STUDIES ON THE COMPARATIVE PHYSIOLOGY OF DIGESTION.

II.—THE MECHANISM OF FEEDING, DIGESTION, AND ASSIMILATION IN Nephrops norvegicus.*

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1. Introduction.

Nephrops norvegicus, the Norway lobster, has been selected as an example for the study of digestion in the Crustacea. It is an animal concerning which surprisingly little appears to have been undertaken, either upon its morphology or on its habits and life history. It is easy to obtain and is, indeed, frequently employed instead of Astacus for examination by junior students. As will be shown later, however, despite external resemblances it differs in many respects from Astacus.

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It is a deep water animal (10 to 60 fathoms usually) and does not readily adapt itself to life in an aquarium, which renders prolonged experimental work somewhat difficult.

The literature on the various aspects of digestion among the Crustacea is so extensive that reference can only be made to the more important papers. Complete bibliographies are to be found in the extensive works of Biedermann and Jordan.¹⁸

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2. Description and Habits of Nephrops norvegicus.

*Nephrops norvegicus* (Leach) belongs to the Class Crustacea, Order Decapoda, Sub-order Reptantia, Section Astacura, Tribe Nephropsidea, and Family Nephropsidae, which includes the three genera Nephrops, Nephropsis, and Homarus.

Living specimens are orange in colour with red and white markings. Storrow,¹⁰ who examined large numbers at North Shields, states that males are found up to 22 cm. in length with an average of 15.6 cm., and females up to 17 cm. with an average of 12.4 cm. M'Intosh²⁴,²⁵,²⁶ also notes the greater size of the males as does Selbie,²⁷ who states that the largest specimen (a male) obtained off the Irish Coast was 24 cm. long, the average length of the males being from 16.5 to 18 cm. and of the females 12 to 14 cm. They have a wide distribution in Northern seas being found in various localities from Iceland (where they form the chief food of the cod) to the Mediterranean, particularly off the coast of Norway,
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in the North Sea, in the Irish Sea, and in the Adriatic. *Nephrops norvegicus* is the only species of its genus found in temperate seas, the only other known species, *Nephrops andamanicus*, occurring in the Indian Ocean at a depth of between 150 and 400 fathoms.

Unlike the common lobster, *Nephrops* never comes inshore. Storrow reports that in the North Sea it is caught mainly between 35 and 42 fathoms and never inside of 33 fathoms, while Selbie says it occurs between 10 and 40 fathoms in the Irish Sea but down to 300 fathoms off the west coast of Ireland (with a maximum recorded depth of 337 fathoms). Specimens have been dredged from between 416 and 450 fathoms off the west of Sicily. Under these circumstances it is not surprising that so little is known of its life history and habits. Calman states that the development is similar to that of *Homarus*, i.e. it is hatched in the Schizopod-stage with natatory exopodites on all the thoracic limbs but with no abdominal appendages, the uropods being the last appendages to be developed. The larvae of *Nephrops* are distinguished, however, by the presence of characteristic long spines on the abdominal somites and telson.

Storrow found that out of 7686 specimens landed at N. Shields only 26.5 per cent. were females, and of these but 5.8 per cent. were berried. The proportions varied, the females being much more numerous in winter although they never exceeded the males; but at this season the percentage of berried specimens was least although, from evidence obtained from animals kept in captivity, it is known that eggs are carried during the winter. Marshall and M'Intosh both note this disproportion in the relative numbers of the sexes. Storrow thinks the females may possibly exceed the males, but that habits of which we have no knowledge lead to the small percentage of females in the catches. Marshall thinks the females migrate farther from land. M'Intosh states that the females may exceed the males if a small trawl is used, but that they escape through the meshes of the larger trawls owing to their small size. Storrow found berried females with young leaving, or ready to leave, the egg from May to September, but particularly in June; while the greatest number
of females carrying recently spawned eggs were found between July and October with the highest percentage in September, so that the period of incubation would appear to be about nine months. From the high percentage of non-berried females found during the winter it is evident that breeding does not occur annually.

The males cast their cuticle chiefly in March and April, while females which have recently cast have been found in every month of the year but especially from June to September, i.e. after hatching of the eggs.

3. Feeding and Mastication.

a. Mouth Parts and Seizure of Food.—The appendages of Nephrops are those of a typical Decapod Crustacean and correspond very closely to those of Astacus, which are well known. It may be noted, however, that in Nephrops the first maxillipede possesses a basipodite which is about three times as long as the coxopodite, the two being about the same size in Astacus; and that in the first maxilla the endopodite is much larger than in Astacus and consists of two pieces instead of one.

