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Anatomy and physiology of digestive tract of Crustaceans Decapods reared in aquaculture.

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Abstract. — *The digestive tract of crustacea is complex. It is composed of a short oesophagum, a stomach with two bags, and internal wall with appendags specialized in grinding of feeds. These hard mastication pieces represent the gastric mill. Setae, filters included in the stomach structure allow the separation between food particles and liquid compounds. Those one are coming over through filters and more on to the digestive gland tubules or mid gut gland. In this organ, several types of cells play specialized functions : absorption, enzymes secretion, stocking function. Some cells of a new type, with undefined function, may be neurosecretions function, have been described recently. The end of tubules of digestive gland exhibits cells with embryonic characteristics. Digestive enzymes of crustacea are diversified : proteases, among which trypsin is the major one, carboxypeptidase, aminopeptidases and a protease of low molecular weight, 11 000, recently thoroughly examined. Enzymes related to lipid metabolism are lipases and esterases. Amylases, maltases, chitinases are well represented.*

Enzyme secretions vary according to factors of external environment. Digestive enzymatic activities are under control of hormones which are about to be checked more in detail.

INTRODUCTION

The digestive tract of some crustaceans decapods has been described with great detail for a very long time; some excellent works have been realized during the last century.

These works are, in their large majority, essentially anatomical, and they have not integrated the fact that they are of a physiological or a zootechnical interest.

With the actual development of the aquaculture of crustaceans, a better knowledge is needed concerning the anatomy and the functions of

the different parts of the digestive tract of the decapod crustaceans, especially those who are candidates to be reared in the future.

The following review is an attempt to clarify the common structures of the digestive tract in the Decapods, and to point out their functions, at the light of some recent researches and new discoveries.

The digestive tract is responsible, for many animals, and crustaceans in particular, for the nutritional function. This function, includes ingestion, transit of nutriments, mechanical digestion, chemical and biochemical hydrolysis, cellular absorption and transfert of excreta, occurs in the digestion tract. This one has several aspects typical of crustaceans. The lumen of digestion tract must be, as in other groups of animals, considered as being located **outside** the animal itself. This concept takes an original connotation for the whole group of crustaceans. This digestive tract has more or less entirely, characteristics of the **tegument** of Arthropoda. The luternal wall of crustacean digestion tract is in fact impregnated, in its fore and hind parts, with complexes of chitin and proteins which are removed at each moult with the exoskeleton.

Another original aspect of crustacean digestive tract relies on the fact that most reserves of the animal are accumulated here. They are utilized at each intermoulting cycle to build up for example, new tissues after ecdysis.

In upper crustaceans groups and particularly in decapods, there exists at the level of stomach walls, a set of hard chewing parts, which are rejected and rebuilt at each moult. Their position and their motility on one part, muscles and nerves which contribute to movements on the other hand, have original characteristics. In fact it is in the stomach that most chewing action on feed particules occurs, and their movements depend on special complex mechanisms.

Even digestive enzymes have their originality, for example special endocrine mechanisms which regulate their synthesis and proteases of low molecules weight. In spite of the diversity in organization schemas of each studied groups, there exists some common structures, at cellular level, which should be considered as characteristics of Crustacea, noticeably, within absorption stocking mechanisms.

Within upper Crustacea, predators and scavengers, sophisticated mechanisms of dilaceration and using calcified parts of stomach, change ingested feeds into very fine food particles. These particles will be selected at filter level which are in several parts of stomach.

Embryogenesis and **organogenesis of digestive** tract studies on organogenesis of the digestive tract of Crustacea are pretty scarce.

During embryogenesis, forgut or stomadeum, and hindgut or protodeum, are differenciated very early during embryo development as in the majority of groups of Crustacea.

Differentiation of digestive **tract during larval** development. After hatching, the digestive tract, very simple at start, becomes complex. Nauplii larvae have, after hatching a non functional digestive tract with a mouth but the **anus** will open after 2 or 3 moults.

This digestive tract is straight and little by little acquires its own movements and enzymatic activities. Its fore part widen into a stomach

sack which differentiates in two side pockets. It is progressively transformed until resembles the tract of the adult. This is true for hard parts which belong to gastric mill and the hepatopancreas.

ANATOMY OF THE DIGESTIVE TRACT
IN HIGHER CRUSTACEANS

General structure

An adult decapod crustacean digestive tube is divided into 3 main parts : fore, mid and hindguts. Generally, the foregut is composed of the oesophagus, and a large part of the stomach where the masticating parts are present. The midgut has no chitin, but contains the many tubuled hepatopancreas which secretes digestive enzymes. The midgut is nearly straight and chitin is present. It is enlarged posteriorly into the rectum and terminates at the anus.

