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NEMATODE FEEDING MECHANISMS. 2. OBSERVATIONS ON *DITYLENCHUS DESTRUCTOR* AND *D. MYCELIOPHAGUS* FEEDING ON *BOTRYTIS CINEREA*

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D. destructor and *D. myceliophagus* behaved similarly when feeding on *Botrytis,* but differed in detail from *D. destructor* feeding on other fungi, as reported by Anderson (1964). Body contractions controlled turgor pressure, but the region where pressure increase was initiated decided different bodily functions: anterior contraction caused gland secretions to be injected into the host and rhythmical posterior contractions caused intestinal movements that mixed the contents. Feeds lasted from 3/4 hr to 2 3/4 hr and were nearly equally divided into injection and ingestion phases. Ingestion was by parts of the posterior of the pharynx pulsating with occasional assistance from the pump in the median bulb, but this eventually led to obstruction of further feeding by locally disrupting the contents of the host. Several cells at the feeding site died after being fed on.

While studying the feeding of *Ditylenchus myceliophagus* J. B. Goodey and *D. destructor* Thorne on the fungus, *Botrytis cinerea* Pers. ex Fr., observations were made that differed from or supplemented those described by Anderson (1964) in his detailed account of the feeding of *D. destructor* on *Chaetomium indicum* and four other fungal species. Anderson found that feeding behaviour differed on different fungi, but he did not use *B. cinerea* or observe *D. myceliophagus.* In the present investigations *D. myceliophagus* behaved similarly to *D. destructor* except that it thrived better on *Botrytis.*

METHODS AND MATERIALS

Botrytis cinerea was grown from spores, or from small blocks of agar permeated by mycelium, on a mixture of 1% Oxoid Ionagar (9 parts) and standard strength Oxoid Potato Dextrose Agar (1 part) contained in modified observation dishes for agar cultures (Doncaster, 1964): a lid of glass instead of Perspex was used because it interfered less with illumination. Cultures were in good condition for observation for about 2 weeks.

Most observations and photography were with Leitz Plano, apochromatic objectives of magnification 100 ×, numerical aperture 1.32 or of magnification 25 ×, N.A. 0.50. Periplanatic eye-pieces of 6 × and 10× were used. Critical illumination was with a Leitz UMK 50 ×, 0.60 N.A., metallurgical objective replacing the normal condenser that had an inconveniently short working distance.

Feeding behaviour was recorded photographically either on 16 mm movie film at different camera speeds or on plates from which prints were made for measurements of the nematodes. Observations were also recorded verbally on magnetic tape.

Intervals between rapidly repeated actions were estimated from ciné film. Because inconspicuous actions could be detected only from movements in projected pictures, the following method was used: at the time of each action, a pencilled dot was made on paper tape that ran at constant speed from a Creed type 25 output punch. Intervals between filmed events were obtained from distances between dots by using a time scale on which 1 sec. was represented by tc/p. cm; where t = speed of tape in cm/sec, c = camera speed and p = projection speed. Most estimates of intervals in test sequences agreed well with direct measurements, but were least accurate when actions were irregular and rapid.

NEMATODE BEHAVIOUR

The nematodes fed for a time at one place and then moved away, usually after a short period of relaxation, to try new feeding sites. The period of feeding at each site is referred to as a "feed". Each feed consisted of three phases of variable duration: penetration by the stylet, injection of secretions and ingestion. Table I shows the durations of the last two phases and of total feeds.

TABLE I

Durations of feeds on B. cinerea *by eight* D. myceliophagus (*Times in minutes*)

Individual	Injection phase	Ingestion phase	Total
1	30	12	42
2	20	51	71
3	21	53	74
4	33	46	79
5	33	60	93
6	57	74	131
7	45	91	136
8	90	65	155
Means	41	56	98

Exploration and penetration

Periods between successive feeds by five different *D. myceliophagus* ranged from 5 min. to 2 hr. The nematodes moved actively through the agar and seemed able to detect the hyphae at distances of 1-2 mm. Often the presence of one nematode feeding seemed to stimulate another to feed or to increase its exploratory activity.

Nematodes about to feed tried different numbers of cells, first by rubbing their lips quickly from side to side over a small area of hyphal surface, then by probes with the stylet, occasionally accompanied by twitching of the median-bulb musculature. They might move to another site after one or both activities or not until they had thrust their spear into a cell and dorsal pharyngeal gland secretions had begun to flow.

Before feeding sites were reached, the dorsal gland duct was more or less distended with secretions. Distension was usually greatest in a reservoir formed

in the fore-part of the median-bulb; it was usually less in the procorpus and always least in the isthmus. A pair of sub-ventral gland ducts enter the lumen of the median bulb immediately behind the pump. They contained indistinct heterogeneous secretions that were not seen to move (Fig. 1). Penetration started with long thrusts of the stylet about twice per sec but thrusting quickened to five per sec and amplitude decreased until the stylet came to rest with about a third of the conus in the host cell. Penetration took from a few seconds to more than a minute and was sometimes accompanied and always followed by the body shortening mainly in the region of the pharyngeal glands and fore part of the intestine (Figs. 3-5, 9).

Phase of injection of secretions

About the time the stylet entered a cell, heterogeneous secretions began moving forward in the dorsal gland duct, distending its anterior end. The median bulb musculature began to twitch usually only after stylet entry: this movement lasted at least 30 sec and in one nematode as long as 30 min. Twitching consisted of irregular un-coordinated contractions, mostly of lateral muscles of the bulb. When those near the reservoir contracted, secretions were forced out in both directions, though mostly forward. Table II (observations 1, 2) shows measurements on two *D. myceliophagus.*

The sub-ventral glands seemed to produce negligible secretions, but during the injection phase, homogeneous dorsal gland secretions progressively accumulated behind the outlet of their duct and formed a distension here termed the anterior reservoir (Fig. 7 A, B). Heterogeneous secretions were not seen to pass into the fungus, but that homogeneous secretions were injected is strongly suggested by the early development of a distinct zone around the stylet tip, the interruption of protoplasmic streaming, the host protoplast coming to appear more densely granular (Fig. 7 A-C), and by several cells at the feeding site dying after the feed. While a globule of homogeneous secretions occupied the anterior reservoir, outflow was assumed, because stopping the flow would be expected to allow the visible secretion constituents to be randomly distributed in the duct. In a minority of nematodes this in fact occurred before posterior pharyngeal pulsations began; pockets of homogeneous secretions occurred at random or drifted backward as Anderson saw regularly and at an earlier stage in *D. destructor* feeding on *C. indicum.* Thus though injection is thought to be usual throughout this phase, it may occasionally be interrupted.

Bodily movements caused by alterations in tonus of the somatic muscles were mostly slight or gradual during the injection phase. Figs. 3-5 show further shortening and fattening of the glandular region of the pharynx in an old female during the first few minutes, but Fig. 9 (Nematode II) shows gradual relaxation of anterior somatic muscles from an early stage of the feed.

Time-lapse film sequences covering entire nematodes and complete feeds show,

besides lateral body movements, irregular slight contractions of the posterior of the body that increased in amplitude about the onset of the ingestion phase.

