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CHAPTER 2

Nutrition and Digestion

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I. Annelida

A. General Considerations

1. Introduction

Except in a very few species, the nutrition and the physiology of digestion in annelids and related groups have been relatively poorly investigated, especially when compared with mollusks or arthropods, or with parasitic invertebrates such as nematodes and cestodes. Moreover, almost nothing is known as far as the nature, properties, and kinetics of the digestive enzymes are concerned. This question ought to be entirely reconsidered in the light of the most recent concepts of enzyme specificity and synthesis. Owing to these numerous gaps in our knowledge of digestive processes, one has to be very prudent before attempting any generalization.

However, considered from an evolutionary point of view, some general facts may be pointed out concerning the extracellular nature of the

digestive processes, and the localization of enzyme secretion and of absorption along the digestive tract.

2. Localization of the Digestive Process

It is generally considered that the primitive form of digestion implies an intracellular process, in which food particles of relatively large size have to be first introduced into the digestive cell prior to being subjected to hydrolysis. It is known that, in Metazoa above the poriferan cellular grade of construction, there are a series of parallel evolutionary tendencies, in different phyletic lineages, in which the extracellular mode of digestion is more and more firmly established. In many classes of mollusks for instance (especially in Bivalvia and Gastropoda Prosobranchia), the intracellular and the extracellular digestion coexist to some extent, only a part of the food matter being hydrolyzed in the lumen of the alimentary canal. In such cases, the "digestive gland" or hepatopancreas is able to perform the absorption by phagocytosis of undigested particles.

As far as we know, annelids seem to be relatively more evolved from this point of view, the digestion of food being generally considered as entirely extracellular (Yonge, 1937; Scheer, 1948; Prosser, 1950).

However, it must be emphasized that some recent observations on polychaetes seem to indicate the possibility of intracellular digestion. In the lugworm *Arenicola marina,* Kermack (1955) observed, by means of a suspension of India ink in seawater, that the epithelium of the glandular region of the esophagus and of the stomach is capable of engulfing particles from the lumen of the gut, while the intestinal and rectal epithelia do not possess this property. She observed that the particles can be transmitted to amebocytes which, while wandering to all parts of the body, digest the food particles.

In *Hermodice carunculata,* a worm of the relatively primitive family of Amphinomidae, intracellular digestion is performed by invading coelomocytes (Marsden, 1963b, 1966). Amoebocytic cells appear to play a role in the absorption of food particles, in both the anterior and the posterior intestines. Pilgrim (1966) recently described "a certain amount of intracellular digestion in the intestine" of the Maldonid polychaete *Euclymene oerstedi.* But the related species *Clymenella torquata* does not seem to perform intracellular digestion, a difference which is attributed to the richer diatomaceous diet of the latter species (Pilgrim, 1966).

It thus seems that the classical concept of the existence of an exclusively extracellular digestion in annelids needs careful reconsideration.

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3. *Specializations Along the Digestive Tract*

The digestive tract of annelids is obviously the organ which is the least dependent on metamerization. Even in less evolved forms or in the most regularly segmented ones, the different parts of the digestive tract are already specialized: the buccal cavity and the pharynx are often transformed into a muscular proboscis, more or less equipped with prehensile structures such as "teeth" or "jaws" in predators. The following regions of the digestive tract are also more or less specialized. Behind a short esophagus, the digestive tract generally appears as a straight and broad tube, somewhat constricted at the level of mesenteries. This tube is classically divided into "stomach," intestine, and rectum. The stomach is sometimes preceded by a crop, or forms a gizzard with thick muscular walls and cuticle. In many species, these regions are undistinguishable morphologically, but can be detected histologically. As a general rule, the epithelium of the digestive tube is formed by secretory cells and absorptive cells; digestion and absorption seem to proceed simultaneously in the greatest part of the digestive tube. The difference between the various regions rests on the relative proportion of the different types of cells: the number of secretory cells tends to decrease gradually from the anterior to the posterior parts of the gut. Thus stomach and foreintestine are mainly the regions of enzyme secretion and food degradation, while the functions of the mid-intestine and hind-intestine are merely restricted to absorption and feces formation. The secretion of the digestive enzymes and that of mucus are considered as being holocrine.

In contrast to what happens in mollusks and arthropods, the digestive system of annelids is characterized by the absence or the poor development of glands or glandular diverticula specialized in the secretion of digestive enzymes, with the exception of the so-called "salivary glands." At the most, the digestive tract sometimes bears more or less developed expansions or ceca, the role of which in the digestive process is often uncertain and will be considered later.

An increase of the total intestinal surface by coiling and looping is only attained in a few sedentary polychaetes (for instance: *Pectinaria*) in which mesenteries are widely reduced. But the increase of the total resorptive surface is more generally realized by the formation of a deep ventral groove, named *typhlosolis*, or in rare cases by the development of cecal expansions.

For a comprehensive description of the gut anatomy in annelids, see Dales (1963).

4. *Direct Absorption of Organic Molecules from the External Medium*

The recent investigations of Stephens (1962a,b; 1963, 1964) pointed out that a number of marine invertebrates, with the exception of arthropods, are capable of removing small organic molecules from the surrounding seawater. It has been suggested that, according to the rate of uptake of amino acids, this absorptive process could significantly contribute to the nutrition of sand- and mud-feeding worms such as *Clymenella torquata* (Stephens, 1963). The absorption takes place across the body wall, without the necessary participation of the gut, because ligations of head or tail do not modify the rate of uptake (Stephens, 1963).

The same phenomenon has been observed in the case of other marine polychaetes (*Nereis limnicola* and *Nereis succinea*) but seems to be entirely lacking in land or freshwater species (*Lumbricus terrestris* and *Placobdella parasitica*). The uptake of glycine from dilute solutions by the two species of *Nereis* is an exponential function of the wet weight of the animal, and declines rapidly when the salinity is reduced below 200 mEq. Cl/liter. This observation, considered together with the inability of freshwater species to remove amino acids from solutions, suggests that the process of amino acid uptake is incompatible with osmoregulation (Stephens, 1964). The latter conclusion is consistent with the findings of Jeuniaux *et al.* (1961a,b) concerning the role of free amino acids as intracellular effectors in other euryhaline species of *Nereis*, and the diminution of the intracellular concentration of free amino acids in response to the adaptation to diluted seawater.

