

## THE PHYSIOLOGY OF DIGESTION IN NEMERTEAN WORMS

Ray Gibson

Departamento de Zoologia,  
Universidade de São Paulo, Caixa  
Postal, 11230, São Paulo, Brasil<sup>2</sup>

### FISIOLOGIA DA DIGESTÃO DE NEMERTINOS

#### RESUMO

Na maioria, os Nemertinos têm hábitos carnívoros ou necrófagos. A digestão do alimento realiza-se em duas fases distintas: a fase inicial é extracelular e ácida, e envolve endopeptidases secretadas pelas células gastrodérmicas. Depois do alimento ser transformado em partículas aproveitáveis, o material, em parte digerido, é fagocitado, e a proteólise ácida continua por algum tempo intracelularmente. Segue-se a segunda fase, que é alcalina e abrange principalmente exopeptidases, mas também, em menor quantidade, lipases e esterases.

As diferenças fisiológicas que ocorrem entre as várias espécies podem ser relacionadas com a posição sistemática das mesmas, e com a organização do tubo digestivo, e parecem ter relação com as regiões da produção dos enzimas e com a natureza das secreções intestinais.

As reservas alimentícias dos Nemertinos são principalmente glóbulos de gordura depositados na gastroderme, mas, há também acumulações suplementares de glicogênio.

#### ABSTRACT

The phylum Nemertea comprises mainly marine organisms, the great majority of which are either carnivorous or scavenging in their feeding habits. From the numerous reports on their natural foods we can conclude that representatives of most invertebrate phyla are eaten by one or another nemertean species, although annelid worms and the smaller crustacean groups are high on their list of priority.

With the exception of a few unusual and unconventional trematode plathyhelminths, the nemertean grade of organisation is the lowest to possess a

<sup>1</sup> This paper was presented at the XXIV Reunião Anual de Sociedade Brasileira para o Progresso da Ciência, held at São Paulo from July 2-8, 1972.

<sup>2</sup> Present address: Department of biology, Liverpool Polytecnic, Byrom Street, Liverpool L3 3AF, England.