Food is seized by the great chelae and passed to the small chelae of the fourth walking legs, or else it is seized directly, either by the latter or by the third pair of walking legs. It is then passed on to the third pair of maxillipeds which lie, bent at the fourth joint and folded upon themselves, covering over the more anterior mouth parts. A row of sharp pointed teeth is borne on the inner surfaces of their long ischiopodites, which are closely applied to one another. The food is gripped firmly between these surfaces and pushed in towards the mouth, the teeth at the same time tearing it up. It is difficult to see what part the remaining maxillipeds and the two maxillae can play beyond passing on the food from the third maxillipeds to the mandibles, as they none of them possess sharp cutting edges or teeth. Herrick, indeed, describing the feeding of the American lobster, states that meat is finely divided by these mouth parts and is passed on to the mouth, after being submitted to the action of the mandibles, in the form of a fine stream of particles. As Jordan points out, this is in
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opposition to the well-established fact that in the Decapods the mandibles play the chief part in mastication. He quotes the evidence of Stamati, who found that flesh was torn into thin strips by the mandibles of *Astacus*. Herrick's account of the movements of various mouth parts is as follows: 

"... the plates of the first pair of maxillæ come together over the lower posterior half of the mandibles. The movements of the masticatory parts of the second maxillæ are synchronous with the beating of the scaphognathite. These project somewhat obliquely over the convex surface of the appendages in front, inward and slightly upward. The large plates of the first maxillipede work up and down, and at the same time inward toward the middle line, describing an ellipse. The second pair of maxillipede move alternately or together, inward and outward, with slight up-and-down movement. The large maxillipede move together, the toothed margins meeting like the edges of a nut-cracker, while the three terminal joints are bent inward and somewhat downward, as in the case of the second maxillipede, so as to meet on the middle line below and hold the food up to the mouth."

The mandibles (fig. 1) lie one on either side of the mouth and largely obscure the opening. Each is attached diagonally by its anterior border (A.M.), the inner end being considerably anterior to the outer end. The inner, or oral, end possesses a semicircular masticatory surface which is divided into two ridges by a longitudinal groove, the outer ridge being provided with a sharp curved cutting edge and projecting over the inner ridge, which is straight and obtusely tuberculated and is continued anteriorly into a process which articulates with the epistoma (E.). A three-jointed palp (P.) is borne on the anterior margin, while a stout tendon is inserted internally into the middle of the posterior margin, providing the connection between it and the large, much branched, mandibular muscle which arises in the dorsolateral wall of the carapace. The contractions of the two muscles pull the mandibles inward and upward, the masticatory surfaces being brought to bear against one another over the mouth and grinding up the food which, at the same time, is pressed into the mouth.
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b. Food.—The only means of forming any idea of the food of *Nephrops* is by an examination of the contents of the gut. The cardiac fore-gut is usually found either partially or completely filled but, owing to the effective masticatory action of the great chelae and mouth parts, it is often difficult or impossible to identify the fragments. As far as can be ascertained these consist chiefly of the following: Torn pieces of muscle, crustacean appendages and parts of carapaces, vertebrae and bones of small fish, hydroid stems, spines, long filamentous strips of algae, and other organic fragments. *Nephrops* may be considered as primarily carnivorous, with a strong preference for animals possessing calcareous shells. If one of several specimens kept in the same tank dies, the survivors immediately proceed to nip off and devour its appendages from the antennæ to the last pleopods, with the exception of the great chelæ and some of the smaller mouth parts. If these animals are examined a day or two later the fore-gut is found full of broken fragments of appendages and the mid-gut and hind-gut filled with a pink coloured mass. With the exception of the algal matter, which may be of considerable length, the largest solid particles are usually about 20 mm. long and 4 mm. wide or roundish masses of some 10 mm. diameter. The grinding action of the “gastric mill” results eventually in the breaking down of these pieces into a fine amorphous powder, the particles of which, by the sifting action of the pyloric fore-gut, are passed into the intestine.


The alimentary canal consists, as in all Arthropods, of three sections, fore-gut, mid-gut (including hepatopancreas), and hind-gut. Of these the first and third are lined throughout with chitin and arise from the embryonic stomodæum and proctodæum respectively. The fore-gut is further subdivided, being composed of an oesophagus, a cardiac fore-gut, and a pyloric fore-gut (using Pearson’s terms), the latter two composing the so-called “stomach”; but, as they do not correspond either anatomically or physiologically to the structures commonly denoted by that term, it is not proposed to describe them as such. Huxley has pointed out that the pyloric fore-gut in
the Crustacea is nearer the heart than the cardiac fore-gut, but these terms have been so extensively employed that it has been considered best to retain them. In an animal 16.25 cm. in length from rostrum to telson, the oesophagus was 1 cm. long, the remaining fore-gut 2.6 cm., the mid-gut 9 cm., and the hind-gut 1.8 cm. The mid-gut in *Nephrops* is the longest portion of the alimentary canal instead of the shortest. Frenzel stated that, with the exception of *Paguristes*, the mid-gut among the Decapods was invariably short, and this view has been largely accepted, although Wallengren has already demonstrated the great length of the mid-gut in *Homarus*, a closely allied genus, whose alimentary system corresponds closely to that of *Nephrops*.