B. Carnivorous Polychaetes

1. *Feeding and Nutrition*

Polychaetes with predatory habits can be considered as being "carnivorous" by opposition to all other forms which feed on microorganisms or decaying food particles suspended in water or in sediment. These carnivorous polychaetes belong almost exclusively to the order of Phyllodocida (including the families Aphroditidae, Glyceridae, Nephthyidae, Scyllidae, Nereidae) and also to the very distinct and probably more primitive orders of Eunicida and Amphinomida.

The carnivorous polychaetes catch their prey by means of the eversible proboscis, often equipped with jaws. These jaws are not used to dilacerate the prey but only to catch hold of them firmly. In *Glycera convoluta*,

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the four jaws are pierced through their length by a fine duct connected to annexed glands, which secrete some poison working as a neurotoxin on the prey (mostly small Crustaceans) (Michel, 1966); the toxic effect is attributed to the presence of amines with indole groups and disulfide groups.

The prey of the carnivorous polychaetes mainly consists of small crustaceans, mollusks, or worms. Many species of Nereidae also feed on algae and on dead animals. The Nephthyidae *Nephthys cirrosa* and *N. hombergi*, on the contrary, are exclusively carnivorous and not at all nonselective detritus feeders, as sometimes stated, a mode of nutrition which is only shown by *Nephthys incisa* (Clark, 1962). Some species are more food-specific: the planktonic Tomopteridae of the genus *Tomopteris* feed on Chaetognaths (*Sagitta*) and on herring larvae (Nicol, 1960). Certain Syllidae (*Autolytus edwardsi*) feed on hydroids. The feeding reaction of the benthic phyllodocid *Eteone heteropoda* has been studied by Simon (1965): its prey consists mainly of small *Nereis succinea* and other polychaetes, which it perceives by following the mucous trail produced by the worm.

Among Amphinomida, the Amphinomidae feed on sedentary animals (tunicates, hydroids, sponges, bryozoans) by means of their ventral proboscis forming a horny rasp, whereas the Spintheridae, flattened disc-shaped worms, live especially on sponges.

2. *Hydrogen Ion Concentration of the Digestive Contents*

Rough pH determinations, performed by Marsden (1963a) in *Hermodice carunculata* (Amphinomidae), suggest that the pH of the digestive contents is slightly alkaline in the anterior intestine (about pH 8), and decreases slowly in the posterior intestine.

3. *Hydrolases*

Only very few data have been published since the pioneering work of Fredericq (1878), who observed the rapid dissolution of fibrin in alkaline and neutral medium by extracts of whole *Nereis pelagica*. In the Amphinomid *Hermodice carunculata*, roughly qualitative tests revealed the secretion of a lipase, an amylase, and proteolytic enzymes acting on gelatin and on "fish flesh" (Marsden, 1963a). The secretion of these enzymes seems to be mainly localized in the anterior intestine, but pharyngeal and esophageal extracts also exhibit hydrolytic activities.

A lipase, or nonspecific esterase, has been detected by the histochemical method of Gomori in the whole intestinal mucosa as well as in the intestinal contents of *Nereis diversicolor* (Lefevere, 1954). Acid and

alkaline phosphatases have also been identified in the intestinal mucosa by histochemical methods.

The gut contents and the extracts of the gut walls of *Hesione pantherina* and *Glycera chirori* are devoid of cellulolytic activity, but a slight cellulase activity has been observed in the gut contents of the eunicid *Eunice aphroditois* (Yokoe and Yasumasu, 1964). Aqueous extracts of the walls of the digestive tube of *Perinereis cultrifera* and *Nephthys hombergi* show a slight chitinase activity (43–58 μg. hydrolyzed chitin/hour/gm. fresh tissues) and a higher chitobiase activity (1600–5800 μg. acetylglucosamine liberated/hour/gm.) (Jeuniaux, 1963). The secretion of chitinase and chitobiase has also been observed in *Aphrodite aculeata* (Jeuniaux, 1963).

Extracts of whole *Nephthys hombergi* contain a lysozyme, which has been purified by Jollès and Zuili (1960), but this enzyme does not seem to play a role in food digestion.

4. Role of the Ceca

In some carnivorous polychaetes, a pair of ceca arise from the base of the esophagus, as in the Nereidae, or from the fore-intestine as in the Syllidae. The role of the ceca is unknown in the Nereidae; those of the Syllidae called "T-shaped glands" are generally filled with water, and are thought to play the role of a "swimming bladder."

In *Aphrodite aculeata,* 18 pairs of well-developed elongated ceca arise from the intestine. A little sieve retains the large particles at the base of each cecum. The blind end of each cecum forms an ampulla. The epithelium is composed of both secretory and absorptive cells, but seems also to function as an excretory organ (Darboux, 1899; Setti, 1900). The ceca are indeed filled with a brownish fluid that can be ejected by the anus in the form of a protective cloud, when the animal is disturbed.

C. Sand- and Mud-Feeding Polychaetes

1. Feeding and Nutrition

These worms feed on living microorganisms or on remains of decaying organisms present in sand or mud. They especially belong to the orders Capitellida (including the families Capitellidae, Arenicolidae, Maldanidae, Opheliidae) and Ariciida. *Owenia fusiformis,* a suspension-feeder Oweniid, is also able to feed by bending over until the crown of tentacles sweeps the surface of the sand (Dales, 1957a); the worms of the genus *Myriochele,* also belonging to the family Oweniidae, feed almost entirely on detritus absorbed from the sediment (Dales, 1957a).