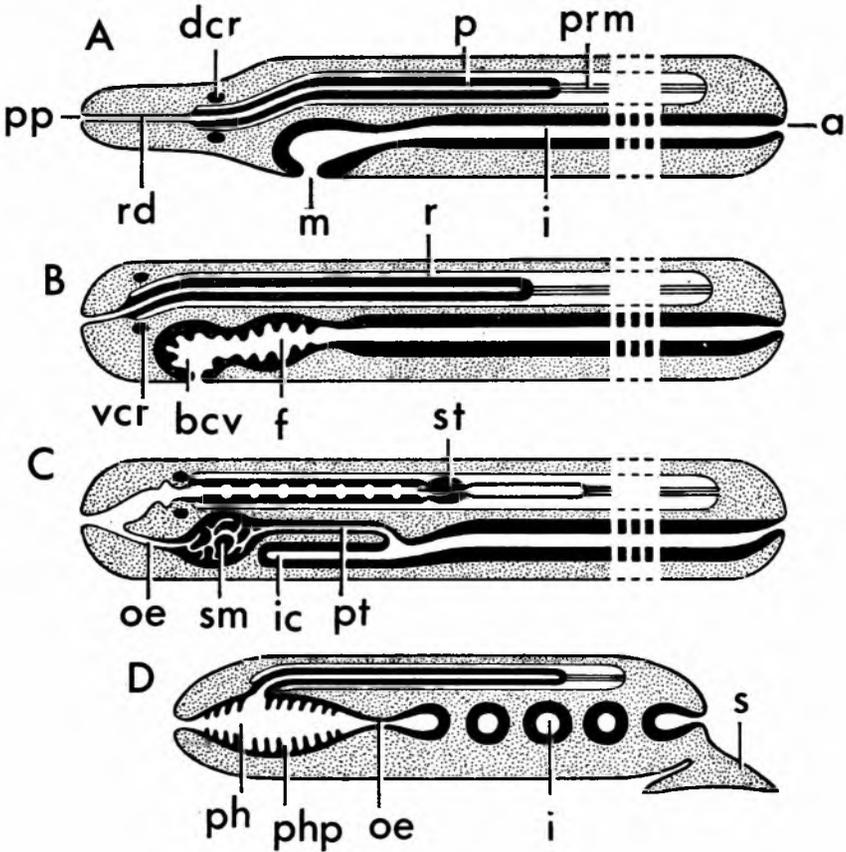


FIG. 1 — Schematic vertical longitudinal sections to show the relationships of the gut and proboscis apparatus within the different orders. A, Palaeonemertea (Cephalothricidae); B, Heteronemertea; C, Hoplonemertea (Monostylifera); D, Bdellonemertea. a., anus; bcv., buccal cavity; dcr., dorsal cerebral commissure; f., foregut; i., intestine; ic., intestinal caecum; m., mouth; oe., oesophagus; p., proboscis; ph., pharynx; php., pharyngeal papillae; pp., proboscis pore; prm., proboscis retractor muscle; pt., pyloric tube; r., rhynchocoel; rd., rhynchodaeum; s., sucker; sm., stomach; st., stilet apparatus; vcr., ventral cerebral commissure. (From Gibson, 1972).

separate mouth and anus to the gut. The arrangement of the alimentary system is of taxonomic importance, simplified diagrams being shown in Figure 1. In all groups the gut is basically divisible into two major regions, separable physiologically as well as histologically, which may be termed the foregut and the intestine. Throughout the various orders a greater uniformity of intestinal organisation is found than of foregut arrangement, the hoplonemerteans in particular possessing such anterior gut elaborations as oesophagus, stomach, pyloric tube and, in some species, an assortment of additional pouches.

The various ways in which food is traced and captured are beyond the scope of this paper, but are summarised by Gibson (1972). In all those species so far studied the food is either taken in intact, alive or dead, or is sucked up by the mouth in a semi-fluid condition. The various regions of the foregut appear, in general, to play no direct part in the enzymic degradation of the food, being apparently responsible only for the ingestive phase of feeding. Gland cells of these regions produce and discharge mucoid substances, which facilitate swallowing, and acidic secretions, which serve the triple purpose of killing the prey, if ingested alive, of initiating the disruption of the food tissues, and of setting up the required pH for the first phase of digestion, which takes place extracellularly in the intestine.

In the foregut of anoplan nemerteans (that is, the Palaeo — and Heteronemertea), species of *Cephalothrix* and *Lineus* have so far been examined histochemically (Jennings and Gibson, 1969), and all appear to possess essentially the same basic physiology. Two major types of gland cells are found, one producing acid mucopolysaccharides, the other containing demonstrable carbonic anhydrase which is believed to be involved in the acid-secreting mechanisms. As food enters the foregut, both types of glands discharge their contents, and the food becomes rapidly mixed up with the glandular secretions. The pH of the foregut contents at this time drops to about 5.0.

Amongst the enoplan species, however, greater physiological variation is found, and although it appears reasonably certain that again mucoid and acidic secretions are produced, they are of a form that react differently to the various histochemical methods employed. The only known exception to this rule so far is the freshwater hoplonemertean *Prostoma rubrum*, which Jennings and Gibson (1969) showed as possessing carbonic anhydrase in certain glands of the stomach. In other species (of *Amphiporus*, *Ototyphlonemertes*, *Paranemertes* and *Tetrastemma*), although the foregut lumenar contents become acidic, the nature of the secretions is as yet undetermined (Jennings and Gibson, 1969; Gibson, 1970 and unpublished observations). *Amphiporus lactifloreus*, in fact, possesses a rather unusual feeding mechanism