Phase of ingestion

Throughout the ingestion phase pulsations occurred in the terminal region of the pharynx (Figs. 2, 8). At their onset the globule of homogeneous secretions in the anterior reservoir began to diminish (Fig. 7 C). In the 7 *D. myceliophagus* observed for correlation of these processes, the globule had disappeared within *ca.* 3 min of the beginning of posterior pharyngeal pulsations, and the apex ot the dorsal duct was left much less distended and containing only heterogeneous secretions (Fig. 7 C, D). Pulsations probably induced the residual homogeneous secretions to flow from their duct into the gut.

Initiation of pulsations was by contraction of muscles inserted anteriorly about the pharyngeal tube and posteriorly, it is thought, between the pharyngo-intestinal cells (so-called "cardia") which were moved at each pulsation (Fig. 8). Contractions pulled the posterior muscular insertions forward, caused the hind end of the pharyngeal tube to jerk backward *ca* 0.5 μ into the intestinal lumen and, perhaps by pressure transmission, the tube was constricted as far forward as the anterior muscular insertions. Differential antero-posterior movements of structures crossing the hind end of the pharyngeal tube (valve? in Fig. 2) suggested they possibly formed an outlet valve.

Hechler (1963), studying the feeding of *Neotylenchus linfordii,* which has no bulbar pump and which similarly pulsates the posterior part of the pharynx, concluded that pulsations represent pumping and Anderson reached the same conclusion for *D. destructor.*

Mean frequencies of posterior pharyngeal pulsations are in Table II (observations 3-5). Later in the feed, when the pump in the median bulb pulsated, muscular contractions in the posterior of the pharynx became irregular, but bulbar pulsations were transmitted to the pharyngo-intestinal junction which moved with low amplitude beats of corresponding frequency.

About the end of the injection phase the posterior third of the body typically tended to straighten before beginning rhythmical cycles of shortening and re-elongation. Harris & Crofton (1957) showed that when the "tail" of *Ascaris* shortened by contraction of the somatic muscles, body turgor was thereby increased. Contractions in *Ascaris* were at a fairly regular frequency of *ca* two per min. Though individuals differed, *D. destructor* and *D. myceliophagus* contracted with comparable frequency (Table II, observations 10-12). That their contractions increased turgor pressure, at first locally, was shown by concurrent constriction of the hind end of the intestine (Figs. 4-6). By pressure transmitted through the mid-intestinal contents, the fore-end briefly enlarged and a sector of the body at the same latitude slightly elongated. Except for its ends the intestine changed very little in diameter. The posterior third of the body then elongated again, thereby re-dilating the hind end of the intestine; this was associated with the fore end

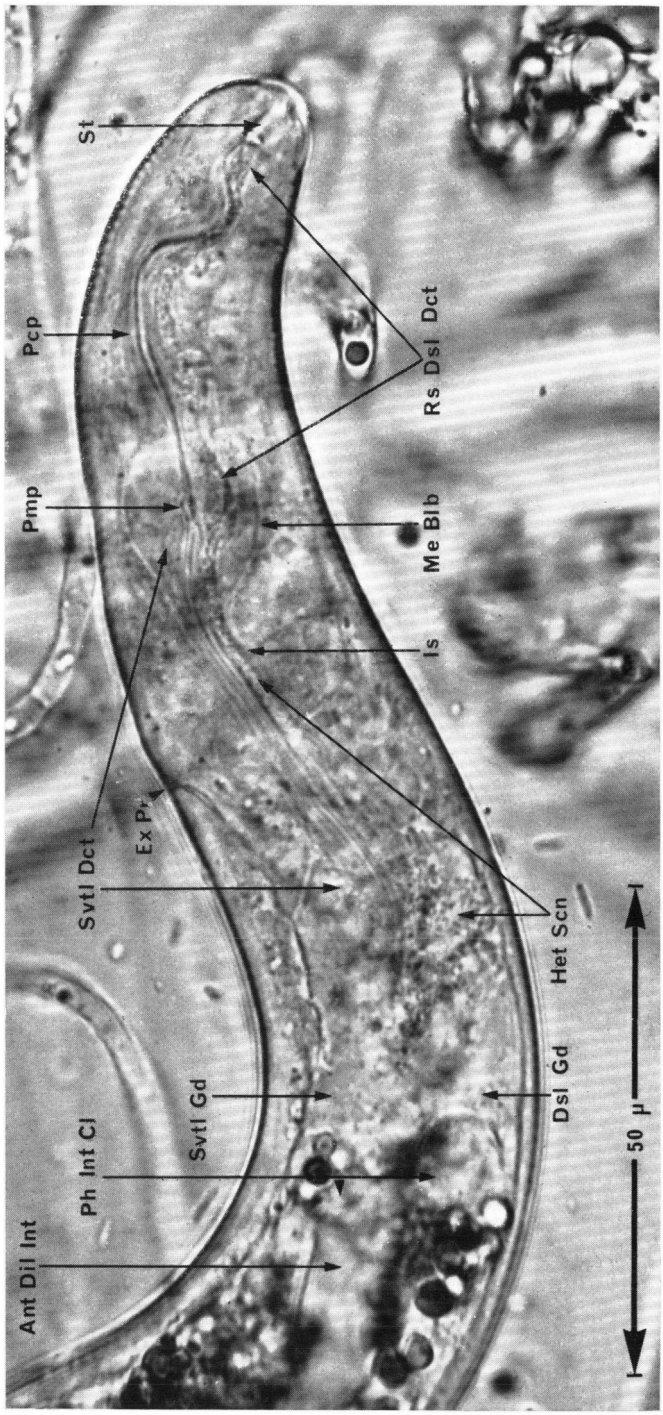

Fig. 1. The pharyngeal region of a *D. myceliophagus* feeding on *B. cinerea*. For abbreviations used in the figures, see the end of this article.