The sand- and mud-feeding polychaetes possess a completely eversible proboscis which never bears jaws. These worms seem to be eating continuously, except at low tide for intertidal species. According to Fox *et al.* (1948), *Thoracophelia mucronata* (Opheliidae) mainly derives its subsistence from the colloidal organic matter adsorbed to the sand, ingesting 24% of their own weight of sand per hour. A worm of about 40 mg. would thus ingest about 84 gm. of sand per year, which represents about 840 mg. of organic matter. In the case of the lugworm *Arenicola marina,* the activity of feeding alternates regularly with defecation, every 45 minutes (Wells, 1953; Kermack, 1955); this rate of feeding and defecation may be influenced, to a considerable extent, by the water content of the sediment (Kermack, 1955).

2. *Hydrogen Ion Concentration of the Digestive Contents*

In *Arenicola marina,* the stomach contents have pH values of about 5.5–6.0, while the reaction is neutral in the intestine (Kermack, 1955). These changes of pH at the level of the stomach affect the viscosity of the mucus, which is less viscous in this region.

3. *Hydrolases*

The stomach is the main seat of starch, fat, and protein digestion in *Arenicola marina* (Kermack, 1955), as in the Maldanidae *Clymenella torquata* and *Euclymene oerstedi* (Pilgrim, 1966). The enzymes are probably secreted not only by the glandular cells of the stomach epithelium but also by those of the esophageal pouches. The digestion involves both extracellular and intracellular processes: the epithelial cells of the stomach are capable of engulfing particles from the lumen (Kermack, 1955; Pilgrim, 1966).

In *Arenicola marina,* the aqueous extracts of the stomach as well as those of the fore-intestine show a very slight chitinase activity (12–16 μg. hydrolyzed chitin/hour/gm. fresh tissues) and a higher chitobiase activity (1270–2700 μg. acetylglucosamine liberated/hour/gm.) (Jeuniaux, 1963); the chitinase activity is thus 10 times lower than in other sand- and mud-feeders such as sipunculids and the earthworms (see below).

4. *Role of the Ceca*

In the Arenicolidae, ceca are present at the junction between the esophagus and the fore-stomach. *Arenicola marina* possesses only one pair of ceca, but other species of the same family are known to possess from two to seven pairs. In *Arenicola marina,* the epithelium of the ceca is richly provided with glandular cells, filled up with zymogen

granules, which suggests the secretion of digestive fluids (Wiren, 1887). The aqueous extracts of these ceca indeed show a strong proteolytic activity on coagulated fibrin, in neutral or alkaline medium, and an amylolytic activity (Brasil, 1903; Kermack, 1955). In other sand- and mud-feeding polychaetes, belonging to the genera *Eumenia* and *Scalibregma* (Scalibregmidae) and *Ammotrypane* (Opheliidae), the cecal epithelium is devoid of glandular cells and seems unable to secrete digestive enzymes (Wiren, 1887).

D. Tentacle-Feeding Polychaetes

1. Feeding and Nutrition

The polychaetes belonging to the order Terebellida (Pectinariidae, Ampharetidae, and Terebellidae) are adapted to feed almost exclusively on the organic deposits forming the uppermost layer of the sediment, by means of a system of tentacles. These tentacles, which are very numerous, are provided with mucous cells and ciliary gutter (for a good morphological description of these organs, see Dales, 1955). The tentacles are extremely extensible in Terebellids: despite their sedentary life in a permanent tube, these worms are thus able to explore a wide surface of sediment around them. The tentacles are sometimes protected in small permanent tubes of agglomerated sand grains, as in *Lanice conchilega*. The mouth is provided with a system of lips, which sort out the particles. Tentacle-feeding polychaetes thus exhibit a more evolved feeding system than sand- and mud-feeders, providing the digestive tube with a much more selected food material, partially cleared of undigestible inorganic particles.

In the order Spionida, there are only two long tentacles on the prostomium, which seem to work like those of Terebellids.

2. Hydrogen Ion Concentration of the Digestive Contents

According to Dales (1955) the pH of the digestive contents of *Amphitrite johnstoni* falls from 7.0 in the esophagus to 6.0 in the fore-stomach. This slight acid reaction is maintained throughout the digestive tract, but rises gradually up to 7.2 in the hind-intestine. In starved worms, a pH of about 7.2–7.4 is found in the whole tract.

3. Hydrolases

In *Amphitrite johnstoni,* hydrolytic enzymes are secreted by the fore-stomach and the fore-intestine, while the muscular hind-stomach acts as a mixer (Dales, 1955) and is said to secrete a "peritrophic membrane." Qualitative tests, performed by Brasil (1904) on *Pectinaria koreni* and by Dales (1955) on *Amphitrite johnstoni,* pointed out the secretion of

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E. Suspension-Feeding Polycha

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lipase, amylase, and proteolytic enzymes in the fore-stomach and in the fore-intestine. The secretion of amylase is especially localized in the first section of the digestive tract (the fore-stomach, in *Amphitrite*) while the proteolytic enzymes are mainly produced by the middle part of the gut (the fore-intestine of *Amphitrite*). The proteolytic enzymes are active only at neutral and alkaline pH (Brasil, 1904).

A cellulase has been found in the aqueous extracts of the whole digestive tract of the terebellid *Loimia medusa* (Yokoe and Yasumasu, 1964).

E. Suspension-Feeding Polychaetes

1. Feeding and Nutrition

Different morphological adaptations to the filtration of the particles suspended in water have been evolved independently by several groups of polychaetes having sedentary habits. The filter used for the collection of the particles can be a velum of mucus, as in *Chaetopterus*, or a feathery crown made of branch or pinnate tentacles in Sabellidae, in Serpulidae and to a lesser extent in Sabellariidae and Oweniidae.[1]

The very peculiar mechanism in *Chaetopterus* has been thoroughly studied by McGinitie (1939). The worm lives in a U-shaped tube, in which water is pumped by the muscular movements of the notopodia of the segments 14 to 16; the water passes through a thick membrane of mucus, occluding the tube, and secreted by a ring of notopodia of the segment 12. Every 15 minutes, the mucus mass is conveyed to the mouth and engulfed. The diameter of the pores of the mucus filter is of about 0.04 μ (McGinitie, 1945). The mechanism of water driving has been thoroughly investigated by Barnes (1964, 1965) in four chaetopterid genera.