Mouth

The mouth is associated with specialized prehensible appendages, maxillula, maxilla, mandibles and maxillipeds. The anterior part of the mouth is reinforced by a hard labrum. There is a localized rare of glandular tissue present on either side of the mouth, as described in *P. aztecus*, made of large epithelial cells and a clear cytoplasm.

Oesophagus

In decapods, it is usually short, straight, positioned vertically and joining the mouth to the stomach. In cross section, an anterior roll can be seen as an extention of the labrum as well as two lateral rolls. The lumen is in an X shape.

It can be noted in the brachyurans (e.g. the crab *Callinectes sapidus*) that the oesophagus penetrates the antero ventral wall of the cardiac stomach. The anterior part tends to be lateral. The pyloric stomach is suddenly directed downwards, at the cardio pyloric juvenile crabs have also a well developed gastric mill, very similar to the adult. In lobsters factor (1981) clearly illustrated that the first larval stage of *Homarus americanus* does not have median, lateral or accessoring teeth in the stomach walls, although they are rigid setae, folds and septae.

For *Crangon sept.* Reynault (1972) showed that the foregut became more complex coinciding with larval growth with a lamellated stomach, which will form the gastric mill between the pylonic and cardiac zones. As with many Caridians, older stages have a reduced or absent gastric mill.

On the other hand, the Brachyurans, Anoriaurans and the Macrourans, the development of the gastric mill occurs during larval metamorphosis.

For *Palaemon serratus*, at the zoea 2 stage, a pair of symetrical tubules parallel to the tract appears and grows towards the rear. At zoea stage 3,

another smaller pair of symetrical tubules develop laterally and forward. At zoea 4, a new pair of tubules develop posteriorly. At stage zoea 5, the number increases to above 10 tubules. This will continue to increase during the whole grow stages of the larvae juvenile.

The thin integument and tissues of the larvae allows for observation of particle movement in the tract. They come and go between the stomach and the lumen, by the use of constricting waves. If the form tubule branches are in the form of an X, with the stomach in the centre, the particles pass from one tubule to the opposite one. If however, the number of tubules is high, observations become very difficult, even impossible. The system is made even more complex by the qualitative action and quantitative of digestive enzymes function. In the Macrourans *(lobster Homarus americanus)* the oesophagus is more ventral, and the cardium tends to be shorter than for crabs. For the rock lobster *Panulirus argus* the oesophagus is practically vertical and penetrates the cardium more posteriorly than in crabs or crayfish.

Histological studies show that the lumen is covered by cylindrical basal epithelium cells, with clear cytoplasm, with average height 40-60 M. This epithelium is itself recovered by a thin hyaline article composed primarily of chitin. Three types of muscle fibres are present in the connective tissue, enveloping the epithelium. The most internal are dialation, the middle are circular and the outer layers longitudinal. A few rare glandulor elements, comparable to tegumentary glands, are found in the oesophagus.

Stomach

The most important and detailed study of decapod stomachs dates back to over a century ago. Mocquard (1883) described more than 60 species, his observations and illustrations are the basis of all works on this topic, although the stomach of many species have never been examined neither detailed.

Penaeid stomachs are the most elongated among decapod stomachs. The oesophagus is associated with the heart region, where it forms a right angle. The stomach pocket has a narrow floor. The cardiac pocket is well developed anterior to the most forward ossicles. Half the anteroventral pocket is thick and calcifield folded towards the front, the intero-lateral cardiac disk which has on its dorsal side a simple and longitudinal of teeth. The pyloric section of the stomach is bent towards the back following a specific angle.

The most distinguishable characteristic in the stomachs of penaeid prawns is the reduction in the number of identifiable ossicles to 14 for *Penaeus* versus 33 in the Reptantia. They are less calcifield as well (Fig. 1).

— Walls

The stomach is covered, on all its inner surface, by chitin protein coat which is of exodermal origin. This coating does not exist in the endodermally derived intestine. As for the vertebrals, the passage from the oesophagus to the stomach is the cardia and pylore from the stomach to

the intestine. The anterior part of the stomach has thin walls, it is flexible a chamber where ingested food is masticated. The posterior region of the cardiac stomach and the pyloric stomach are reinforced and supported by a number of articulated calcorious pieces, disks and ossicles. There are thick due to a coat of chitin.