Material was fixed in Bouin's fluid which gave excellent results in the majority of cases. Flemming's solution was used to demonstrate the presence of fat, and corrosive sublimate gave a good fixation of the hepatopancreas, although the best results were obtained by fixing small pieces of the gland in 30 per cent. alcohol containing 5 per cent. of corrosive sublimate and then transferring to higher strengths of alcohol, each of which contained a similar proportion of corrosive sublimate. In order to obtain good sections of heavily chitinised regions such as the oesophagus, the pyloric fore-gut, and the anus, the tissues were decalcified for two days in 70 per cent. alcohol containing 3 per cent. of HNO₃, then softened in a 10 per cent. solution of soft soap in 70 per cent. alcohol for three days, and embedded in paraffin wax in the usual way. The pyloric fore-gut, an extremely heavily chitinised region, was cut without difficulty after this treatment. Sections were stained with Delafield's haematoxylin and erythrosin, with Heidenhain's iron-haematoxylin, and with picric-indigo-carmine or Van Gieson.

*a. Mouth.*—The mouth (fig. 1) consists of a longitudinal opening (M.) situated on the ventral aspect of the head. Normally it lies hidden behind the mandibles (Mn.) and can only be seen clearly after either or both of these have been removed. The chitinous plate immediately anterior to, and on either side of, the mouth is known as the epistoma (E.), and this is raised on its middle posterior margin into a transverse...
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thickened ridge which gives attachment to the labrum (L.) or upper lip. This is a shield-shaped structure which overhangs the anterior half of the mouth and which is continued up the oesophagus as a well-pronounced ridge (fig. 2, L.R.). Posteriorly, the mouth is bounded by a pair of winged membranous projections which lie external to the mandibles and unite in the middle line to form the metastoma (Mt.) or lower lip. This is also continued, but as a low ridge, in the oesophagus, and so are the two lateral lips (L.L.).

b. Oesophagus.—The mouth leads into a short thick oesophagus (fig. 4, O.) which passes almost directly upwards and opens into the capacious cardiac fore-gut from which it is separated by a ring of valvular flaps. In transverse section (fig. 2) the lumen is almost obliterated by the presence of the four longitudinal ridges (L.R., M.R., Lt.R.) which are separated by deep furrows. The labral ridge is much the most prominent of these.

The epithelium (E.) consists of a layer of narrow cells about 60 μ in length, which are bounded externally by a thick layer of chitin 50 μ thick and consisting of two distinct layers, an outer deeply staining layer about 4 μ thick, and a thick hyaline inner layer. Beneath the epithelium is a thick layer of connective tissue (C.T.) composed of a network of reticulate fibres with numerous small nuclei. External to this lies a thick ring of circular muscle fibres (C.M.), the constrictor muscles, and both internal and particularly external to this are

Fig. 1.—Nephrops. Mouth, left mandible and edge of carapace removed. × 2. A.M., line of articulation of mandible; E., epistoma; L., labrum; L.L., lateral lip; M., mouth opening; Mn., mandible; Mt., metastoma; P., palp.
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broad bands of longitudinal muscles (L.M.). There are also fibres which pass across the connective tissue and between the epithelial cells to become attached to the inner surface of the chitin, and are known as the dilator muscles (D.M.). Blood sinuses (B.S.) are present, especially outside the circular muscle layer.

Embedded in the connective tissue just beneath the epithelium lie great numbers of round glands—the tegumental or so-called oesophageal or salivary glands (T.G.). These consist of a rosette of conical cells (fig. 3, G.C.) their narrow ends pointing inward, and each with a large nucleus (N.) near the base. There is a small cavity (C.) in the centre, and this is continued into an intracellular duct (D.) which passes between the epithelial cells and through the chitinous layer to open into...
the lumen. The whole gland is invested by a capsule of connective tissue cells (C.C.). The gland cells are found in three states. They may be vacuolated, or may contain a mass of darkly staining, probably zymogen, granules, which again may be present in a diffused condition throughout the cells, particularly near the base, or as a dark ring round the apex of the cells (as in fig. 3). The first probably represents the resting condition, and the second and third respectively the elaboration and discharge of the glandular secretion.

Concerning the function of these glands little is known. Similar glands have been shown to be present in many Decapods over the entire surface of the body. Those present on the pleopods of the females have been named cement glands by Herrick and others, and considered responsible for the sticky secretion which binds the developing eggs to these appendages. They have been found in the oesophagus in all Decapods that have been examined—notably by Vitzou and Wallengren. They have also been found in the hind-gut of these animals, although Frenzel denies that they are present in the hind-gut of Scyllarus.

The majority of authors have described those present in the oesophagus as salivary glands, although Huet is the only author who advances any physiological evidence; he found that an extract of the oesophagus reduced starch. Other workers have called them intestinal glands, Lang thought they possessed an excretory function, while Herrick considers that, although primarily of a glandular nature, they may have a secondary sensory function, and that their presence in the mouth and oesophagus, which are undoubtedly highly sensitive regions, provides the animal with a sense of taste.

