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Morphology and physiology of digestive epithelia in *Decapod crustaceans*

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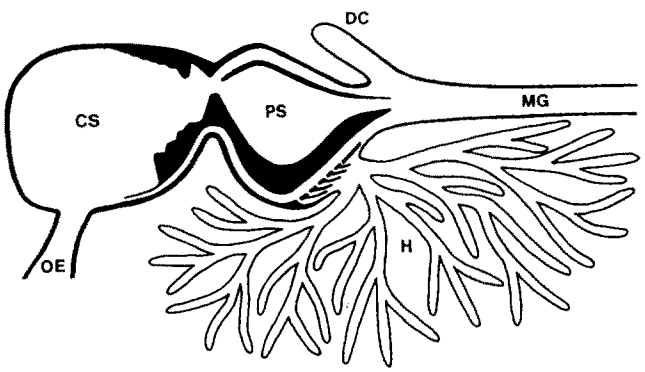
Abstract. The anatomy and cellular composition of the digestive tract of decapod crustaceans is in many aspects considerably different from the vertebrate system. These differences include primarily the gastric mill and a sophisticated filter apparatus in the stomach and the hepatopancreatic tubule system with its bi-directional movement of fluids. Further differences are the lack of a strongly acidic pH and pepsin in the stomach. Consequently, many of the physiological processes are fundamentally different as well, particularly the physical and chemical processing of the feed and the synthesis, storage and mode of action of the digestive enzymes. The hepatopancreas is a central organ of metabolism and includes functions which, in vertebrates, are confined to intestine, liver and pancreas.

Key words. Digestive tract - Decapoda - Stomach - Hepatopancreas - Digestive enzymes - Nutrient absorption - Vitellogenesis - Xenobiotics.

Introduction

The digestive tract of Decapoda is composed of a cuticle-lined foregut (oesophagus and stomach), a cuticle-free midgut with dorsal and ventral caeca (hepatopancreas) and a cuticle-lined hindgut. The hepatopancreas is the most voluminous of these organs and includes a variety of physiological functions. This paper summarizes the morphology and physiology of the digestive epithelia of decapods and emphasizes major differences to digestion in vertebrates. The results are mainly based on my own research on the shrimps *Penaeus monodon*, *Palaemon elegans* and *Troglocaris schmidtii* and the freshwater crayfish *Astacus astacus*.



Schematic diagram of the anterior digestive tract of decapod crustaceans. Thick lines indicate cuticular coated parts. CS: cardiac stomach; DC: dorsal caecum; H: hepatopancreas; MG: midgut; PS: pyloric stomach.

Results and discussion

Morphology and physiology of foregut and hindgut

The cuticle-lined foregut opens anteriorly at the mouthparts and is posteriorly followed by the midgut. The mouthparts hold the feed and tear away smaller pieces. These pieces are then lubricated at the entrance of the oesophagus by a mucus rich in acid mucopolysaccharides which is secreted by subtegumental glands. The oesophagus proper is a short tube and channels the feed into the stomach.

The first chamber of the stomach, the cardia, is armed by a gastric mill composed of solid cuticular teeth [1]. This mill masticates the feed (physical breakdown) and mixes it with the digestive fluid which is always present in the stomach. The digestive fluid contains a variety of proteinases, lipases and carbohydrases as well as fat emulsifiers and is responsible for the chemical breakdown of the feed molecules. In the second chamber of the stomach, the

pylorus, the chymus is filtered through a complicated cuticular filter apparatus. Particles bigger than 50-100 nm are retained by the filter setae and transferred to the midgut for defaecation. The filtrate is transported into the hepatopancreas for absorption of the nutrients.

The hindgut can be short in some species but long in others. It serves for the transport of residual waste material to the exterior and perhaps for ion transport [1].

Morphology and physiology of midgut and hepatopancreas

The midgut includes the midgut tube, the dorsal anterior and posterior midgut caeca and the hepatopancreas. The midgut tube can be long like in penaeids or short like in freshwater crayfish. It consists of a single cell type [1]. Main functions are apparently the formation of the peritrophic membrane which envelops the faeces and water uptake during moulting. The anterior caecum is actually the blindly-ended beginning of the midgut. It includes plenty of mitotic stages and delivers new cells to the midgut tube. The function of the posterior caecum is unclear.

The hepatopancreas is by far the most voluminous organ of the digestive tract and covers intestinal, hepatic and pancreatic functions. It is composed of several hundred blind ending tubules and adjoining collecting ducts which terminate in the antechamber. The antechamber has direct luminal continuity with the pyloric stomach and the midgut. Each hepatopancreas tubule consists of a single-layered epithelium and is enveloped by a close-meshed muscle network. The epithelium includes four cell types, embryonic E-cells at the tips of the tubules and mature R-, F- and B-cells along the tubules. All mature cell types bear a microvillous border and have direct contact to the tubule lumen and the haemolymph [2]. Aged cells are discharged from the epithelium either at the junctions of the tubules with the collecting ducts or in the antechamber.

R-cells cover intestinal and hepatic functions. They are responsible for absorption and catabolism of nutrients and storage of nutrient reserves [2]. The nutrients are internalized from the tubule lumen by molecular transport across the membranes. Carriers are known for glycogen and amino acids. Nutrient absorption is correlated with proliferation of smooth endoplasmic reticulum in the R-cell apex and a high activity of acid phosphatase and unspecific esterases in the same cell region. R-cells can store large amounts of the nutrient reserves glycogen and lipid [2] to provide energy for periods of starvation, moulting or reproduction. An exceptional mode of storage of nutrient reserves was observed in the cave-dwelling shrimp *Troglocaris schmidtii*. In this species parts of the hepatopancreas are converted into large lipid storing chambers [3]. R-cells are further involved in storage excretion of copper from both the haemocyanin metabolism and the environment [4]. Copper is deposited as inert sulfite within subapical lysosomes. It remains in the epithelium until natural discharge of the aged cells. R-cells also deliver lipoprotein particles into the haemolymph particularly during vitellogenesis [2].

F-cells include mainly pancreatic functions. They are the site of synthesis of digestive enzymes as revealed in *Astacus astacus* by immunohistochemistry with antibodies against the proteolytic enzymes astacin [5], trypsin and carboxypeptidase. After synthesis the enzymes are not stored intracellularly as inactive pro-enzymes within zymogen granules like in vertebrates. Instead, they are immediately discharged into the tubule lumen and transported to the cardiac stomach. There they await the next meal in an active form. The enzymes of decapods are well adapted to this unusual mode of storage since they are remarkably stable. F-cells are further involved in detoxification of iron [4] which is deposited within supranuclear lysosomes. Proliferation of the rough endoplasmic reticulum after exposition of shrimp to insecticides indicates also an involvement of F-cells in detoxification of organic xenobiotics.

The main function of B-cells is still obscure. Morphology suggests any degrading function. B-cells may clear the tubule lumen from remnants of digestion inclusive of exhausted digestive enzymes [2].

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