The mucosa is similar to that of the oesophagus. The walls are complex with various size lamellae, depending on its location. Threads and needles in the interior of the stomach also vary in size depending on their location. Dorsally, there is a saddle shaped gland, the cells resembling blood cells. This gland is considered as an haematopoetic organ.
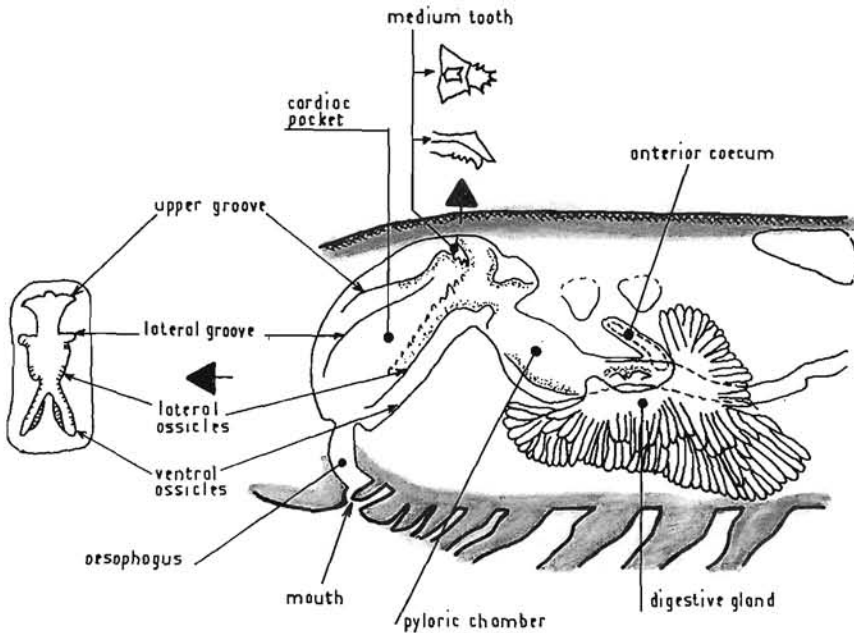

Fig. 1. — Drawing of the stomach of Penaeid crustacean.

— *Mastication parts of the stomach*

Geoffroy (1709) was the first to mention the presence of « dents stomacales » in Crustaces podophtalmaires (Crustacean with stalked eyes). Among the general characteristics of the digestive tract, it has been stated earlier that the anterior and posterior parts are coated with chitin protein material and associated with the exoskeleton, thus they participate in the periodical moults as well. The internal surface of the anterior part of the digestive tract is thus armed with protrusions capable of grinding the food. These projection are sometimes calcified and become skeletal articulated pieces of varying forms. Each piece is moved by individual muscles located outside the wall, and controlled by a group of characteristic nerves. These pieces and folds have group specific forms. Their internal surface are not smooth, and these invagination constitute a complex valvular system, particularly marked in the posterior region of decapod stomachs.

After Geoffroy, these masticating parts were studied by famous anatomists, like Reaumur (1712), Cuvier (1805), Milne-Edwards (1834) and Heckel (1836). The system was well described over the post century. It would seem that the stomach armature can be compared to a three branched claw through which the food must pass to reach the pyloric region (Milne Edwards 1834). On the other hand, Huxley (1857) compares the masticating parts to a mill, and the pyloric region to a filtre. Here, only fine particulate matter can pass and be digested. Thus decapod crustaceans can be considered filterfeeders.

These masticating parts have roles which are quantitatively and qualitatively different, depending on their respective positions. The first fifteen pieces located in the cardiac pocket, is often called the gastric mill. The anterior parts, stronger and more calcified, are ossicles called teeth. The second set of 18 pieces at most smaller and less calcified, participate in the filtering function of the pyloric region.

Many observations have led to recognize that the effectiveness of a stomach is in part due to its complexity. More over, the complexity of the mandibules varies inversely to that of the stomach.

The masticating parts are mobile, and with their respective movements, grind food into a soup of fine particles.

The general shape of the stomach and the position of its masticating parts varies from species to species. It is thus impossible in this context to give detailed descriptions of different species types, remembering also that many decapod species have been little studied in this field. Additionally the number of ossicles varies in decapods. The Brachyuran having much more.

— *Function*

It was thought that, for decapod Crustaceans, digestive liquids from the secretory gland flowed forward along ventral channels, and that digestion took place in the anterior pocket. The secretions, along with the food particles would then be carried towards the rear. They were to be filtered in the ventral section of the stomach, the finest particle and liquid products passing into the hepatopancreas tubules where absorption took place.