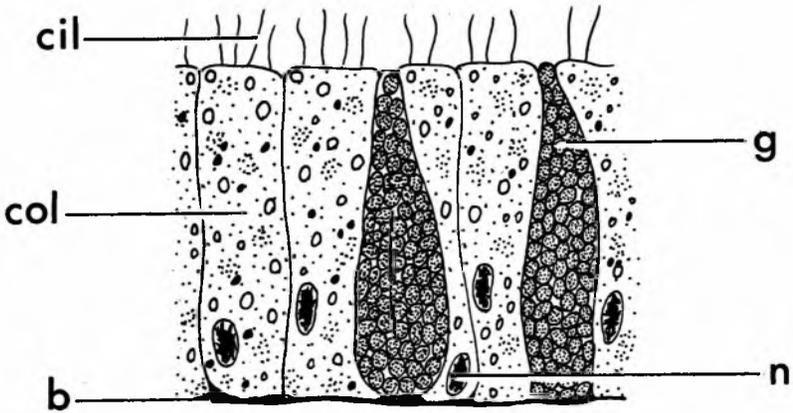


FIG. 2 — Diagrammatic representation of part of a heteronemertean intestine to show the typical gastrodermal appearance. *b.*, basement layer of gastrodermis; *cil.*, cilium; *col.*, columnar cell; *g.*, gland cell (endopeptidase producing); *n.*, nucleus of columnar cell.

which involves stomach eversion, and it is quite clear that the foregut secretions of this species are capable of histolysing the body contents of the gammarid prey. Whether this histolysis is achieved purely by acidic secretions, or whether some enzymic involvement is present, we do not yet know.

Food thus reaches the intestine in an acidic medium, and, to a greater or lesser extent, fragmented. Within the intestine only one group of extracellularly-acting enzymes have so far been positively identified, these being endopeptidases of the cathepsin-C type<sup>3</sup>. Within the anoplan groups these enzymes are produced and discharged by the gastrodermal gland cells (Fig. 2) and function at a pH optimum of about 5.5-6.0. However, in the hoplonemertean enoplans physiological changes are again found, and in most species studied the gland cells do not contain demonstrable endopeptidases (recent work has shown that psammobiontic Brazilian species of *Ototyphlonemertes* are an exception to this generalisation: Gibson, unpublished). In the hoplonemerteans endopeptidases can, however, be found in vesicular spheres produced within the ciliated columnar cells of the gastrodermis. These spheres, which are proximally situated in the resting gut, migrate distally when food enters the intestine and discharge their contents between the microvilli and cilia of the columnar cell surfaces (Fig. 3). The gland cells discharge their contents at the same time, and it is argued on logical grounds that, although no enzymes have yet been identified in their secretions, they are most likely to be proteolytic in form because of the predominantly carnivorous nature of the worms.

The later stages of digestion are the same, apart from differences in duration, for all species so far investigated. When the intraluminal material is broken down sufficiently enough to be phagocytosed, food is taken into the columnar cells and distinctive food vacuoles are formed. Phagocytosis is achieved, at least in the one species investigated (*Lineus ruber*), by lamellar outgrowths engulfing luminal material in the form of enclosed spheres, which then sink internally as indicated in Figure 4, which is based upon a description given by Jennings in 1969.

Intracellular digestion takes place in two distinctive phases, although there is both spatial and temporal overlap between the two. Initial intracellular digestion again involves endopeptidases, and all the evidence so far is that these enzymes are derived from the gut lumen mixture, and not directly secreted for use at the intracellular level. Acid phosphatases have been found in

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<sup>3</sup> This is certainly true for the carnivorous or scavenging species, but the atypical commensal bdellonemerteans, with a modified diet, do not possess demonstrable endopeptidases in their digestive enzyme complement (see Gibson and Jennings, 1969).