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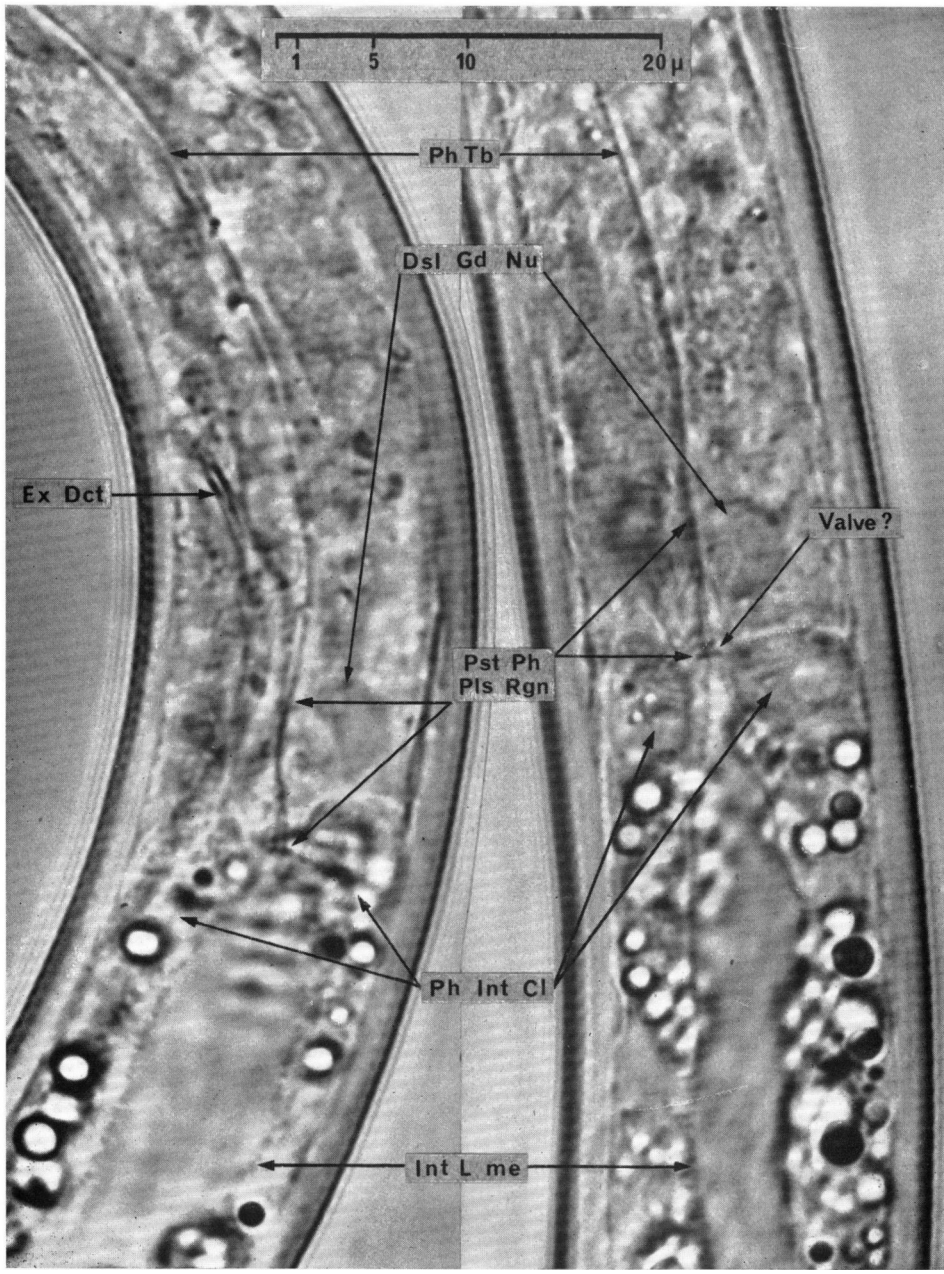
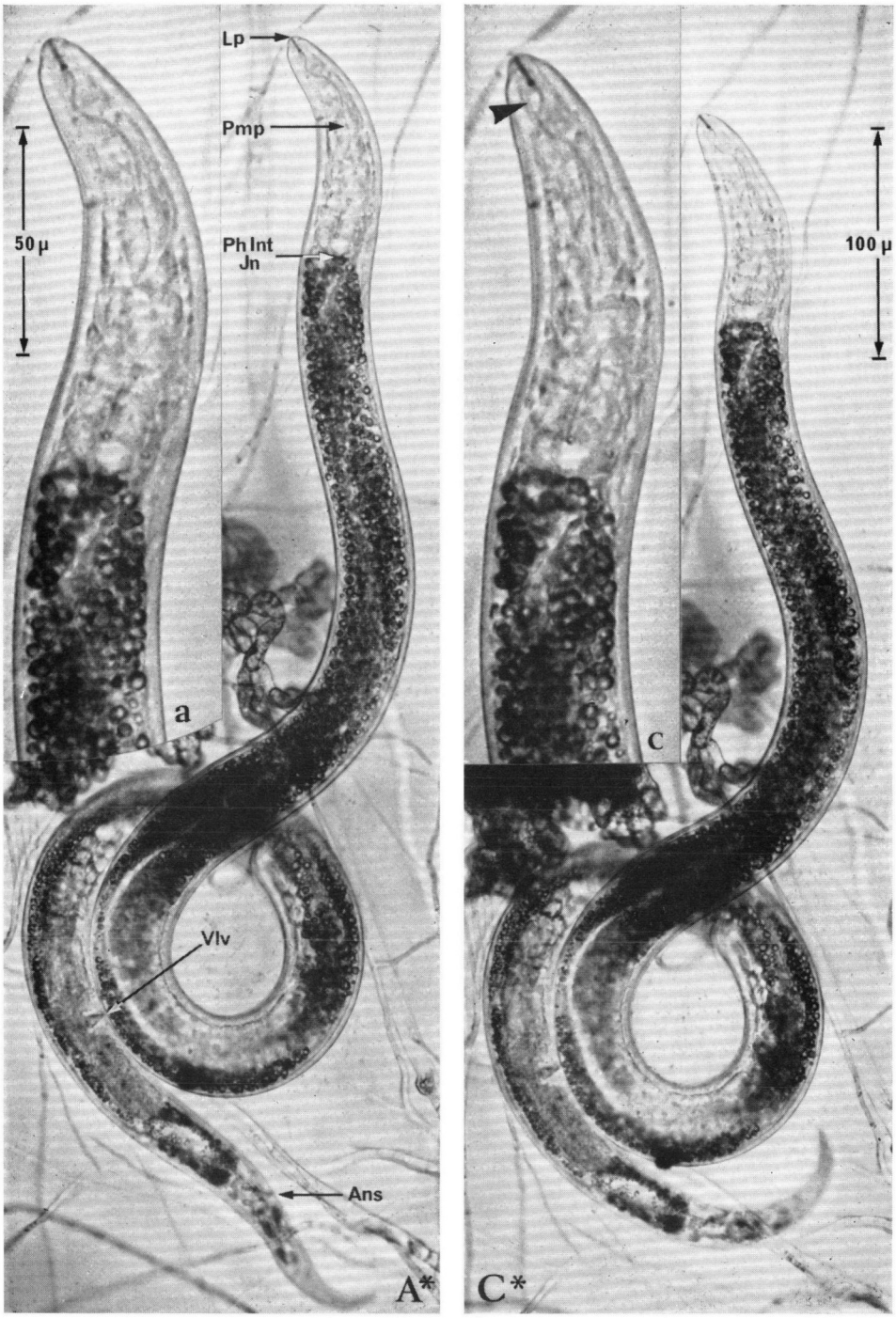


Fig. 2. Details of posterior pharyngeal and anterior intestinal structures of two live *D. myceliophagus*.



Figs. 3-5. A *D. myceliophagus* photographed before, during and after a feed, showing changes in bodily proportions at different stages. The pharyngeal region is shown enlarged (insets). Numerical data are in Fig. 9 (asterisked).

Fig. 3 A, a. While stylet thrusting a few seconds before the feed began. C, c. Five minutes later; note the pharyngeal region has shortened and thickened and secretions have begun to swell the dorsal duct's anterior reservoir (pointer).

