the tubes placed in different positions in the dish. Series of counts were recorded for both light and dark situations. The experiment was repeated three times with different pupae and tubes. The data indicate that pupae produce a volatile substance which is attractive to hypopi (Table 1). Mites are attracted as readily in the dark as in the light (*8*).

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8. This work was supported by National Science Foundation grant G9934, made to the senior author. We acknowledge with gratitude the statistical analysis prepared by Dr. Allan M. Burkman of this College, and the identification of the mite by Dr. Roscoe D. Hughes, Medical College of Virginia. The photograph was prepared by Mr. Luis de la Torre of our department.

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Licking Rates of Albino Rats

Abstract. Local licking rates of eight albino rats, when the rats were given tap water at the end of a short runway after 23 hours of water deprivation, averaged a little over seven licks per second. Small variations within sessions were found, rates being slightly but consistently higher at the beginning than later on in sessions. Inter-session and individual differences were also observed, but were only of the order of one lick per second. Within practical limits, it appears that licking rates of rats are constant.

When licking rates of four albino rats were measured by means of a cumulative recorder, it was reported that "the local rate of drinking an acceptable solution was constant for each animal," and that the "local rates of responding remained between five and six licks per second for all animals under all conditions" (*1*). The animals drank by licking the fluid under test from a drinking tube with a 3-mm opening. The data reported were utilized to show that local licking rate, or rate of consummatory behavior, is not a function of size of reward and hence cannot be related to other behavior variations which do accompany changes in reinforcement magnitude (*2*).

The statements about the constancy of licking rates are, however, imprecise.