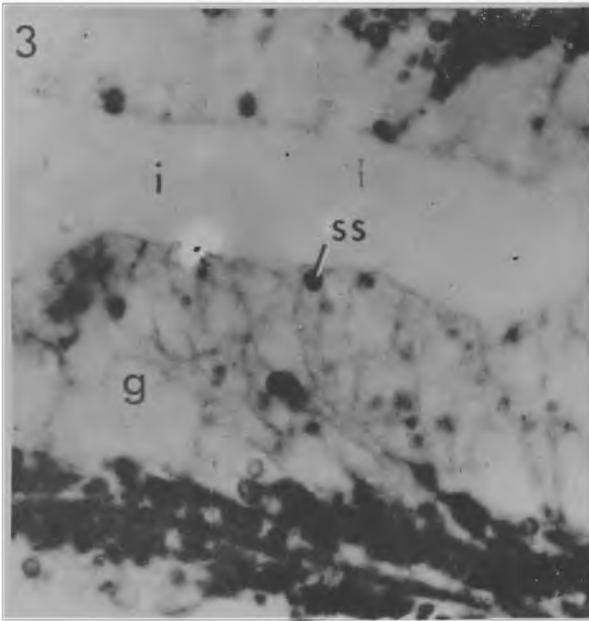


FIG. 3 — Longitudinal vertical section through a portion of a hoplonemertean intestine, showing the endopeptidase-containing secretory spheres (*ss*) within the columnar cells of the gastrodermis (*g*). The upper left sphere is about to discharge its contents into the intestinal lumen (*i*). Mallory, x 300.

the food vacuoles and surrounding cell cytoplasm at this time and are believed to be involved in the maintenance of the correct pH necessary for endopeptidase activity to continue. Later the second, and final, intracellular stage can be demonstrated, this primarily involving alkaline phosphatases and exopeptidases, again acting in the food vacuoles. Unlike the endopeptidases, the exopeptidases never act in the gut lumen and can only be demonstrated within the gastrodermis at the appropriate phase of digestion.

Three other enzyme groups are known to occur in the gut, although the emphasis placed upon these appears, as might be expected, to be a minor one. Esterases, carbohydrases ( $\alpha$ -amylase) and lipases have mostly been demonstrated in conjunction with the second, alkaline, stage of intracellular digestion, although the amylases and esterases may function in the earlier period. Lipases have so far only been positively identified in two species, the heteronemertean *Lineus ruber*, when fed on a high fat content diet (Jennings, 1962), and the hoplonemertean *Ototyphlonemertes evelinae* (Gibson, unpublished), which appears to possess greater quantities of the enzymes under normal circumstances. It seems probable that most, if not all, nemertean species possess these other enzyme groups in minor proportions.

One unique pattern of nemertean digestive physiology is known to occur in the entocommensal bdellonemertean *Malacobdella grossa* (Gibson and Jennings, 1969). Briefly, in this species an alteration in the type of diet to one that includes a high proportion of plant material (phytoplankton), has resulted in a shift in the emphasis placed upon the digestive enzyme groups. Thus endo — and exopeptidases have not been found in the gut, being replaced by carbohydrases and esterases. In *Malacobdella* there is evidence that the gastrodermal gland cells secrete an  $\alpha$ -amylase-like carbohydrase, a major alteration from the apparent circumstances found in their hoplonemertean relatives.

A completely different method for the uptake of nutrient materials was suggested by Fisher and Cramer (1967) for the heteronemertean *Lineus ruber*. This was the direct absorption of amino acids and glucose across the epidermis, a mechanism that might involve the proteolytic and other enzymes known to occur in the epidermal layers of many species (Jennings and Gibson, 1969; Gibson, 1970, 1972). However, the acquisition of food in such a manner is likely to be of only secondary importance in nemerteans and, if present at all, will merely serve a supplementary role to the use of the gut.

Food reserves are present in nemerteans, although their nature has been but superficially investigated. In all the species examined to date the major food reserve is fat, deposited principally within the gastrodermis as small globules, but also occurring with less frequency in other parts of the body.