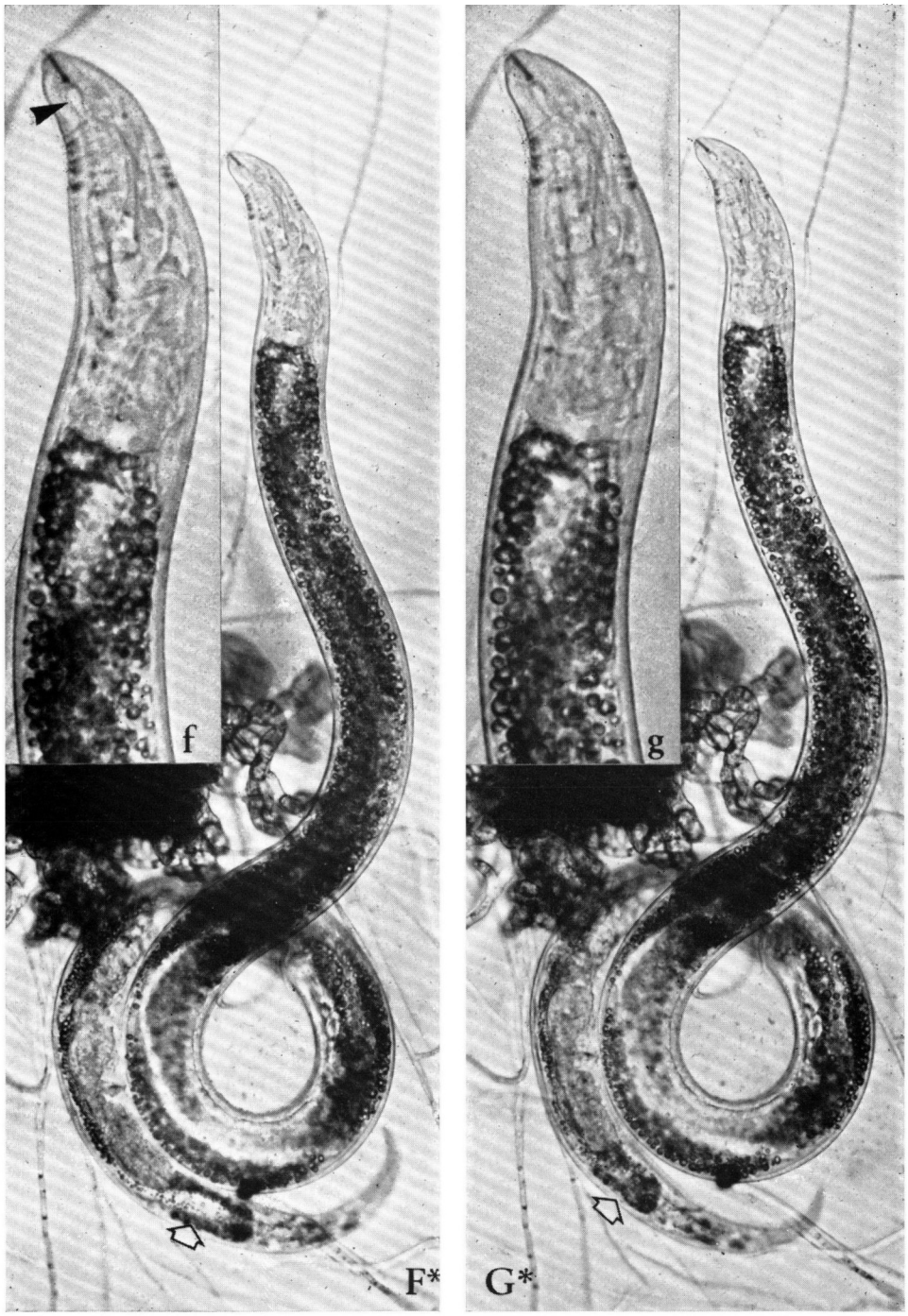


Fig. 4 F, f. Late injection phase at 25 minutes. Note the short, thick pharyngeal region and secretions accumulated in the anterior reservoir (narrow pointer). G, g. The beginning of the ingestion phase at 35 minutes. Note that secretions have begun to leave the anterior reservoir. An early "tail" contraction has constricted the posterior of the intestine (broad pointer).

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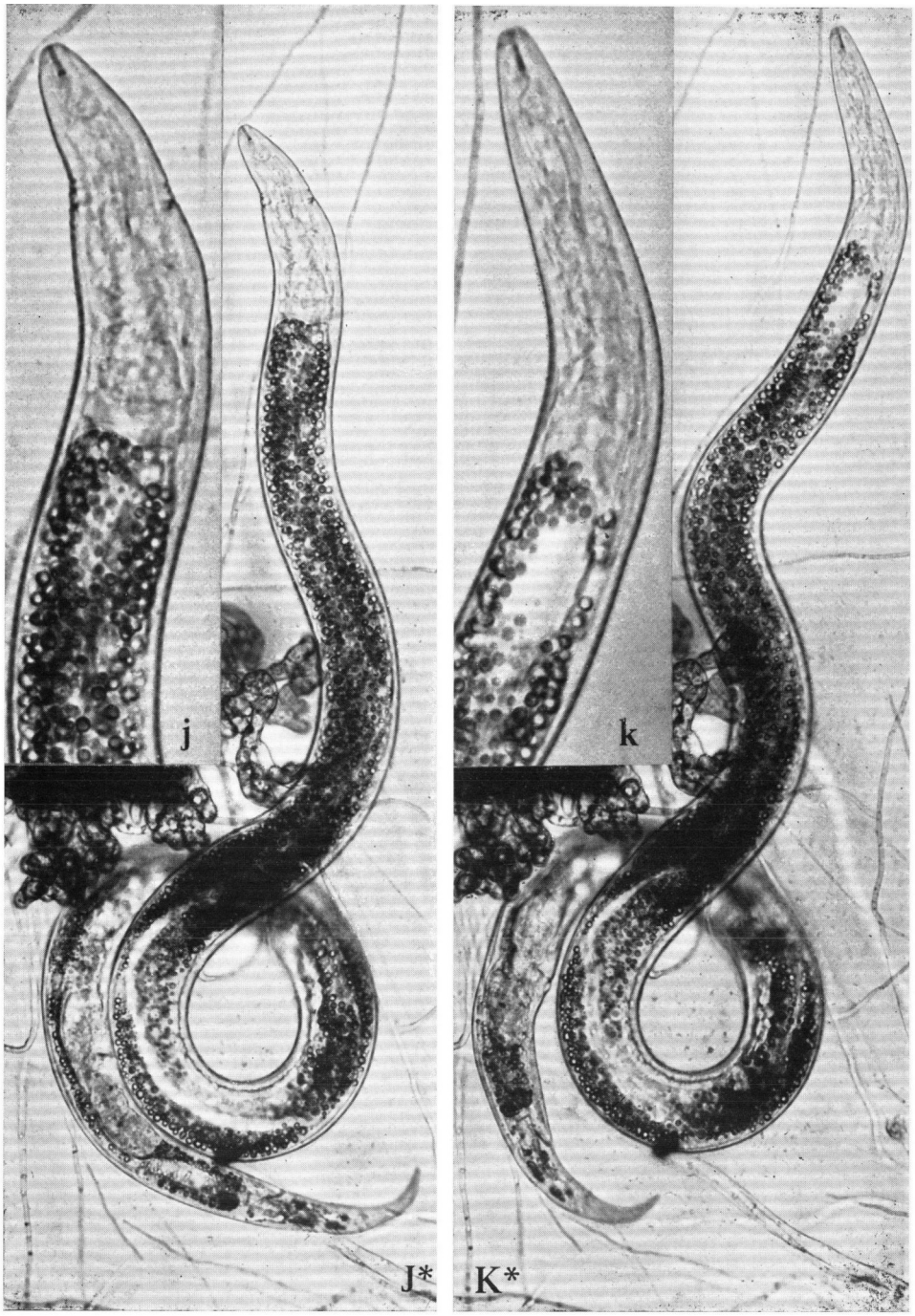