In Nephrops both labrum and metastoma are packed full of
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the glands, which are continued in decreasing numbers along the oesophagus for the proximal two-thirds of its length. They are also present in great numbers in the hind-gut (see fig. 15). An extract of the oesophagus or of the hind-gut gives a strong reduction of starch, but so do extracts of the cardiac fore-gut and the mid-gut, which contain no glands. Moreover, the hepatopancreas discharges a powerful amylolytic enzyme which passes forward into the cardiac fore-gut, and renders any accessory supply of ferment unnecessary. It is difficult to accept Herrick's view that organs of this typically glandular type can have a sensory function. Previous writers who have regarded them as salivary or intestinal glands have overlooked the important fact that in the alimentary canal they are found only in the fore-gut and hind-gut, i.e. always in association with chitin. They have probably nothing whatever to do with digestion, but they may discharge a sticky secretion which entangles the food (although they contain no mucin) or may possibly have some function connected either with the secretion or preservation of the chitinous lining.

c. Cardiac Fore-gut.—The cardiac fore-gut (fig. 4) is a large sac-shaped structure having an average capacity of about 5 c.c., and occupying the greater part of the anterior cephalothoracic cavity. It possesses a thick chitinous lining consisting of two layers, an outer darkly staining layer of an average thickness of 110 μ, and an inner light coloured layer of 10 μ. This is secreted by an epithelium consisting of narrow cells some 55 μ deep. Beneath this there is a layer of connective tissue containing circular and longitudinal muscles. The chitinous lining is calcified in certain regions, thus giving rise to a series of ossicles which serve for support, and also form the masticatory apparatus or gastric mill. The complete series of ossicles present in the fore-gut of the Decapods and the groups of muscles attached to them have been described by Parker,80 Mocquard,87 Albert,1 Williams,43 and others, and no attempt will be made in this paper to do more than describe the mechanism of mastication, Huxley's16 nomenclature being followed.

Extending over the roof of the cardiac fore-gut there is a broad median cardiac ossicle (figs. 4 and 5, C.) to the middle of
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the posterior margin of which is attached a narrow bar, the urocardiac process (U.). This passes backward and downward and its posterior end is strongly calcified forming the brown recurved median tooth (M.T.). Articulating with the dorsal surface of this tooth is the prepyloric ossicle (fig. 5, Pr.P.) which passes forward above the urocardiac process to articulate with the pyloric ossicle (P.), which forms the roof of the anterior region of the pyloric fore-gut. Attached to either side of the posterior margin of the cardiac ossicle is a stout curved rod,

the pterocardiac ossicle (Pt.), while extending from the ventral end of this to the anterior lateral margin of the pyloric ossicle is the zygocardiac ossicle (Z.). Medially, the zygocardiac ossicles are produced into a pair of brown strongly calcified lateral teeth (L.T.) possessing elongated grinding surfaces (fig. 5) characterised by transverse ridges—the whole giving the appearance, as Huxley has aptly observed, of an elephant’s molar.

Two sets of muscles are primarily responsible for the
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working of the gastric mill, a pair of anterior gastric muscles (A.G.M.) which arise in the extreme anterior dorsal region of the cephalothorax, and are inserted in the anterior surface of the cardiac ossicle, and two pairs of posterior gastric muscles (P.G.M.) which arise just anterior to the cervical groove and are inserted in the sides of the pyloric ossicle.

Huxley states that the movement of the gastric mill is brought about by the combined effect of these two sets of muscles, the median tooth being forced downward and forward, the articulation between the prepyloric and pyloric ossicles acting as a hinge, and the two lateral teeth forced inward and forward as a result of the forward pull of the pterocardiac ossicle and backward pull of the pyloric ossicle, which between

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**FIG. 5.—Nephrops. Median view of fore-gut. x 2.** A.P.C., ant. pyloric chamber; C., cardiac ossicle; C.F., cardiac fore-gut; C.P.V., cardio-pyloric valve; D.C., dorsal caecum; D.F., dorsal fold; D.V., dorsal valve; G.F., gland filter; H.P.D., hepatopancreatic duct; L., labrum; L.S., lateral food stream (left side); L.T., lateral tooth; L.V., lateral valve; L.V.V., lower ventral valve; M.G., mid-gut; M.G.F., mid-gut filter; M.T., median tooth; O., oesophagus; P., pyloric ossicle; P.P., post-pectineal ossicle; Pa., pads; Pr., press; Pr.P., prepyloric ossicle; Pt., pterocardiac ossicle; R., ridge of gland filter; U., urocardiac process; V.G., ventral groove; V.V., ventral valve; Z., zygocardiac ossicle.
them force the zygocardiac ossicle into a more horizontal position (fig. 5). The three teeth are thus brought sharply in contact with one another breaking up anything that may be lying between them. Mocquard, however, observed the movements through the transparent carapace of a living *Stenorhyncus*, and states that the movement is produced almost entirely by the movement of the anterior gastric muscles. On the relaxation of the muscles the teeth resume their normal position owing to the elasticity of their joints, and also to the contraction of the cardio-pyloric muscle (C.P.M.), which stretches from the posterior margin of the cardiac ossicle to the upper edge of the prepyloric ossicle.