In Serpulidae and Sabellidae, the current of water passing through the branchial crown is produced by cilia of the crown; other ciliary tracts lead the particles to the mouth. In *Sabella pavonina*, a mechanical sorting of the particles occurs on the branchial filaments, in such a way that only the smallest particles can reach the mouth (Nicol, 1930). According to Dales (1957b), free-swimming algae generally escape from the pinnules; fanworms such as *Spirorbis* seem thus only capable of filtering inert particles of detritus down to 1–2 μ. As pointed out by Dales (1957b), this is perhaps one explanation of the abundance of fanworms at the mouths of estuaries where there is much fine detritus in suspension.

In all these cases, the respiratory system is coupled to the feeding

[1] As already stated, *Owenia fusiformis* is able to feed either by collection of suspended particles by a ciliary current produced by the ciliated crown, or by taking up larger particles in the sediment with the lips (Dales, 1957a).

system, a disposition which is well exploited by other microphagous sedentary animals such as lamellibranchs and tunicates.

Values of filtering rates, expressed by unit total fresh weight, have been recorded by Dales (1957b) for *Myxicola infundibulum* (0.10 liter/hour/gm.), *Sabella pavonina* (0.39 liter/hour/gm.), *Pomatoceros triqueter* (1.40 liters/hour/gm.). *Hydroïdes norvegica* (0.90 liter/hour/gm.), *Spirorbis borealis* (0.95 liter/hour/gm.) and *Salmacina dysteri* (2.09 liters/hour/gm.). The largest species thus have lower filtering rates per unit of weight than the smallest. When expressed as a function of the weight of the branchial crown alone, the filtering rates of these species are not significantly different and are comprised between 1 and 5 liters/hour/gm. (Dales, 1957b).

2. *Hydrogen Ion Concentration of the Digestive Contents*

In *Sabella pavonina,* the pH tends to increase slightly and progressively from the stomach (about 6.8–7.0) to the middle of the intestine (about 8.0–8.2 in the region of the segments 70–80). Then, the pH falls progressively, reaching a value of 6.5 in the rectum (Nicol, 1930).

3. *Hydrolases*

In *Sabella pavonina,* an amylase with pH optimum of 6.8 is more active in the stomach, while proteolytic enzymes with an optimum pH of 7.8 are more active in the intestine (Nicol, 1930). Carbohydrases acting on saccharose and lactose have not been detected (Nicol, 1930).

Other polysaccharidases are, however, involved in the digestive processes of some suspension-feeders: in *Sabellarstarte indica* (Sabellidae), the walls of the digestive tract secrete a relatively high amount of cellulase (Yokoe and Yasumasu, 1964); chitinase and chitobiase are secreted by the walls of the stomach and of the fore-intestine of *Spirographis spallanzanii* (Jeuniaux, 1963).

The activity of the chitinase (88 μg. chitin hydrolyzed/hour/gm. fresh tissues) and that of the chitobiase (1680 μg. acetylglucosamine liberated/hour/gm.) are approximately equal to those found in the earthworms. Cellulases and chitinases obviously play an important role in the digestion of cell walls, cuticles, or metaplasmatic membranes of planktonic animals and plants or of particles of decaying organisms.

Arylsulfatases, acting on dipotassium 2-hydroxy-5-nitrophenylsulfate and on potassium nitrophenylsulfate, as well as a β-glucuronidase acting on *p*-chlorophenylglucuronide monohydrate, have been detected in extracts of the whole body of *Chaetopterus variopedatus* (Corner *et al.*, 1960). Owing to the fact that these enzymes are predominantly secreted by digestive glands and tissues of mollusks and other invertebrates,

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F. Oligochaetes

1. *Feeding and Nutrition*

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it is presumed that they play a role in the digestion of *Chaetopterus*. However, the exact nature of the natural substrates on which arylsulfatases and β-glucuronidases actually act is still unknown.

F. Oligochaetes

1. Feeding and Nutrition

Feeding habits are more diversified among oligochaetes than is generally believed. In the small freshwater forms, many species belonging to the families Naïdidae (*Naïs, Aulophorus, Chaetogaster*) and Lumbriculidae (*Agriodrilus*) are active predators and feed mainly on small rotifers, crustaceans, and worms. Other Naïdidae and all the Tubificidae live at the bottom of ponds, lakes, and rivers, and are mud-feeders. The tubiculous species belonging to the genus *Ripistes* (Naïdidae) use the long setae of the anterior part of the body to collect all kinds of detritus on the surface of the sediment; the detritus is then wiped off in the mouth.

The Enchytraeidae form an important part of the biomass of the litter, in which they feed on dead leaves and decaying plants and animals. The "earthworms" belong to about nine different families grouped into the two orders of Prosopora and Opisthopora. All kinds of "earthworms" have generally the same habits; however, the species living in the uppermost part of the soil (for instance *Eisenia foetida*) feed mainly on the dead vegetation of the litter, while the species burrowing, in the deeper layers (for instance *Lumbricus spp.*) ingest considerable amounts of soil. The mixing of soil particles with fragments of partially digested organic matter and with mucus in the digestive tract of earthworms plays an important role in the humus formation (Darwin, 1881).

The soil-eating earthworms feed not only on the dead organic matter of the soil, but also on microorganisms constituting the pedofauna, such as nematodes (Stöckli, 1958). Soil protozoa seem to constitute an essential part of the diet of *Eisenia foetida:* a sterilized soil recolonized by fungi and bacteria alone fails to support normal growth of *Eisenia* from the egg to maturity, while inoculation of suspensions of motile forms of soil protozoa allows the complete development of the worms (Miles, 1963). The passage of the soil through the digestive tract of the earthworms is accompanied by a sharp modification of the bacterial flora, both qualitatively and quantitatively; it thus appears that certain bacteria are digested, such as *Escherichia coli,* while others can only develop in the excrements of the earthworms. The feces are known to contain a bacterial flora often much more abundant than that of the fresh soil (Swaby, 1950; Kollmannsperger, 1956; Brusewitz, 1959; Parle, 1963).