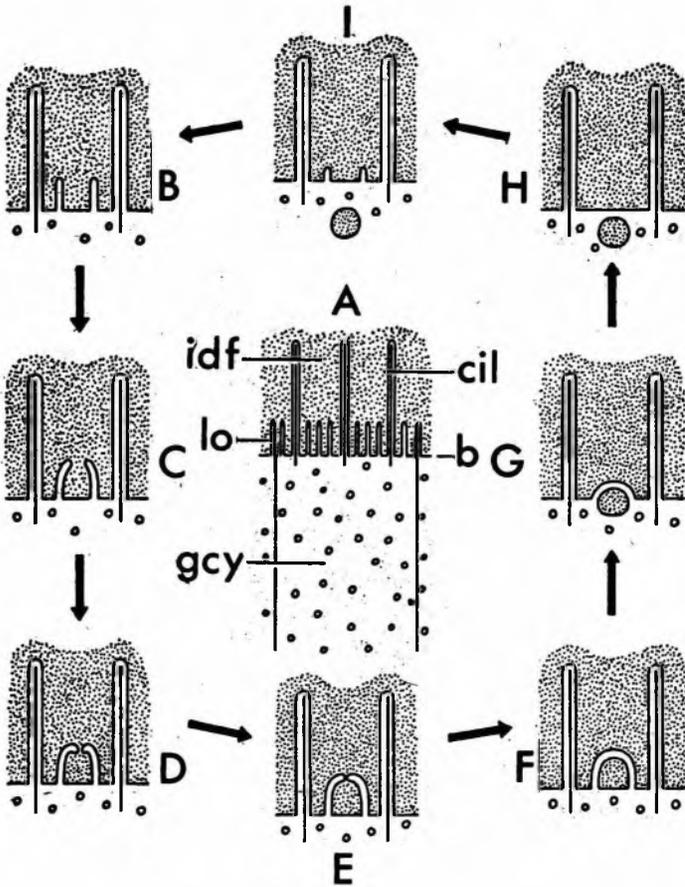


FIG. 4 — Diagrammatic representation of the mechanism whereby food material is phagocytosed and passed into the intestinal columnar cells. A, Component parts of the distal region of a typical columnar cell; B-E, Outward extension of plasma lamellae; F, Fusion of adjacent lamellar tips; G, H, Food vacuole being passed back into cell; I, Phagocytosis completed, new plasmal lamellae forming. *b.*, gastrodermal boundary; *cil.*, cilium; *gcy.*, gastrodermal columnar cell; *idf.*, intraluminal partly digested food material; *lo.*, plasmal lamellar outgrowth. (From Gibson, 1972).

The fat deposits are supplemented by smaller quantities of glycogen with a similar distribution (Jennings, 1960; Gibson and Jennings, 1969; Jennings and Gibson, 1969; Gibson, 1970).

In conclusion we can say that although comparatively few species of nemerteans have had their digestive physiology investigated in detail, there do seem to be indications of certain patterns emerging. Thus for the group as a whole digestion occurs in two stages, an extracellular and acidic proteolytic stage that is continued for a time at the intracellular level subsequent to phagocytosis, and an intracellular alkaline phase involving not only proteases but also other enzymes of other groups. The greater physiological variation found in the hoplonemerteans may be indicative of phylogenetic relationships, but it is far too early to state this with any degree of certainty. What differences do occur in the physiological patterns of nemerteans can, however, be related to their systematic position and level of gut organisation.

#### ACKNOWLEDGEMENTS

I wish to express my sincere thanks to the Brazilian National Research Council (Conselho Nacional de Pesquisas) of Rio de Janeiro, the University of São Paulo, and the Royal Society of London for providing the financial assistance that enabled my wife and I to visit and work in Brazil.

I am also indebted to Professor Diva Diniz Corrêa for providing facilities within the 'Departamento de Zoologia', to Professor Paulo Sawaya for facilities within the 'Departamento de Fisiologia Geral e Animal', and to Mrs Eveline du Bois-Reymond Marcus for translating the summary into Portuguese and, more especially, for her invaluable and willing assistance, both socially and scientifically, given throughout our stay in São Paulo.

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