There are many other series of muscles present, both extrinsic, which serve to dilate the oesophagus and fore-gut, and intrinsic (like the cardio-pyloric muscle), which run between the various ossicles and act as constrictors. All these muscles are innervated by stomatogastric nerve which is formed by the union of two branches, one from each of the oesophageal commissures.

Just beneath the lateral teeth are small teeth, one on either side, and posterior and ventrally pairs of hairy pads (Pa.), which serve to guard the entrance to the pyloric fore-gut. Running along the floor of the cavity, from the opening of the oesophagus to that of the pyloric fore-gut, is a ventral groove (V.G.), supported by a pair of post-pectineal ossicles (P.P.), the entrance being guarded by two rows of stout setæ. It is by means of this groove that communication is maintained between the fore-gut and the hepatopancreas, the hepatopancreatic secretion passing forward, and dissolved matter backward, through this channel. On either side of the groove are lateral pads covered with setæ which incline towards the pyloric opening.

d. Pyloric Fore-gut.—Passing backwards and downwards from the posterior dorsal aspect of the cardiac fore-gut is the curved pyloric fore-gut. Externally its two most prominent features are the dorsal caecum (D.C.), which comes off as a diverticulum from the anterior end of the mid-gut and passes forward over the roof of the pyloric fore-gut, dividing into two portions distally; and two rounded lateral pouches (G.F.)—
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the ampoules pyloriques of Mocquard—which project from the ventral surface, one on either side, and contain the gland filter.

Internally the structure is very complicated and to understand the relations of the various parts reference should be made to fig. 5. It has long been known that this region serves as a filtering apparatus, but Jordan, working on Astacus, was the first to demonstrate the significance of the various parts, and since then Williams has given an excellent description of the anatomy and physiology of the "stomach" of the lobster. The cardio-pyloric opening is almost obliterated by the presence of a massive ventral fold—the cardio-pyloric valve (C.P.V.)—and two smaller dorsal folds (D.F.), all of which are thickly covered with forward directed setae, particularly at the edges. Posteriorly these three surfaces meet (although for purposes of clearness the figures shows them drawn apart), but anterior to this outpouchings of the pyloric wall form an anterior pyloric chamber (A.P.C.). There are three channels along which finely divided particles can pass, a mid-dorsal channel (consisting really of two dorsolateral channels) commencing behind the median tooth and passing between the dorsal folds and named the mid-gut filter (M.G.F.) by Jordan, and two lateral channels (L.S.), one on either side of the cardio-pyloric valve, commencing near the anterior end of the lateral teeth and formed by the longitudinal folding of the outer walls of the pylorus immediately below the anterior pyloric chamber. There are also a pair of ventral channels, one on either side of the base of the cardio-pyloric valve, which form the continuation of the ventral groove, lead into the gland filter (G.F.), and contain the hepatopancreatic secretion together with food matter either in solution or in the form of exceedingly fine particles.

The mid-gut filter runs backward and downward to open into the mid-gut at the base of the dorsal cæcum and on either side of the dorsal valve or Trichter (D.V.), a chitinous projection which runs backward into the mid-gut. The two lateral streams, after passing the cardio-pyloric valve, unite and pass between two muscular plates, this region being termed, by Jordan, the press (Pr.). The chitinous walls of these plates are drawn out posteriorly into lateral valves
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(L.V.), each possessing two terminal teeth; these also pass for a short distance into the mid-gut, although not so far as the dorsal valve.

Ventral to the press lies the gland filter (G.F.). This is a chitinous structure consisting of two semicircular plates (fig. 6),

![Diagram 6](image)

Fig. 6.—Nephrops. Gland filter. × 12. A., anterior; C.P., chitinous plate bearing rods; C.P', chit. plate, under surface; F., free ends of rods showing inward directed setae; L.A., line of attachment of rods to chitinous plate; L.V.V., lower ventral valve; R., ridge; V.V., ventral valve.

![Diagram 7](image)

Fig. 7.—Nephrops. Filter apparatus; I., inner surface; O., outer surface; R., chitinous rods; S., setae.

concave on their dorsal surfaces, which unite in the middle line to form a prominent ridge (R.). This ridge is prolonged posteriorly into a ventral valve (V.V.), and an even longer posterior prolongation of the chitinous plates below forms a lower ventral valve (L.V.V.). Arising along the anterior border, and passing transversely across the surface of the
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Chitinous plates are a series of chitinous rods each of which bears a row of fine setae on its inner edge (fig. 7), the whole forming a most effective filtering apparatus. The rods are attached for the first third (L.A.) of their extent and are then free from the underlying plate; thus, owing to the curved shape of the plates, a section taken through the middle (fig. 8) shows the rods attached to the ridge and also to the outer end of the plates but free between.