Fig. 5 J, j. During median bulb pumping, at 40 minutes. Elongation of the "tail" has re-dilated the posterior of the intestine and constricted it anteriorly (cp. Fig. 4 G). K, k. Departure at 42 minutes. Note great elongation of the pharyngeal region, dilation of the intestine anteriorly and "tail" contraction.

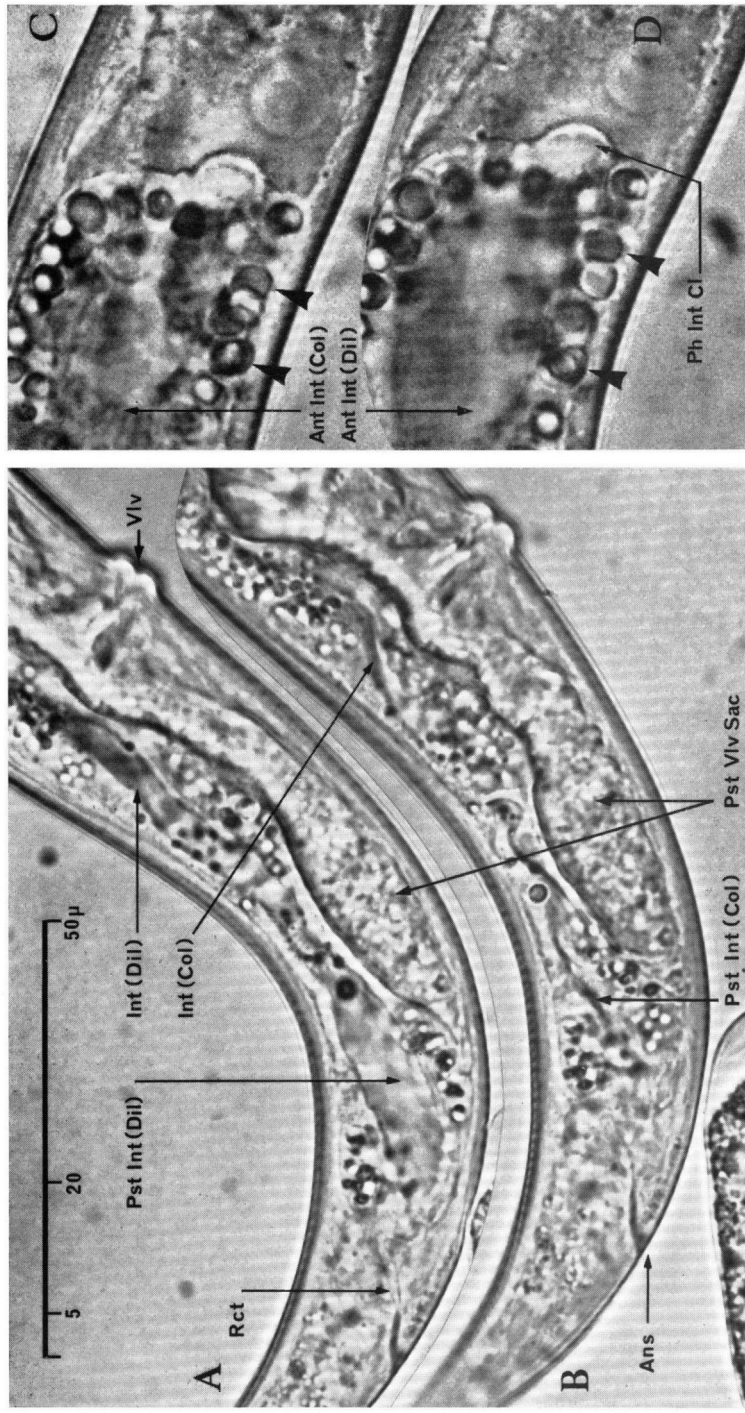

Fig. 6. A. B. The "tail" region of *D. myceliophagus* relaxed (elongated) (A) and contracted (B), causing respectively, dilation of the posterior of the intestine (A) and its constriction (B). C. D. Another *D. myceliophagus*. The anterior of the intestine is constricted at "tail" relaxation (C) and dilated at "tail" contraction (D). Note elongation of the intestinal wall in D (pointers).