It is now believed that the system works differently. Food enters the stomach and moves towards the rear along the dorsal wall of the anterior pocket, then they pass through the gastric mill where they are ground before entering the pyloric pocket. The food is continually worked by lateral outgrowths (teeth and ossicles) and return anteriorly to pass through the system again. The liquid phase flows antero-posteriorly along ventro-lateral sides leading to the principal channels of the pyloric pocket excludes any particles larger than 1ñm of the secretory gland. A filtre is located in the ventral region. These non digestible particles are rejected into the hindgut.

It is possible that chemical digestion begins in the stomach, helping to reduce the size of the particles. Transit time of food products lasts a few second, not exceeding a minute. Food may rapidly pass through the anterior diverticulum located dorsally to the pyloric pocket. Here, enzyme activors may be secreted in the stomach pH modified (Fig. 2).

Decapod crustacean stomachs have varying degrees of complexity. Ossicles and the gastric mill are often absent in Caridians, but are most complex for Brachyurans. There seems to be though compensatory factors : less the stomach contains ossicles more the mandibular appendages are complex.

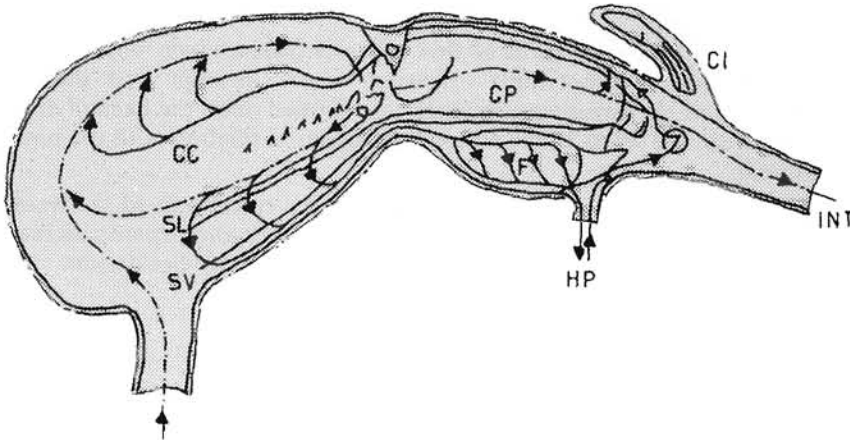These alimentary rejects not digested by internal filters become faeces.

Fig. 2. — Diagram on circulation of digestive fluids in the stomach of Penaeid Crustacean.

Hepatopancreas or midgut gland

The hepatopancreas is considered a major organ in decapods, used in many metabolic functions : synthesis and secretion of digestive enzymes, absorption of digested dietary products, production of mineral reserves and organic substances, lipid and carbohydrates metabolism, role in distribution of stored reserves during the intermoult cycle, catabolism of organic compounds. In most decapods, it forms a pair of glands, occupying on either side of the stomach a large volume inside the cephalothorax. It represents 2-6 % of the total body weight. Each section is composed of 2-3 well distinguished lobes, associated with connective tissue. A network of longitudinal and circular muscles has been described for several species.

Generally, each half of the hepatopancreas opens into the digestive tract via principal ducts. Each duct divides into secondary and then tertiary tributaries until they end in small tubules that constitute the glandular mass.

In Penaeids, the collecting chamber is teardrop shaped and progessively elongates during growth (Nakamura and Yonekura, 1980).

Liquid and digested material exchange between the gland and the midgut occurs either anteriorly, lateraly or ventrolaterally.

The colours of the hepatopancreas is variable — brown, red, green, yellow, blue or tan — and depends mainly on the stored reserves. i-carotene, zeaxanthine and astaxanthine are the pigments present.

Around each hepatopancreatic duct are fine circular and longitudinal fibres, which are responsible for the movement of liquid and cells throughout the organ. Each duct must empty into the stomach the secretions produced by the gland and then fill up with digested material which will be absorbed. These muscular fibres allow for peristaltic and longitudinal movements of each duct, which have lumens of small dimensions.

The detailed innervation of this organ is little known. The crayfish *Cambarus virilis*, haemolymph irrigation occurs through first defined vessels (such as the hepatic artery) then less defined ones, the haemolymph flows between the ducts in the fibroelastic tissue in relation with the basal membrane.

The hepatic artery, after leaving the anteroventral part of the heart, divides into two and takes the haemolymph towards the hepatopancreas, thus being in close relation to the general haemolymph circulation.

Midgut coecae

In addition to the two hepatopancreatic masses, several decapod crustaceans possess coecae of variable length depending on the species. The crab *Cancer* has three elongated tubular coecae, two anterior symetrical ones, the other posterior. The lobster *Homarus* only has one short anterior coecum.