The relation between the various structures in this region is shown in fig. 8. The walls of the press are seen to consist of thick pads containing lateral muscles (L.M.), which run from the under surface of the mid-gut filter (M.G.F.) to the upper surface of the filter chamber (G.F.C.). The contractions of these muscles drives the chitinous walls together and forces
the particles of food or faeces backward, possibly at the same time squeezing liquid or fine particles downward through the filter. The mid-gut filter consists of two lateral pouches lying saddle-like over the top of the press, and practically cut off from the cavity of the latter by the close approximation of the chitinous edges lining the entrance. Dorsal to this lies the cavity of the dorsal caecum (D.C.). The filter apparatus lies beneath the press, the ridge (R.) rising in the middle and preventing large particles from passing into the filter chamber. The dorsal walls of the two sickle-shaped filter chambers (G.F.C.)

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secrete a thick semicircular ridge of chitin covered with numerous large setae.

All particles which are not pressed through the filter are forced gradually backward along the mid-gut filter and press and so into the mid-gut, being guided free of the openings of the hepatopancreas by the dorsal, lateral, and lower ventral valves (the ventral valve does not extend so far as the openings, as shown in fig. 9).

Communication is maintained between the ventral groove of the cardiac fore-gut and the hepatopancreas by means of the two ventral channels, one on either side of the cardio-

Fig. 9.—Nephrops. Trans. section at entrance of hepatopancreatic ducts into mid-gut. × 12. D.V., dorsal valve; F., food channel; F.G.E., fore-gut epithelium; G., groove for passage of hepatopancreatic secretion; H.P.D., hepatopancreatic duct; H.P.E., hepatopancreatic epithelium; L.V., lateral valves; L.V.V., lower ventral valve (attached to epithelium); M.G.E., mid-gut epithelium.
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pyloric valve, which pass into the filter chambers, the contained fluid passing over the anterior fixed end of the rods and setæ but having to filter through their posterior free border into channels (fig. 9, G.) which pass backward on either side of the lower ventral valve up to the openings of the two hepatopancreatic ducts. As we have seen, the solid particles in the channel above (F.) are prevented from passing down and blocking the passage by the presence of the valves. Huxley thought these valves were to prevent the regurgitation of food into the fore-gut, while Cuénot thought the Trichter passed the rough particles directly from the fore-gut into the hind-gut in those Decapods where the mid-gut is short, thus preventing injury of the short and delicate mid-gut—a function which it obviously could not fulfil in Nephrops. As will be seen later, the hepatopancreas, besides being a secreting, is also an absorbing, organ, and the presence of the valves and of the beautiful filter apparatus prevents anything but dissolved or exceedingly fine matter from passing into it—a most necessary condition, since the presence of even small particles would suffice to obstruct the fine ducts.

6. Hepatopancreas.—Behind the cardiac fore-gut the greater part of the cavity of the cephalothorax is occupied by the paired hepatopancreas (fig. 4). This is a brown multilobular gland, each half of which is arranged in three main lobes, anterior, posterior, and dorsal, and is made up of a mass of fine blind tubules which open into three chief ducts—one from each of the three main lobes—these in turn uniting in a common hepatopancreatic duct which opens into the anterior end of the mid-gut.

The lobules are surrounded by a thin layer of connective tissue inside which lie the tubules and interstitial cells which form the mass of the gland. In transverse section (fig. 10), each tubule is seen to be composed of the following elements: a surrounding coat or tunica propria (T.P.), a basement membrane (B.M.), an epithelium consisting of two distinct types of cells and varying in height from 20 to 100 μ, and an inner striated border (consisting of the "Stabchen" of Frenzel). The epithelium consists of ferment cells (F.C.) and absorption cells (A.C.) (the liver or fat cells of Weber and earlier
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The former contain small vacuoles and a darkly staining secretion. The secretion may or may not occupy the entire cell, but is invariably present around the large nucleus which contains a prominent nucleolus. After fixation with Carnoy’s fluid the secretion assumes a fibrillar appearance. Particularly near the distal end of the tubules these cells contain large clear vacuoles (C.V.) with a slight granular content near the centre, and these have been described by Schneider, Frenzel, and others as “ripe” ferment cells (Blasenzellen). It must be pointed out, however, that the darkly staining secretion is frequently to be found being discharged into the lumen (see ferment cell on left of fig. 10), and that the clear vacuoles are by no means so common in Nephrops as in Astacus. The absorption cells are more numerous and usually longer than the ferment cells. A small round nucleus without any very prominent nucleolus is situated about the middle of the cells which, when fixed in Flemming’s solution, are found to contain a great number of small fat globules. As will be shown later, there is ample evidence to prove that these cells are absorptive in function.