2. *Anatomy and Function of the Different Parts of the Gut*

In oligochaetes, the digestive tract differs considerably from the classical simple straight tube of annelids. A muscular, dilatable, more or less protrusible pharynx is often equipped with pharyngeal glands (= "salivary" glands) producing mucus. The esophagus bears the so-called "calciferous" or "Morren" glands; they do not play any role in digestion but are concerned with pH regulation of the blood and with the regulation of the blood cationic composition (Myot, 1957; Gansen, 1963). These glands excrete calcareous spheroliths in the lumen of the digestive tract; the calcium carbonate often crystallizes into vaterite crystals at the level of the hind-intestine (Gansen, 1963).

The esophagus leads into a stomach which, in earthworms, is divided into a crop and a muscular gizzard, lined with a thick cuticle. The gizzard is reduced or absent in aquatic forms. The epithelium of the stomach is richly provided with glandular cells, secreting mucus and enzymes (Gansen, 1963).

The fore- and middle-intestine are chiefly concerned both with enzyme secretion and with absorption, while the hind intestine is exclusively devoted to absorption. The surface of the intestine is increased by the typhlosolis, a dorsal involution of the intestinal wall. Additional glands are found in the intestine of some Enchytraeidae and Megascolecidae.

3. *Hydrogen Ion Concentration of the Digestive Contents*

The H ion concentration is kept nearly constant in the whole digestive tract of *Lumbricus terrestris* (Robertson, 1935; Heran, 1954). The pH lies between 6.5 and 7.5 in the pharynx, esophagus, crop, gizzard and in the fore-intestine. A slightly more alkaline reaction (7.6–8.0) is recorded from the region corresponding to the segments 60–80, but the reaction is neutral in the hind-intestine and in the rectum (Heran, 1954). Similar results have been recorded by Puytorac and Mauret (1956) for *Allolobophora savignyi* and by Kagawa (1949) for the Japanese earthworms *Pheretima communissima* and *P. divergens*.

4. *Hydrolases*

a. Earthworms. Proteolytic Enzymes. In *Lumbricus terrestris* (Heran, 1956) and *Eisenia foetida* (Gansen, 1963), the mucosa of the crop, gizzard, and fore-intestine (up to the portion corresponding to the sixtieth segment in *Lumbricus*) secrete proteolytic enzymes. The proteolytic activity decreases sharply in the mucosa of the middle- and hind-intestine.

Heran (1956) has studied the activity of the enzymic glycerin extracts

of crop and intestine of *Lum*
at pH values between 4 and 8
was found to be maximum at tw
and 7.7–8.3. The author conclu
enzymes secreted simultaneous
opinion relies also on the fact
pected two enzymes vary acc
epithelium used: the extracts of
while those of the other parts
at alkaline pH. However, no a
sumed two enzymes.

Both types of proteolytic ac
1956). According to Gansen (
activity of the proteolytic enz
and fore-intestine extracts, an
nitrocasein/90 min./mg. protei
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In *Pheretima elongata* (Meg
wall, at the level of segments 1
as substrate, with an optimu
the activity has not been meas
protease, when kept at 5° for
proteolytic activity of the same
and at pH 8.7, is enhanced by
and by asparagine as well as
ferricyanide and calcium chlo
such as sodium fluoride, sodi
have no effect. Glycerol, fructo
as well as bile and bile salts se
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The pharyngeal (= "salivar
organs. In *Lumbricus* and *All*
pharyngeal epithelium are beli
lem and Winne, 1899; Keilin, 1
(1963) did not find any evi
in that part of the gut.

5. *Saccharidases*

a. Amylase. An amylase is s
tract of *Lumbricus terrestris* a
being found in the fore-intestin
foetida, the amylase activity

of crop and intestine of *Lumbricus terrestris* on casein as substrate, at pH values between 4 and 8.5. In every case, the proteolytic activity was found to be maximum at two different pH levels, respectively 5.2–5.7 and 7.7–8.3. The author concluded that there are two distinct proteolytic enzymes secreted simultaneously by the different parts of the gut. This opinion relies also on the fact that the relative proportions of the suspected two enzymes vary according to the portion of the glandular epithelium used: the extracts of typhlosolis are more active at pH 5.6–5.7, while those of the other parts of the intestinal walls are more active at alkaline pH. However, no attempt has been made to isolate the presumed two enzymes.

Both types of proteolytic activity increase during starvation (Heran, 1956). According to Gansen (1963) in *Eisenia foetida,* the maximum activity of the proteolytic enzymes has been found in crop, gizzard, and fore-intestine extracts, and corresponds to 40–43 mg. hydrolyzed nitrocasein/90 min./mg. protein N at pH 7.3, and to 14–18 mg. hydrolyzed nitrocasein/90 min./mg. protein N at pH 5.6, at 37°.

In *Pheretima elongata* (Megascolecidae), the extracts of the intestinal wall, at the level of segments 15–25, show a proteolytic activity on casein as substrate, with an optimum pH of about 8.7 (Kamat, 1955); but the activity has not been measured below pH 7.5. The stability of this protease, when kept at 5° for 24 hours, is maximum at pH 8.7. The proteolytic activity of the same extracts, measured on casein as substrate and at pH 8.7, is enhanced by cystein-HCl, aspartic and glutamic acids and by asparagine as well as by sodium cyanide, potassium ferro- and ferricyanide and calcium chloride. Other amino acids, and other salts such as sodium fluoride, sodium nitroprusside and magnesium sulfate have no effect. Glycerol, fructose, galactose, glucose, lactose, and maltose as well as bile and bile salts seem to produce inhibitory effects (Kamat, 1957).

The pharyngeal (= "salivary") glands are mainly mucus-producing organs. In *Lumbricus* and *Allolobophora,* these glands and the whole pharyngeal epithelium are believed to secrete proteolytic enzymes (Willem and Winne, 1899; Keilin, 1920). In *Eisenia foetida,* however, Gansen (1963) did not find any evidence of secretion of digestive enzymes in that part of the gut.