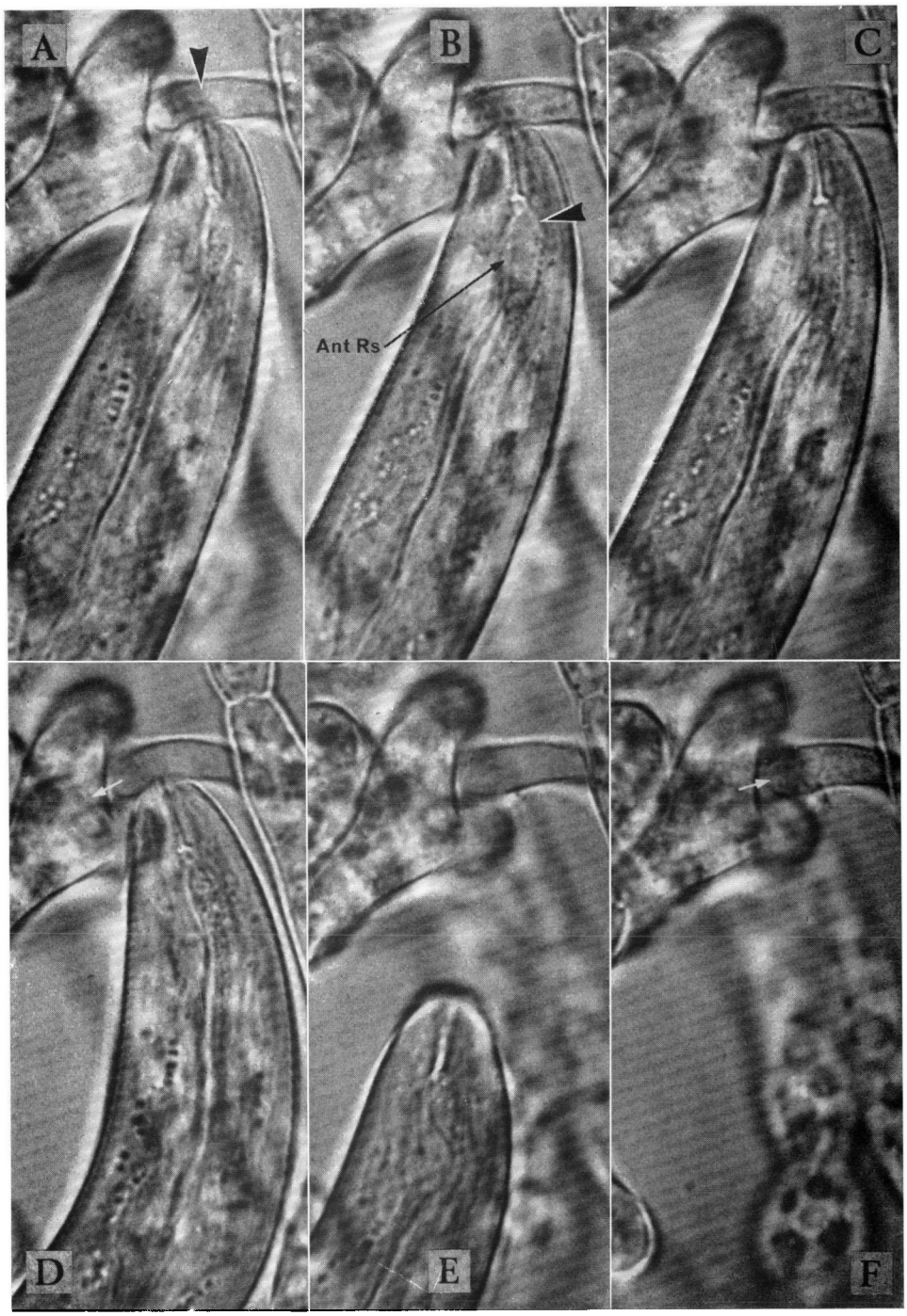

Fig. 7. Selected frames from film of a complete feed by *D. myceliophagus*. A. While penetrating the food cell. B. Near the end of the injection phase. Note homogeneous secretions swelling the anterior reservoir (pointer) and compare heterogeneity of the host protoplast in A (pointer). C. Three minutes later the homogeneous secretions have disappeared. D. Near the end of the pumping stage that terminated the feed; "granules" in the food cell have just moved towards the parent mycelium (arrow). E. The nematode's departure 2 minutes later. F. Four minutes later, the "granules" have flowed back into the food cell.

TABLE II

Actions associated with feeding: timed frequencies per minute (/m) or per hour (/h)

Observations	Species	Individual	Description of action	Number of actions timed	Mean frequency	Frequency range	Standard deviation per observation	Standard error of mean
1	*D. myceliophagus*	1	Twitching of median bulb musculature following stylet's penetration of food cell	15	77/m	10-300/m	71	± 18
2	Ditto	2	Ditto	18	103/m	54-200/m	34	± 8
3	*D. destructor*	1	Posterior pharyngeal pulsations (before pumping by median bulb)	19	81/m	43-100/m	22	± 5
4	*D. myceliophagus*	3	Ditto	24	90/m	67-120/m	15	± 3
5	Ditto	4	Ditto	28	76/m	50-100/m	19	± 4
6	*D. destructor*	2	Pulsations of the median bulb pump terminating the feed	47	257/m	231-300/m	18	± 3
7	*D. myceliophagus*	5	Ditto	50	267/m	222-316/m	24	± 3
8	Ditto	6	"Tail" contractions (vigorous) during injection phase	13	28/h	6-69/h	19	± 5
9	Ditto	7	Ditto	9	21/h	5-78/h	23	± 8
10	Ditto	6	"Tail" contractions (vigorous) during ingestion phase (before oviposition)	34	122/h	95-150/h	14	± 2
11	Ditto	7	Ditto	74	78/h	8-120/h	19	± 2
12	Ditto	6	"Tail" contractions (vigorous) during ingestion phase (after oviposition)	55	68/h	9-128/h	28	± 4

collapsing in different degrees. Sometimes collapse was momentarily almost complete, but the intestine soon returned to its partially dilated resting state. However, differences between individuals in the way their intestines collapsed strongly suggested this was caused hydrostatically and not by contraction of intestinal muscles as Anderson thought.

The wall of the fore part of the intestine (Fig. 6 C, D) showed great flexibility and during the phase of bodily elongation it often folded inward, almost obliterating the lumen, but it stretched considerably while the body contracted. Though the hind part of the pharyngeal gland mass was sometimes shifted by intestinal movements, the flow of secretions was only slightly affected.

During the last 2-15 minutes of the ingestion phase, and sometimes sporadically earlier, the pump in the median bulb pulsated after a short period of muscular twitching. The twitching gradually developed into co-ordinated contractions that dilated the pump irregularly at first, but soon rapidly and steadily. Frequencies of pumping are in Table II (observations 6 & 7). Pumping seemed eventually to disturb the fungal protoplast in such a way that feeding was obstructed, for after different periods of nematode activity, visible constituents of the fungal endoplasm began to flow. However the movement differed from normal streaming, yet was not directly caused by the nematode pumping, because particles in the penetrated cell flowed past the nematode's stylet, not towards it. Sometimes

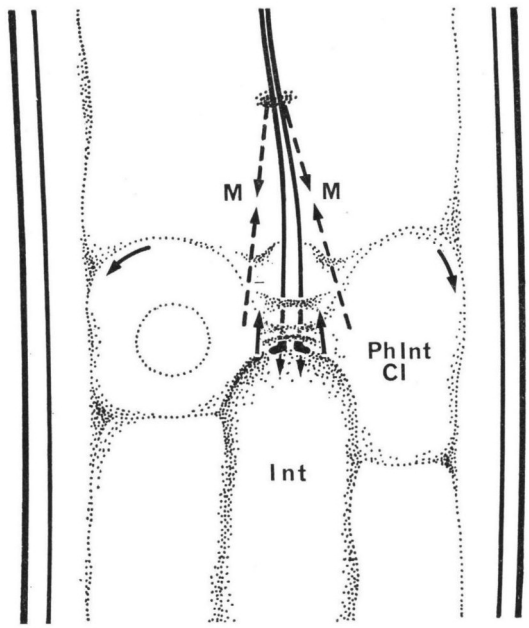

Fig. 8. The posterior pharyngeal pulsatory region. Arrows denote directions of observed movements of structures at each pulsation. The arrows at M show directions of muscular contraction.

movement first appeared in the parent mycelium and particles were carried towards the feeding site before a reverse and final flow began beyond the point of penetration. Whether the final flow was towards or away from the parent mycelium, it usually occurred after the nematode had not only stopped pumping but departed; it led to cytoplasm exuding from the penetration hole (Fig. 7 D-F). Nematodes usually left within 2 or 3 min of the onset of endoplasmic movement and the way they detached their lips from the hyphae by writhing from side to side showed that their lips had adhered tightly to the hyphae. Only after detachment could they withdraw their stylets.