Intestine

The intestine extends all along the abdomen, from the posterior end of the stomach and terminates generally at the anus. The lumen made of secretory cells produces a mucuous substance which coats the non digested products from the stomach, then aiding their movement within the tract. The peritrophic membrane which envelops the excreta is found in nearly all crustaceans. Its synthesis and production cause a loss in the nutritional energetic costs of crustaceans.

Hindgut : rectum and anus

The hingut of decapods is located in the posterior half of the 6th abdominal segment and includes the rectum and anus. There is usually a gland present in this segment, oval shaped, a continuation of the midgut lumen. It is located dorsally and has a folded epithelium. The distal portion of this gland is in continuation with the hindgut.

A particular structure has been described in Penaeids two parallel channels form the hindgut lumen, and join with the rectum, where they come together to form a single channel.

The proximal third of the hindgut lumen is much larger than the last third, and the mucosa forms the internal folds. The rectum has a small

diametre and opens externally at the anus, between the telson and the uropods.

In Penaeids, the hindgut originates at the rectal gland which is dorsally located, and comprises the rectum and anal canal (Fig. 3).
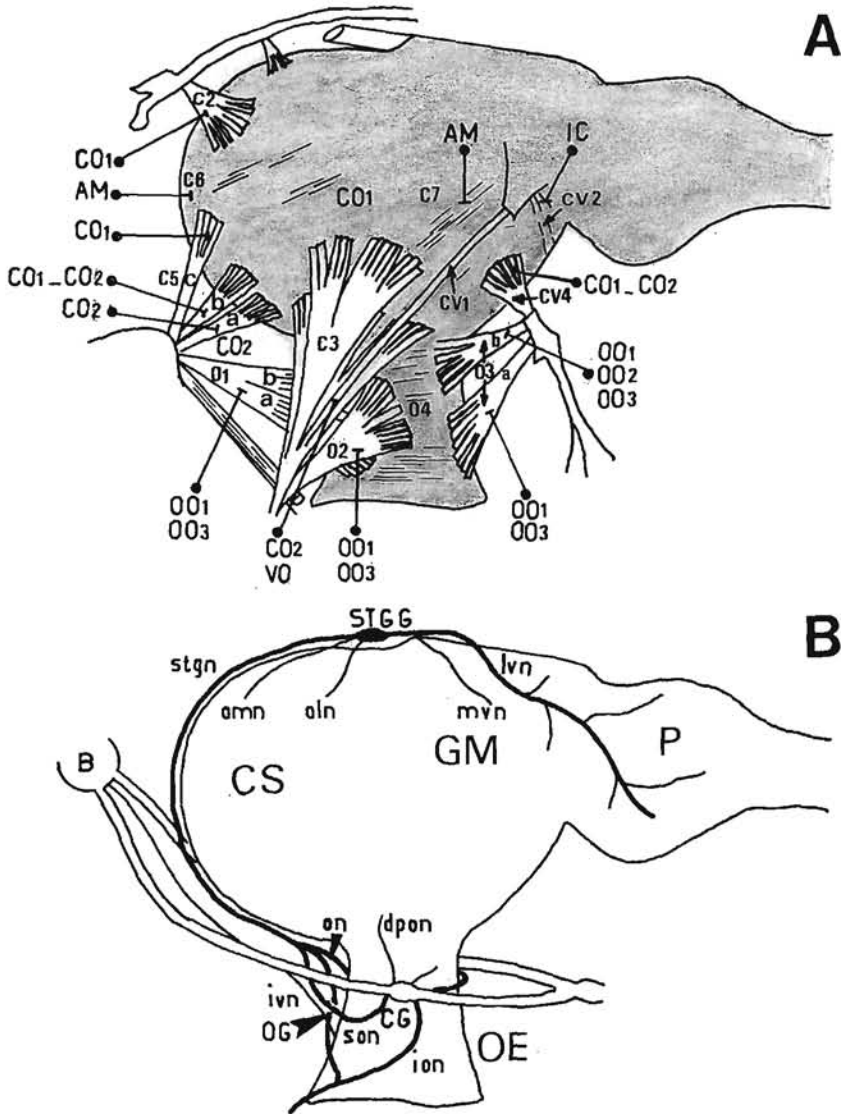

Fig. 3. — Neuromuscular organization of the foregut

A) Lateral view of the foregut with oesophageal and cardiac sac muscles. For each muscle, the motoneurones are indicated.