The tunica propria is a structureless membrane in which lie embedded a network of muscle fibres. Pump has studied

![Diagram of Nephrops transverse section through hepatopancreas.](image-url)
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the nature of the muscle net in the hepatopancreas of the higher Crustacea with great care, and has shown it to be composed of a series of simple or branched circular fibres (Ringfasern), which pass round the tubule parallel to one another, and are connected to each other by longitudinal connections. The longitudinal fibres are of three types, thin unstriated fibres (Bindefaden) which come off at all angles to the circular fibres, broader striated fibres coming off at right-angles to the circular fibres (Bindefasern), and similar fibres coming off at other angles (Spaltfasern). In *Nephrops* all these elements can be distinguished although there is no branching of the circular fibres, and the two types of striated longitudinal fibres are (as is usual) few in number compared with the unstriated fibres.

Triangular blood sinuses (B.S.), containing masses of cells, are present between the tubules. It is easy to demonstrate their nature by the method employed by Jordan and earlier workers. Two c.c. of a saturated solution of ferrous lactate in sea-water are injected into the abdomen of a living animal which is then replaced in water for twenty-four hours. Portions of the hepatopancreas are then removed and fixed in 95 per cent. alcohol containing 5 per cent. of a solution of ammonium sulphide. Paraffin sections are prepared and treated with a 10 per cent. solution of potassium ferrocyanide for ten minutes, with a very dilute solution of HCl for one hour and then with borax carmine. The mass of the sections is stained red, but the cells of the blood sinuses stand out a vivid blue—*i.e.* the iron solution has been caught up in the blood stream and carried into the blood sinuses including those of the hepatopancreas.

The hepatopancreatic ducts do not differ in their structure from the tubules.

*f.* Mid-gut.—The mid-gut runs directly backward through the posterior half of the cephalothorax and the abdomen until it meets the hind-gut, a short distance from the anus. Besides the hepatopancreas, it possesses two diverticula, anteriorly the dorsal caecum which passes over the roof of the pyloric fore-gut, and posteriorly a dorsal diverticulum (fig. 13) which comes off at the junction of the mid-gut and hind-gut, and passes
backwards along the roof of the hind-gut for half its distance, then turns downward, sometimes on the right side, sometimes on the left, to the ventral surface, where it passes forward for a short distance before turning back and ending blindly on the dorsal wall of the hind-gut. Food passes freely into both diverticula which have the same histological structure as the mid-gut, and furnish additional absorptive surfaces.

The mid-gut (fig. 11) is a narrow thin walled tube plentifully supplied with blood-vessels from the abdominal artery. It is lined by epithelial cells about 40 µ deep, and possessing a striated border (S.B.) and elliptical nuclei. Other round, more deeply staining, nuclei (B.C.) surrounded by a thin layer of cytoplasm are also present—usually near the base of the epithelium. These are the basal cells of Frenzel, and in his opinion are young cells which give rise to new cells to replace any that have been destroyed. This is the most probable explanation of their presence. They are frequently to be observed in various stages of division. Frenzel thought that division took place amitotically, and this would certainly seem
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to be the case very often; but in one case a definite mitotic figure (fig. 12) has been observed, although the spindle fibres could not be distinguished.

Beneath the epithelium (E.) lies a thick undulating basement membrane (B.M.), under that a layer of circular muscle fibres (C.M.) about 20 μ thick, and outside that a layer of longitudinal fibres (L.M.) among which lie many blood sinuses (B.S.), the whole being from 60 to 80 μ thick. At both ends of the mid-gut (fig. 9) the epithelium is thrown into a series of longitudinal folds which are continued into the cæcum and into the diverticulum (figs. 8 and 14).

g. Hind-gut.—The hind-gut (fig. 13) is a short stout tube which curves down from the end of the mid-gut to open to the exterior by the anus (A.) which lies on the ventral surface of the telson. Immediately behind its union with the mid-gut it is raised into a well-marked swelling (G.S.), formed by a great accumulation of tegumental glands.

Transverse sections (fig. 14) through the hind-gut show the following structure: The epithelium is raised into a series of six longitudinal ridges (L.R.) bounded by cells (E.) about 55 μ deep which possess basal nuclei and secrete a thin layer of deeply staining chitin (C.). Bundles of longitudinal fibres (L.M.) occur, but only within these longitudinal ridges, and branches can be seen passing from them between the epithelial cells to be inserted into the chitin. The remainder of the ridge is filled in with connective tissue, and contains occasional blood sinuses. Around the whole there is a broad band of circular muscle fibres (C.M.) about 80 μ thick, and outside that
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a thin layer of connective tissue containing blood sinuses and a few longitudinal muscle fibres (O.L.M.).

It will be noted that the arrangement of the circular and longitudinal muscles is different in the mid-gut and hind-gut. The relation between the two regions is most clearly shown in a longitudinal section through their junction (fig. 15). The junction between the two sets of epithelial cells occurs at the base of a forwardly projecting ridge (R.) of the hind-gut. The

thin circular muscle layer (C.M.) of the mid-gut is continued, but becomes greatly enlarged in the hind-gut, while the longitudinal muscles (L.M.) pass over and through the mass of glands (T.G.), which make up the glandular swelling, and are continued as a thin external layer round the hind-gut. The inner longitudinal muscles (I.L.M.) (the section passes through two longitudinal grooves) are seen to arise directly from the chitin of the hind-gut and to pass back as a broad band, with occasional connecting fibres passing between them and the outer muscle layer.