5. *Saccharidases*

a. Amylase. An amylase is secreted by all the regions of the digestive tract of *Lumbricus terrestris* and *Eisenia foetida,* the maximum activity being found in the fore-intestine (Heran, 1956; Gansen, 1963). In *Eisenia foetida,* the amylase activity of tissue extracts is comprised between

15 mg. "glucose" liberated/3 hours/mg. protein N in the hind-intestine, and 47 mg. "glucose" liberated/3 hours/mg. protein N in the fore-intestine, at pH 7 and 37°. The optimum pH of *L. terrestris* amylase lies at about 7.2; starvation produces an increase in the amount of amylase found in the enzymic extracts (Heran, 1956).

b. Oligosaccharidases. The aqueous extracts of the intestinal walls of *Lumbricus terrestris* (Li and Shetlar, 1965) and those of *Dendrobaena octaedra* and *Allolobophora caliginosa* (Nielsen, 1962) contain a very wide variety of glycosidases: α-mannosidase, α- and β-galactosidase, α- and β-glucosidase (including invertase) and, in the case of *L. terrestris,* a β-glucuronidase and a trehalase. An invertase has also been found in the gut of *Helodrilus caliginosus* (Jewell and Lewis, 1919). It must be stressed, however, that these enzymes (except for β-glucosidase) are also found in muscle extracts, although in lesser amounts (Li and Shetlar, 1965); it is thus not clear whether these oligosaccharidases are actually secreted in the gut lumen and play a role in the extracellular digestion process or not.

A β-*N*-acetyl-D-glucosaminidase has not been found in *Lumbricus* intestinal wall (Li and Shetlar, 1965) although extracts of these tissues, as well as intestinal contents, show a relatively high chitobiase activity (2080 μg acetylglucosamine liberated/hour/gm. fresh tissues) (Jeuniaux, 1963). The activity of the glycosidases of *Lumbricus terrestris,* at pH 4.1 and 40°, using *p*-nitrophenylglycosides as chromogenic substrates, has been determined by Li and Shetlar (1965); expressed in micromoles nitrophenol liberated per 30 minutes per milligram protein, the following figures are given: α-mannosidase: 18.90; α-galactosidase: 11.64: β-galactosidase: 8.20; α-glucosidase: 0.91; β-glucosidase: 0.69; β-glucuronidase: 0.48. The optimum pH of all these glycosidases is said to lie between 3.0 and 4.5.

c. Polysaccharidases. In addition to amylase, other polysaccharidases able to hydrolyze structural polysaccharides are secreted by earthworms. A lichenase has been found in aqueous extracts of the whole digestive tract of *Helodrilus caliginosus* (Jewell and Lewis, 1919).

Using a viscosimetric method and carboxymethyl cellulose or chitosan-hydrochloride as substrates at pH 5, Tracey (1951) identified a cellulase and a chitinase in whole extracts of a series of earthworms belonging to the following genera: *Allolobophora, Dendrobaena, Eisenia, Lumbricus,* and *Octolasium;* a cellulase has been found in *Bimastus* and *Eiseniella* species (Tracey, 1951) and in *Pheretima* sp. (Yokoe and Yasumasu, 1964).

In *Lumbricus terrestris* and *L. rubellus,* the secretion of chitinase is located at the level of the middle intestine; the chitinase activity

amounts to 145 μg hydrolyzed chitin/hour/gm. fresh tissues (Devigne and Jeuniaux, 1961). Despite the presence in the gut of a chitinolytic bacterial flora showing marked differences with that of the soil, the chitinolytic enzymes found in the digestive tract are predominantly elaborated by the intestinal tissues themselves. This conclusion arose from experiments in which earthworms were reared in a sterile medium to which antibiotics had been added. After 1 month, the chitinolytic intestinal flora showed wide variations, without any alteration of the chitinase activity of the intestinal wall extracts and digestive contents (Devigne and Jeuniaux, 1961).

The activity of the *Lumbricus* intestinal chitinase is optimum at pH 5.0, decreases slowly with increasing pH, but is rapidly inhibited below pH 4.0 (Devigne and Jeuniaux, 1961).

b. Other Oligochaetes. According to the histological observations of Szarski (1936a,b), the carnivorous Naïdidae, especially those belonging to the genus *Chaetogaster,* are able to digest proteins, fats, and starch, principally in the fore- and mid-intestine; staining methods suggest the existence of an acid reaction (pH 1–2) in the contents of the stomach.

As far as Enchytraeidae are concerned, α-glucosidases, including invertase and trehalase, β-glucosidases, α-galactosidase, β-galactosidases, and amylases can be detected in extracts of the whole *Cognettia sphagnetorum* (Nielsen, 1962). Invertase, trehalase, lactase, and salicinase have been identified in *Fredericia hegemon* (Nielsen, 1962). The synthesis of β-glucosidase and β-galactosidase by the intestinal walls has been demonstrated in *Mesenchytraeus glandulosus* (Nielsen, 1962). The secretion of trehalase would probably allow the digestion of fungus spores, found by the enchytraeids in the litter.

G. Leeches (Order Hirudinea)

1. Feeding and Nutrition

Three modes of feeding can be recognized among leeches. The leeches of the suborder Pharyngobdellae (Erpobdellidae, Trematobdellidae) are carnivorous and feed on worms, insects, or mollusks. They swallow the whole prey. They possess a muscular, noneversible pharynx but no jaws, and their digestive tract is simple, without diverticula.

The leeches of the suborder Rhynchobdellae (Glossiphoniidae and Piscicolidae) penetrate the tissues of their prey using an eversible proboscis; they are more or less specific parasites of fishes, tadpoles, frogs or mollusks, sometimes even of crocodiles and turtles. The digestive tract consists of an enlarged crop, bearing some six pairs of diverticula, and a short intestine with four pairs of short diverticula.