B) Lateral view of the stomatogastric nervous system. B, brain; CG, commissural ganglion; CS, cardiac sac; GM, gastric mill; OE, oesophagus; OG, oesophageal ganglion; P, pylorus; STGG, stomatogastric ganglion; amn, anterior medical nerve; DPON, dorsal posterior oesophageal nerve; ION, inferior oesophageal nerve; IVN, inferior ventricular nerve; LVN, lateral ventricular nerve; MVN, medical ventricular nerve; ON, oesophageal nerve; SON, superior oesophageal nerve ; STGN, stomatogastric nerve.

MICROSCOPICAL ANATOMY

Oesophagus

The walls are made of an epithelium covered with a 140 μm thick cuticle, itself subdivided in a homogenous exocuticle and an internal horizontally indented, and separated by a strongly PAS positive zone.

For *Scylla serratus* (Barker and Gibson, 1978), this cuticle is covered with fine canals (3 μm diametre), leading to gladular structures of 70-130 μ diametre, their secretions flowing towards the oesophageal lumen.

Their number decreases the stomach, where there are none.

The oesophageal musculative is made of bands of acidophilic circular fibres, 200 μm thick, and longitudinal fibres.

Stomach

The walls histologically resemble those of the oesophagus but the tegumentary glands do not exist and the muscle elements are more massive and differentiated Oka (1967) gave a good description of *Penaeus orientalis* stomach.

Hepatopancreas

The functions of this species variable shapped gland are diverse : absorption, enzyme secretions, storage, etc. It is evident that different types of epithelial cells are present to assure these functions.

The presence of characterized by microvilli cells indicate an absorption function which has been well described in several decapod groups. Secretory glands are also present, characterized by vesicles which rupture in the digestive tract. These two types of cells coexist in the midgut of lower crustaceans. For higher crustaceans, the different types of cells are differentiated at the apex of the hepatopancreas tubules, and their specialization increases towards the base of the tubules.

Classical cell type nomenclature is as follows :

— E cells : embryonic characteristics, apical
— R cells : described by Hirsch and Jacobs (1928, 1930) or Restrellen, which have a storage function;
— F cells or Fibrenzellen, have a fibrous appearence;
— B cells or Blasenzellen, have a secretory function, and contain one or more important secretory vacuoles.

These are confirmed and more detailed by Gibson and Barker (1979).

The E cells of the crab *S. serrata* are 25 μm tall and 5 μm wide. The proximal nucleus has a 4-5 μm diametre. Their apical surface shows no brush border. They are very often in the mitosis phase.

The R cells, of dimension 60 μm X 10 μm, are more abundant, and contain multiple vacuoles, filled with osmiophilic lipids. Their brush border is 1-2 μm tall. Small calcareous deposits and glycogen spheres are

also present. Ultrastructurally, these spheres are less electron dense than other deposits.

The immature R cells located near the apex of the hepatopancreas tubules are clear and of similar size to E cells, with numerous mitochondria apically and a well organized Golgi body basically. Their small nuclei contain less chromatin, and the endoplasmic reticulum (ER) is limited to several zones only. The microvilli are dense and well arranged. The mature cells have lipid droplets and glycogen particles. They are characterized by vacuoles which will progressively form a supranuclear inclusion containing metals such as copper, zinc and sulphur as well as other less abundant ones.

F cells are basophilic, and slightly larger (50-90 μm) than R cells. These cells are found in the central region of the tubules, between the R and B cells. The cells have a fine brush border, and a PAS positive vacuole near the nucleus.

B cells may reach a height of 30 μm and certain a large oval vacuole, with a maximum with of 50 μm. A group of numerous small vacuoles located near the apical surface, just below the brush border, may coalesce with the larger vacuole. Sometimes, entire B cells are found in tubule lumen.

More recently, a new type of cell - M cell - have been described in the hepatopancreas of *P. semisulcatus* (Al-Mohanna and Nott, 1985). They neighbour the base of the tubules, and have a storage function. They are rich in proteins, and are large vacuoles. Their spherical shape and their position differentiates them from the other epithelial cells. Their exitence, appearence and reserves vary throughout an internal cycle.

The association between the various cells have lead to several different interpretations. The most classical being R cells derived from E cells on the one hand, and B cells from E and F cells, on the other. Enzymes may be produced by several types of cells, at least F and B cells.

Crustaceans have different types of digestive secretions, a part from intracellular digestion. In most cases, the secretion is holocrine, that is the entire contents are rejected into the lumen. But merocrine secretions, or continual enzyme production by specialized cells, and apocrine secretions occuring near the apex have also been described.