During the final pumping phase or earlier, the whole pharynx gradually re-elongated (Figs. 3-5, 9). From the appearance of the ends of the intestine, it seemed that tonus in most nematodes was somewhat relaxed before they moved off, but some, e.g. the one in Fig. 5, kept their rear muscles contracted for some minutes.

Effects of feeding on host cells

Conidia, young cells with vacuolated protoplasts or older cells were chosen as food, but not greatly vacuolated, senile cells. Unlike Anderson's observations, terminal cells were not avoided. When nematodes fed on hyphae in which streaming was conspicuous, this soon stopped. In the larger cells the protoplast near the nematode's stylet became variously altered; some showed a dome-shaped zone around the tip of the stylet, bounded by "granules" that became increasingly conspicuous, but "granulation" in others seemed to follow paths across the cell or to become general.

When, after the nematode's departure cell contents exuded, the exudate seemed to consist mainly of the zone that had surrounded the stylet tip. Streaming was not seen again after feeds, though time-lapse films were taken of two such hyphae 5 and 16 hours later. Sometimes penetrated cells and up to five consecutive cells adjoining them became shrunken within *ca* 4 hr and their contents lost all recognisable structure in less than 12 hr, but not all cells up to the hyphal tip always died.

DISCUSSION

Harris & Crofton (1957) suggested that the great similarity of form among nematodes is mainly determined by mechanical factors and that the cylindrical body, equipped with longitudinal but no circular somatic muscles must, while retaining flexibility, be turgid to provide the necessary force against which the muscles can work. Using *Ascaris,* they showed that turgor depends on the state of muscular tonus and on the geometric arrangement of the inelastic fibrillar component of the cuticle. This is such that a shortening of the body length is less than compensated by increase in girth and body volume is made less, but because the body contents are incompressible, any increase in tonus of the longitudinal muscles increases turgor pressure. They postulated that despite the inelastic nature

of the fibrils themselves, they can by their arrangement and associated musculature function as an elastic structure; limited changes in body length need not therefore reflect changes in volume.

Inglis (1964) stated that no fibrillar component of the cuticle is present in most nematodes, but in their cuticles longitudinal flexibility nevertheless greatly exceeds radial flexibility, so that increased tonus in the longitudinal muscles will still tend to increase body turgor.

Harris & Crofton calculated that internal pressures throughout the group should be of the same order and independent of body size, but Inglis considered it would be less in nematodes lacking cuticular fibrils. Harris & Crofton suggested that movement of different parts of the body is often co-ordinated by transfer of fluids caused by local pressure changes and that complicated nervous co-ordination is lacking. Doncaster (1962) suggested that local pressure changes assisted inversion of the bulb flaps in *Pelodera* and *Rhabditis* sp. and Mapes (1965), using *Panagrellus silusiae,* showed defaecation to occur at a critical body volume. However, pressure changes in the "tail" and pharyngeal regions in *D. destructor* and *D. myceliophagus* control other functions: shortening of the body at the beginning of the feed (Figs. 3, 4 & 9) is associated with forward movement of gland secretions, which accumulate in the anterior reservoir and some pass into the host. It is reasonable to conclude that shortening the anterior increases pressure on the glands and causes their secretions to flow, but the lack of septa that could localise pressure differences in the pseudocoelom suggests that pressure fluctuations there become general throughout the body. When the posterior of the body shortens, hydrostatic pressure is initially increased there, but the effects differ from those of shortening the anterior: the hind end of the intestine is collapsed and because the intermediate intestinal region allows free passage of fluid, the volume of the anterior end is increased. There is visible movement of pseudocoelomic contents also, but this is restricted to the hind end. Thus it seems that when contractions occur posteriorly it is mainly the intestinal fluid that restores equilibrium of hydrostatic pressure in the body.

The relationship between the hydrostatic pressure of the fungus and that of the nematode would give useful information on the feeding process, but these have not been measured directly. Harris & Crofton found the hydrostatic pressure of fresh *Ascaris* in 30% sea water at 38-39° C., fluctuated between 16-225 mm Hg: mean *ca* 70 mm Hg (= 0.092 atmo.) and they postulated that pressures of the same order of magnitude would be general in nematodes, regardless of body size. Thatcher (1942) calculated the mean osmotic potential of *B. cinerea* hyphae to be 29.8 atmos., that of the culture medium used in these observations was 2.0 ± 0.4 atmos. The theoretical suction pressure and turgor pressure would therefore be about 28 atmos., but H. L. Penman (personal communication) suggests that this bears no relation to the actual hydrostatic pressure of the fungus which he considers could be of the same order as that of the nematode. The bodies of *D. destructor* and *D. myceliophagus* seemed always to shorten immediately before a feed

(Fig. 9 A, B, Nematodes I & II) and it must be assumed that, for secretions to be injected, the hydrostatic pressure of the dorsal gland and duct was thereby increased to exceed that of the fungus.

The host endoplasm stopped streaming soon after the stylets entered, suggesting that nematode secretions altered the properties of the protoplast in ways favouring