Among the Gnathobdellae (Hirudidae and Haemadipsidae) are the true hematophagous leeches (*Hirudo, Hirudinaria, Macrobdella*), the buccal cavity of which is equipped with three strong jaws, used to make incisions in the prey's skin.[2] The pharynx is not eversible; between its muscular masses, numerous unicellular glands, called "salivary" glands, secrete a substance, hirudin, which prevents the clotting of the blood. Other species have only weak jaws and feed as typical carnivores (*Haemopsis, Philobdella*). In the typical blood-sucking species, such as *Hirudo medicinalis,* the crop extends from the eighth segment to the eighteenth, and bears a pair of ceca at the level of each segment. The last pair is the longest, and lies parallel to the intestine and the rectum. In the nonblood-sucking species, only the posterior pair of ceca is well developed (Mann, 1962).

The adaptation of the true blood-sucking leeches to an exclusively hematophagous diet is realized at the anatomical level by the possession of jaws, providing a precise cutting device, of a muscular pharynx acting as a pump, and of a series of greatly distensible gut diverticula, in which the blood of one single meal can be stored for a long time. On the biochemical level, blood-sucking leeches show a high degree of adaptation in the secretion of a powerful anticoagulant, hirudin, by the "salivary glands," and in the presence of a monospecific symbiotic intestinal flora, which seems to assume the main proteolytic role, a problem which will be considered later (see Section 3,a).

Hirudin, a specific inhibitor of thrombokinase, has been purified and analyzed by several authors (Yanagisawa and Yokoi, 1938; Jütisz *et al.*, 1963). Its formula is $C_{30}H_{60}O_{20}N_8$, with a molecular weight of 852. Jutisz *et al.* (1963) have isolated two different forms, α and β-hirudin, which differ in their solubility properties, but which have the same mobility upon paper electrophoresis.

In addition to hirudin, the "salivary" glands seem to secrete a histaminelike substance, which acts by causing a dilatation of the capillaries around the wound; they are also said to secrete some anesthetic (Lenggenhager, 1936; Lindemann, 1939).

Thanks to these anatomical and biochemical adaptations, blood-sucking leeches are able to feed only once every 3–6 months, and to digest slowly the blood taken in during one meal. The weight of the blood sucked in by a leech *Hirudo medicinalis* amounts generally to 3–4 times the weight of the leech, one the basis of fresh or dry weight (Pütter, 1907, 1908; Büsing *et al.*, 1953).

[2] They can also occasionally feed on other organic sources than blood: *Macrobdella decora,* for instance, can feed on the eggs of the salamander *Ambystoma maculatum* (Cargo, 1960).

As far as sucking response of *Hirudo medicinalis* is concerned, experiments in which leeches were allowed to feed through an artificial membrane have shown that blood can be substituted to a considerable extent by a solution of glucose (1 mg./ml.) in 0.15 *M* NaCl, or by solutions of D-galactose, L-sorbose, L-arabinose, and D,L-glyceraldehyde. Potassium chloride abolishes the sucking response (Galun and Kindler, 1966).

2. *Digestive Enzymes in Carnivorous Species*

The carnivorous leeches ingest either whole prey or tissue fragments that they pump by using the proboscis. In all these leeches, bacteria are said to play some role in the digestive processes, but this statement lacks experimental demonstration. In the nonhematophagous Hirudidae *Haemopis sanguisuga,* several exopeptidases have been detected, but no endopeptidase; among the former enzymes, a dipeptidase acting on glycylglycine and a carboxypeptidase acting on chloracetyltyrosine have an optimum pH of 7.8; an aminopeptidase acting on leucyldiglycine showed an optimum pH between 7.6 and 8.2 (Graetz and Autrum, 1935). Extracts of the gut walls of the same species contain a lipase, the pH optimum of which is comprised between 8.2 and 8.4 (Autrum and Graetz, 1934).

Lichenase and amylase are cited in the gut of the leech *Dina sp.* (Erpobdellidae) (Jewell and Lewis, 1919).

3. *Digestion in Blood-Sucking Species*

a. Protein Digestion. Surprisingly enough, proteolytic enzymes are said to be entirely lacking in extracts of gastric mucosa of blood-sucking leeches (Graetz and Autrum, 1935; Büsing *et al.*, 1953). It is sometimes believed therefore that extracellular digestion does not exist in these leeches, the hemoglobin being directly absorbed by the cells and degraded intracellularly into globin and hematin (Harant and Grassé, 1959).

According to Büsing (1952) and Büsing *et al.* (1953), the digestion of the blood proteins is realized by a symbiotic bacterial flora, composed of a single species, *Pseudomonas hirudinis,* which is able to produce antibiotics, thanks to which the development of other kinds of bacteria in the crop is inhibited. This statement relies on the *in vitro* observation of the slow production of "soluble" nitrogen from blood inoculated with *Pseudomonas,* and upon the fact that Chloromycetin introduced into the crop of leeches inhibited any blood digestion. However, it is not quite clear how the bacteria *in vivo* realize the digestion of the blood proteins, nor how this digestion can be profitable to the host, whereas

extracellular proteolytic enzymes are said to be lacking in the digestive contents. It seems that this problem requires further examination.

b. Esterases. Autrum and Graetz (1934) failed to obtain any evidence of lipase secretion in the crop of the leech *Hirudo*. Büsing (1952) claims that the digestion of fat is realized, as that of proteins, by the symbiotic *Pseudomonas hirudinis*. This bacterium can indeed be grown in a culture medium containing only tributyrin as source of carbon, and reduces rapidly the fat concentration of the medium.

c. Saccharidases. The only saccharidase to be reported from the enzymic digestive equipment of the leeches is a hyaluronidase (Hahn, 1945), which is probably produced by the "salivary" glandular cells of the pharynx, and acts as a spreading factor. The mode of action of the leech hyaluronidase is distinct from that of the hyaluronidases found in testicular extracts, snake venoms, and microorganisms, which split the endohexosaminidic bonds of hyaluronic acid. The hyaluronidase of *Hirudo medicinalis,* on the contrary, hydrolyzes the endoglucuronidic linkages of hyaluronic acid. The oligosaccharides produced from hyaluronate by leech hyaluronidase indeed are tetrasaccharides with uronic acid forming the reducing end group (Linker *et al.,* 1957, 1960).