Midgut and digestive coecae

The cells of the portion of the digestive tract located between the foregut and the rectum, that is between the posterior end of the cephalothorax and the junction of the 5th and 6th abdominal somites, and these of the digestive coecae have been described for *Homarus* and *Cancer* by Mykles (1979). The epithelium is made of simple layer of cubic cells covered with a thick cuticle. The nucleus is basal, and associated with 1-2 nucleoli. Additionally the lateral membranes of adjacent cells are highly interdigitate, which enhances the epithelial cohesion. That cohesion is reinforced by three types of specialized intracellular junctions, the most remarkable being the *macula adherens*, located level with the lateral membranes (separated by 9-10 nm) and have very electron dense material.

The cells possess microvilli and the basal cytoplasm contains numerous mitochondria, and a smooth ER. Elongated vacuoles, called pleomorphic vacuoles, most probably are at the origin of the peritrophic membranes [sone think that this material secretes peritrophic membranes].

At the base, nerve cells are present, possibly neurosecretory in function, haemocytes and other cells with possible endocrine functions.

Water and salts can pass through the epithelium, at rates depending on the stages of the intermoult cycle (Mykles and Thearn, 1978).

Hindgut

The epithelial cells have numerous mitochondria in their apical cytoplasm. It is probable that the epithelium is associated with water and ion transport. Water absorption in this part of the digestive tract helps compact and transfer excretia. This zone plays an important role in osmoregulation of different species, complementing the exchanges occuring in the gills.

DIGESTION PHYSIOLOGY

Mechanical digestion

Crustaceans often choose their prey or food with respect to dissolved substances emitted from these into the water, and detected by chaemoreceptory organs located around the mouth and anterior appendages. Larval stages or planctonic species choose adequate particles with the help of filtres and basket systems located on their anterior appendages.

Chemical digestion

Several digestive enzymes were studied last century (Hoppe-seyler, 1877). Few species however have to be studied in detail using modern techniques. Several proteases have been studied in detail, for Penaeid species, and the crayfish *Astacus* for example.

The carboxypeptidases A and B, and trypsic activity have been studied by gates and Travis (1969, 1973) and by Galgani et al. (1984). For Penaeids, some aminopeptidases and dipeptidases have been identified. Decapods also have a light (11000 molar mass) protease that is very active (Pfleidener et al., 1967; Swilling et al., 1985, Galgani et al., 1985).

In decapods only, a slight collagenolytic activity is detected, in the crab *Uca*, it was studied by Eisen et al., (1973).

Trypsine represents by far the principal proteolytic activity. It is composed of 6 isoenzymes, with a molar mass of 25000 daltons (Galgani et al., 1985). The trypsine sequence has been revealed by Zwilling and Tomaseck (1970) and Titani et al. (1983). It is about 50 % homologous with beef trypsine.

Chymotrypsine is present in small amounts, sometimes absent (Eisen et al., 1973), aminotransferases have been shown to exist in the crab *Carcinius maena* (Chaplin et al., 1967).

Carbohydrates and polysaccharide digesting enzymes exist in all those crustaceans already studied : amylases, saccharases, maltases, laminarinases, chitinases, even cellulases in certain species.

Amylase (endo-i-1, 4- glucanase) is also present. For *Palaemon serratus*, this enzymes molar mass is 50000 (Van Wormhoudt, 1980), and composed of 2-3 isoenzymes, depending on geographic location. This polymorphism can even be greater, *P. elegans* has 7 i *amylase* isoforms. Three glucuronidases (23500, 275000, and 370000) exist in *P. serratus* (Treller and Ceccaldi, 1976).

Cellulose digestion by crustaceans enzymes is not clearly demonstrated except in wood borers like *Limnoria* (Ray and Julian, 1952).

Laminarinases or i-1,3-glucanases digest the storage polysaccharides or laminarines present in algae, fungi and marine protists. This family has been little studied in crustaceans.

Chitinases and chitobiases are present in all these crustaceans studied. For predators, this allows the digestion of pray exoskeletons or their own after ecdysis. A chitobiase of molar mass 110-125000 was studied by Brun and Wojtowicz (1976). These enzymes related to chitin digestion have been studied by Jeuniaux (1963) and Muzzaelli (1977).

Multiple functions oxydases (MFO) and nitroreductases were found in the hepatopancreas of the lobster by Elmamlouk and Gesser (1976).

At last, deoxyribonucleases, ribonucleases of molar mass 33,000; 25,000 respectively and phosphatases have been studied in several species.

But lipases have been little studied. Numerous esterases (ca.20) exist in each species however their specificity needs to be better understood. Lipid digestion and absorption is greatly aided by the presence of emulsifying agents with properties close to those of bile (Holwerda and Vonk, 1973).

The optimal pH for the activation of enzymes varies, but is, in many cases, higher than for vertebrates, and especially for mammals. The values range from 5.5 to 9.