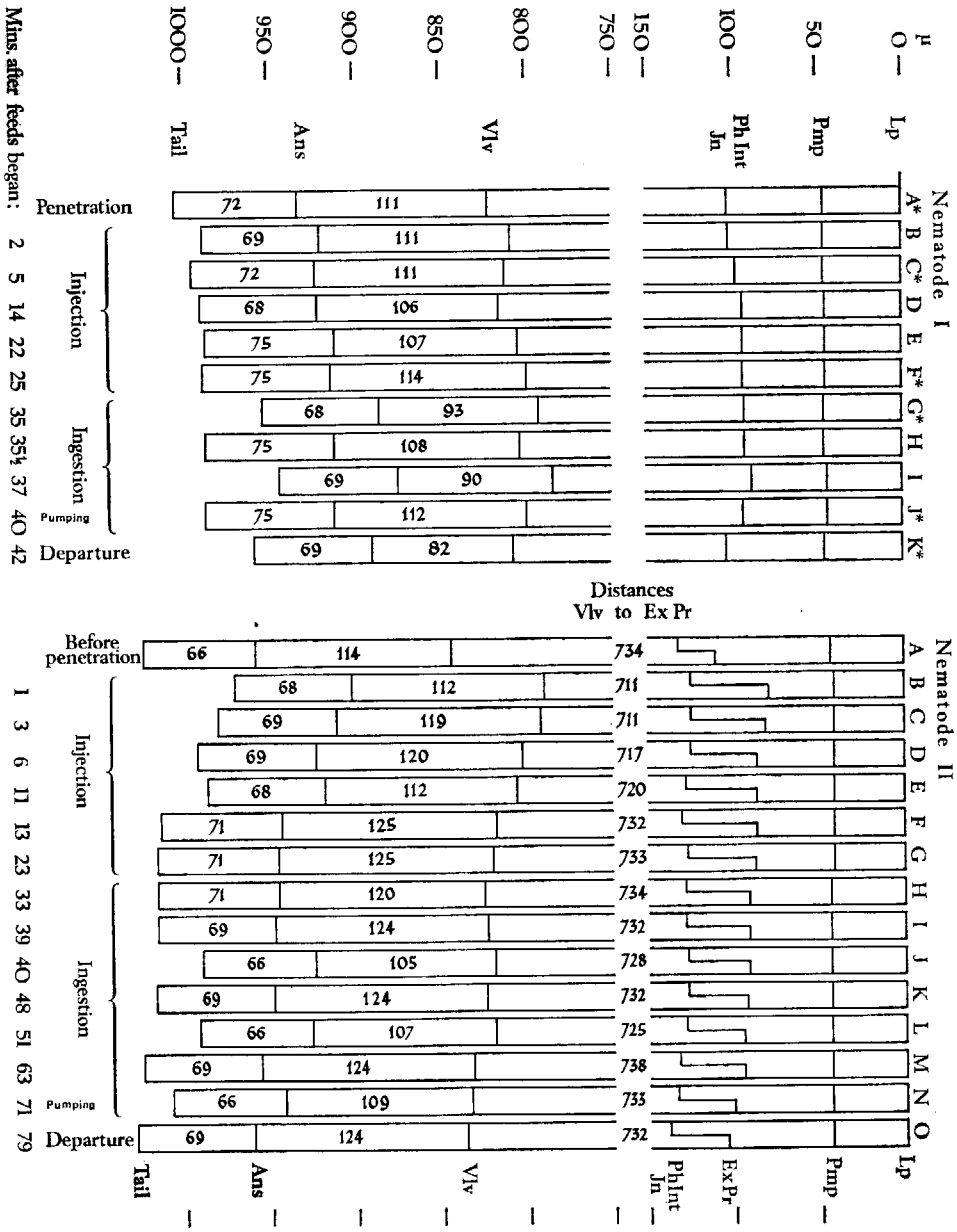

Fig. 9. Distances (in μ) between alimentary structures and body wall structures measured from series of photographs of two *D. myceliophagus* before, during and after feeding (Data asterisked are from Figs. 3-5).

its ingestion by the nematode: changes in colloidal properties or gelation seem possible. Gelation would minimise the risk of solid or viscous ingredients blocking the stylet aperture during ingestion. Moreover, the sudden endoplasmic streaming resulting from vigorous pumping and apparent obstruction of further feeding might be explained as breakdown of a thixotropic or otherwise unstable gel structure. In these circumstances ingestion might have to be accomplished with the minimum disturbance.

The posterior pharyngeal pulsations must represent either gentle pumping, as suggested by Anderson, or some mechanism to control the speed of ingestion if the food is under greater pressure than the nematode's turgor. The former implies ingestion by muscular activity; the latter the presence of valves closed by muscles. Circular muscles are thought to exist in nematodes only in the reproductive tract, but Wright (1965) showed that part of the pharynx of *Xiphinema index* can be constricted by radial muscles. However, if homogeneous secretions in the anterior reservoir are ingested by pulsation of posterior structures in the pharynx, these structures probably actively pump.

From film of the *D. myceliophagus* in Fig. 7 it was calculated that *ca* 460 pulsations occurred while homogeneous secretions emptied from the anterior reservoir, of capacity *ca* 100 cu.μ. An estimate of the capacity of the posterior pharyngeal pump from photographs (other *D. myceliophagus*) was *ca* 0.5 cu.μ (length of tube seen to collapse *ca* 4 μ; its mean diam. *ca* 0.4 μ). A pump of this size and of just over 40% efficiency would empty the reservoir in the observed time.

The use of the bulbar pump at later stages suggests that fluids are less readily obtained from the fungus as feeding proceeds.

Anderson described movements of the fore end of the intestine and suggested that they helped the intestinal contents to mix, as well as possibly assisting ingestion, but he neither showed them to depend on opposite movements of the hind-gut, nor that they became regular only during the ingestion phase when both food and pharyngeal secretions are thought to pass into the gut. A model showing the effectiveness of such a system in mixing fluids consists of a narrow glass tube with a rubber teat at each end. The system can be filled with unmixed fluids of different colours and one teat is fitted collapsed. When the teats are squeezed alternately, the fluids mix; they do so quickest when the difference between teat capacity and tube capacity is greatest.

Contractions of the hind end of the body causing intestinal movements also constricted the reproductive tracts of females and moved eggs therein. Table II (observations 10, 12) shows an example of contractions becoming slower after oviposition. However, they occurred with greater or lesser frequency in all nematodes, including males, throughout the ingestion phase.

I thank Mr. J. H. A. Dunwoody for calculating standard errors and standard deviations of frequencies of actions, Mr. C. W. Fearne for the loan of the Creed

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ABBREVIATIONS USED IN THE FIGURES

Ans.	Anus	Nu.	Nucleus
Ant.	Anterior	Ph.	Pharynx, pharyngeal
Blb.	Bulb	Ph. Int.	Pharyngo-intestinal
Cl.	Cell(s)	Pr.	Pore
Col.	Collapsed	Pst.	Posterior
Dil.	Dilated, dilatable	Pcp.	Procorpus
Dsl.	Dorsal	Pls.	Pulsatory
Dct.	Duct	Pmp.	Pump
Ex.	Excretory	Rct.	Rectum
Gd.	Gland(s)	Rs.	Reservoir
Het.	Heterogeneous	Rgn.	Region
Int.	Intestine, intestinal	Scn.	Secretions
Is.	Isthmus	St.	Stylet
Jn.	Junction	Svt.	Subventral
L. me.	Lining membrane	Tb.	Tube
Lp.	Lips	Vt.	Ventral
Me.	Median	Vlv.	Vulva, vulval

ZUSAMMENFASSUNG

Der Mechanismus der Nahrungsaufnahme bei Nematoden. 2. Beobachtungen an Ditylenchus destructor *und* D. myceliophagus *beim Fressen an* Botrytis cinerea

Beim Fressen an *Botrytis cinerea* verhielten sich *Ditylenchus destructor* und *D. myceliophagus* ähnlich, unterschieden sich aber in Einzelheiten von dem Verhalten von *D. destructor* an anderen Pilzen, wie es von Anderson beschrieben wurde. Körperkontraktionen kontrollierten den Turgordruck, aber je nach dem Abschnitt, in dem der Druckanstieg begann, wurde über verschiedene Funktionen entschieden: Kontraktionen des Vorderendes veranlaßten, daß Drüsensekrete in den Wirt injiziert wurden, und rhythmische Kontraktionen des Hinterendes riefen Darmbewegungen hervor, die den Darminhalt vermischten. Ein Freßvorgang dauerte ¾ bis 2¾ Stdn. und war in die nahezu gleich langen Phasen „Injektion" und „Aufsaugen" unterteilt. Das Aufsaugen geschah durch das Pulsieren des hinteren Ösophagusabschnittes mit gelegentlicher Unterstützung durch die Pumpe im Medianbulbus. Diese konnte jedoch infolge lokaler Zerreißungen des Inhaltes der Wirtszelle zu einer Hemmung der Nahrungsaufnahme führen. Mehrere Zellen an der Fraßstelle starben nach dem Saugen ab.

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