H. Myzostomida

This class comprises only forms which all live on echinoderms (mainly Crinoids). A few species are endoparasites, but most of them live as ectoparasites or commensals. They feed on the plankton retained on the host's ambulacres. They possess a muscular pharynx, separated by a sphincter of the "stomach" or "middle intestine," which bears 2 to 5 pairs of highly ramified diverticula. Some glands, called "salivary glands," open in front of the proboscis. The ceca appear to play mainly an excretory function (Jägersten, 1940; Platel, 1962). The "salivary glands" are extremely rich in ribonucleoproteins and secrete mucopolysaccharides (Platel, 1962). Nothing is known about digestion.

II. Echiurida

A. Feeding and Nutrition

The species belonging to the genera *Echiurus, Urechis,* and *Ochetostoma* live in U-shaped tubes burrowed in mud or sand of the bottom of the ocean. A current of water throughout the tube is created by the rhythmic contractions of the body, and water is pumped through the anus in the thin-walled hind-intestine, which thus functions as a respiratory sac. But, contrary to what happens in Chaetopterids, the

respiratory and feeding systems are not coupled. The food material consists of detritus that the animal collects on the bottom, using its proboscis. The proboscis does not correspond to a protrusible pharynx, but to a prostomium, derived from a region anterior to the mouth. The proboscis bears a ventral groove richly supplied with mucus cells and ciliated cells; the food particles entangled in the mucus film are conducted to the mouth by ciliary motion.

The feeding system of *Urechis* species is entirely different. Mucus is secreted by a ring of mucus glands located on the body at a short distance from the mouth; by secreting mucus continuously during its slow retraction into the deeper region of the tube, the animal creates a long and expanded food-collecting funnel, the bottom of which is occupied by the proboscis and the mouth. The distal extremity of the funnel is fastened to the wall of the burrow. By muscular movements of the body, water is pumped into the tube and is filtered on the mucus net. Finally, the mucus net is swallowed by the worm. The pumping periods vary from a few minutes to an hour, with respect to the relative amount of suspended particles in water (McGinitie, 1939, 1945). By experimental feeding with substances of different particle size, it has been calculated that the mesh openings of the mucus net are of about 40 Å in size, as are those of the mucus bag of the polychaete *Chaetopterus*. The mucus net of *Urechis* thus appears to form an efficient straining apparatus (McGinitie, 1945).

B. Hydrogen Ion Concentration of the Digestive Contents

In *Ochetostoma erythrogrammon*, the pH of the gut contents rises from 7.6 in the crop to 8.2 in the mid-gut, and 8.0 in the rectum (Chuang, 1963).

C. Hydrolases

The study of *Ochetostoma erythrogrammon*, a detritus feeder, by Chuang (1963) has added much to our previous limited knowledge on this matter, based on the paper of Gislen (1940) who observed the presence of proteolytic enzymes, amylase, and esterase in the intestinal contents of *Echiurus echiurus*.

Confirming the existence of these hydrolases in *Ochetostoma*, Chuang (1963) showed that they are almost exclusively active in the alkaline zone of the pH scale, with a pH optimum of 7.5 for the esterase, of 8.0 for the amylase and of 8.5 for the protease. These enzymes thus appear to work *in vivo* in the vicinity of their optimum. The activity of amylase is the highest at the level of the foregut and mid-gut, while

protease and esterase are more active in mid- and hind-gut. The proteolytic enzymes are active on gelatin, casein, fibrin and ovalbumin, but not spongin; the esterase splits olive oil as well as benzyl-*n*-butyrate and butyl acetate.

Among carbohydrases, no cellulase, lactase, invertase, or inulinase was found; maltase has been detected, but in small amounts. This lack of carbohydrases, other than amylase and maltase, would probably reduce the ability of *Ochetostoma* to digest the plant detritus constituting its food (Chuang, 1963). It must be stressed, however, that a relatively high cellulolytic activity is recorded from the "gastric juice" and the extracts of gastric walls of *Urechis unicinctus,* when carboxymethyl cellulose is used as substrate (Yokoe and Yasumasu, 1964).

III. Sipunculida

A. Feeding and Nutrition

The sipunculids generally live in shallow water; a few species are found in deep water. Most species burrow in the sediment, but they do not build a tube; some species inhabit holes in rocks or empty shells of mollusks.

The mouth opens at the distal end of the introvert, which bears a crown of ciliated tentacles. The food particles are caught by the tentacles, either in the surrounding water or on the surface of the sediment; they are entangled in the mucus secreted by the tentacles and carried to the mouth. The tentacles having little if any sorting function, the digestive tube is filled with a big mass of sand; the sand often represents a half of the dry weight of the whole animal, in the case of *Sipunculus nudus.*

The anatomy and histology of the digestive tube of *Phascolosoma elongatum* has been described in detail by Stehle (1952, 1953).

B. Hydrolases

Digestion and resorption proceed exclusively in the descending whorls of the digestive tract (Cuénot, 1900; Arvy and Gabe, 1952).

Apart from the histochemical work of Arvy and Gabe (1952) on the digestive tract of *Phascolion strombi,* the digestive enzymes of Sipunculida have been rarely studied.

A low cellulolytic activity has been recorded from extracts of the whole digestive tract of *Physcosoma* sp. (Yokoe and Yasumasu, 1964). The intestinal contents of *Sipunculus nudus* show a definite chitinolytic activity (20–116 μg. hydrolyzed chitin/hour/ml.), while the extracts of the washed gut walls were shown to contain a chitinase (110–125 μg.

hydrolyzed chitin/hour/gm. fresh tissues) and a high amount of chitobiase (7000–11,520 μg. acetylglucosamine liberated/hour/gm.). The equipment of sipunculids thus appears, as far as polysaccharidases are concerned, to be similar to that of sand- and mud-feeding polychaetes and oligochaetes.

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