Reserves

Absorption occurs in the cells, cylindrical and elongated, with a brush border. They contain droplets associated with carotenoid pigments, glycogen, calciumphosphate crystals (especially during the period immediately preceeding exuviation). Vacuoles containing irregular copper corpsules are detected with an electronic microscope. Zinc and magnesium are also present (Al. Mohanna and Nott, 1985).

Their content,(the content of these metals) varies along the intermoult stages, reaching their maximum concentration at stages C4-D0. The storage of material and its reuse immediately after exuviation to reconstitute new tissues is a major key in crustacean physiological equilibrium.

BACTERIAL FLORA OF THE DIGESTIVE TRACT

Their importance is very variable from one group to another. Generally, there is no true symbiosis as it occurs in termites for example.

Digestive tract bacteria can be a source of food or vitamins, or perhaps produce themselves digestive enzymes. But, as the food has a very short transit time in the digestive tract (Repper, 1978) such a direct enzymatic role would be rather limited.

WAYS OF USE OF NUTRIENTS

When a crustacean nutritional balance is established, the erse physiological functions undertaken by the animals must be accounted for a part of the ingested food assimilated and used :

— for mechanical energy, e.g. locomotion;
— for reproduction, especially in the biosynthesis ovarian tissue, or of testes;
— for proper growth, e.g. energy used for moulting hepatopancreas reserves, synthesis of muscular tissue, production of exuviae;
— for the synthesis of the peritrophic membrane;
— for osmotic regulation (e.g. chemical energy used for the maintenance of internal balance) and for excretion.

The other part is not assimilated, and is rejected excreta, or sometimes regurgitated after sorting in the gastric mill.

CONTROL OF THE DIGESTIVE FUNCTION

Variation

The mechanisms for digestion adaptation to variations in environmental factors and food characteristics constitutes an important chapter in the ecophysiology and ecobiochemistry of crustaceans (Ceccaldi, 1982, 1986).

Digestive enzymatic activities vary with the time of day and night, following internal circadian rhythms, with two peaks per day, depending on the phases of the intermoult cycle, but also on the phases of vitellogenesis. Larval development stages affect, both qualitatively and quantitatively, digestive enzymes, where amylases are first present in high concentration, then slowly giving way to proteases towards the middle of the larval to life. This is synchronous with changes in their diet.

In adults, food untake induces an increase in digestive enzyme secretion. The affinity of amylase and trypsine for their substrate is based on temperature, this being measured *in vitro*. Maximum affinity corresponds to optimum temperature of the species. Light photoperiod and quality also has an effect on enzyme activity, and also regulates the

circadian clocks. Van Wormhoudt and Malcoste (1976) showed that green wavelength acts as a stimulant whereas red wavelength acts as an inhibitor.

Amylase and protease activity is modulated by the composition of the diet (Lucien Brun et *al.*, 1984). This activity increases with respective increases in glucides or proteins in the diets, either natural or artificial, given to the animals. Above an optimum percentage, around 5-10 % for glucides and 40-50 % for proteins, their activity begins to decrease. Histologically, R- cells do not change shape during the 1-2 h. post-feeding. Then the smooth ER rapidly develops, and the Golgi system becomes very active and produce small multivesicular bodies. After 12 hours, the R- cells loose their hemidesmesomes, the ER becomes smaller, and the cells return to their original shape.

Control

Hepatopancreatic secretions are controlled by hormones. There is a double mechanism in the eye-stalk. A stimulant, of molar mass 500 daltons, containing 20-OH ecdysone is present. An inhibitor must also exist, acting on the Y-organ to inhibit production of ecdysteroids; its activity varies with the seasons and with the intermoult cycle. For *Palaemon serratus*, gastrine cholecystokinine have been found in the eye stalk, near the X, organ (medulla terminalis), the X organ (medulla externa) and the sinus gland. Similar peptides are present in the walls of the stomach (Favrel and Van Wormhoudt, 1986). For *Penaeus japonicus* quantitative and qualitative variations in these peptides have been observed after feeding.

These peptides have a role in the decapod stomach nervous system for example in the lobster, they act on the muscles controlling the rythm of the gastric mill teeth.

CONCLUSION

Zoological knowledge of crustaceans has lead to much research. However, more scientific studies have to be initiated in this field as well as an increase in crustacean physiological and biochemical knowledge (Ceccaldi, 1982). The discoveries and results of these studies will have an important impact in the field of marine biotechnics.

At last, these studies will lead to improvements in aquacultural development, exploitation management, and better understanding of the distribution.

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