Besides those present in the swelling, tegumental glands
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are found in small numbers in the longitudinal ridges and, owing to their position in the hind region of the gut, it has been suggested that they secrete a substance which binds the faeces together. They are identical with the glands already described in the oesophagus, and there seems little doubt that their function, be what it may, is the same.

![Diagram of Nephrops](image)

**Fig. 15.—Nephrops. Long section through junction of mid-gut and hind-gut. x 52.** C., chitin; C.M., circular muscle; D., lumen of mid-gut diverticulum; E., epithelium of mid-gut; E', epithelium of hind-gut; H.G., lumen of hind-gut; I.L.M., inner long muscles of hind-gut; L.M., long muscles; M.G., lumen of mid-gut; R., ridge at junction of two sections of gut; T.G., tegumental glands.

**h. Anus.—** The anus (fig. 16) is a longitudinal opening on the ventral surface of the telson. It is lined by long epithelial cells which secrete a thin layer of chitin. Beneath the underlying basement membrane are situated a few tegumental glands (T.G.), and bundles of longitudinal muscle fibres (L.M.), which are the continuation of the inner longitudinal fibres of the hind-gut, and become attached to the chitin lining the margin of the aperture as soon as they come in contact with it, i.e. the ventral bundles becoming attached first and the...
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dorsal bundles last. The six longitudinal grooves of the hind-gut give place to an irregular undulation, and at the same time the longitudinal muscles have lost their regular arrangement. The circular muscle layer is absent. Miller states that circular arching fibres are present in the anus of *Cambarus* while longitudinal fibres are absent. This is certainly not the case in *Nephrops*. There are series of radial muscles which stretch between the anus and the dorsal and ventral body walls, being attached to the chitin at each end. There are only a few thin dorsolateral fibres (D.R.M.), but the ventrolateral fibres (V.R.M.) are both numerous and thick. On either side of the anus lie longitudinal areas formed of especially flexible chitin, to which are attached muscles from the anus and, apparently, from the ventral body chitin (M.S.). When the anus is open (as in the figure) these areas are thrown into deep grooves or sulci (S.), owing to the contraction of the various fibres attached to their apices. At
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other times they take the form of shallow troughs. There is nothing in the nature of a sphincter muscle, and the probability is that the anus is opened by the contraction of the radial fibres, which tend to pull out the anal walls and pull up the sulci, the folding of which allows the lips of the anus to come apart. As soon as the muscles relax the natural elasticity of the chitin will cause the lips to come together again and so close the opening.

5. Movement of the Food through the Gut.

Food is pressed into the mouth by the mouth parts and then passed up the oesophagus, and into the cardiac fore-gut by the action of the constrictors and dilators of the oesophagus. It is retained in the cardiac fore-gut by the presence of the valves at the opening of the oesophagus, and it is passed upwards and backwards between the lateral pads towards the gastric mill. This movement is brought about by the action of the muscles of the cardiac fore-gut, and helped by the fact (pointed out by Williams) that the setæ of the cardiac fore-gut all point towards the gastric mill. Mastication takes place and the fragments become mixed with the hepatopancreatic secretion which passes up from the ventral groove. Digested matter and minute fragments are carried back by the same channel into the pylorus where the fluid is strained through the gland filter, liquid and minute particles passing through it and so into the hepatopancreas, while larger particles are carried up into the cavity of the press and finally into the mid-gut. The passage of dissolved matter into the hepatopancreas can be demonstrated by feeding animals on methylene blue or carmine and examining them twenty-four hours later when the interior of the hepatopancreas is found deeply stained. The forcing out of the secretion and taking in of the dissolved matter is brought about by a rhythmical contraction and expansion of the hepatopancreatic tubules. The circular muscle fibres cause contraction, and the relaxation of these together with the contraction of the striped longitudinal fibres cause expansion. Meanwhile, all undissolved particles in the fore-gut are ground up until they become small enough to pass the cardio-pyloric valve by way of the mid-gut filter or lateral
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channels. In the pylorus the action of the press forces them backwards into the mid-gut.

Definite peristaltic and antiperistaltic waves can be detected in the mid-gut, especially after the gut has been excised and placed in a flat dish of sea-water for observation. Owing to the slender character of the longitudinal muscles the movements are not very pronounced, but they are unmistakable and occur both spontaneously and after suitable stimulation. Both Miller and Alexandrowicz have demonstrated the presence of an extensive nerve plexus, somewhat resembling Auerbach's plexus in the vertebrates, in both mid-gut and hind-gut in other Decapods, and it is this, presumably, which controls peristalsis. By this means matter is forced into the hind-gut. Peristaltic movements are much more pronounced in this region. Spontaneous convulsive movements, apparently quite independent of those of the mid-gut, occur more or less periodically, the contractions taking place from three to five times per minute, each one being followed by an opening of the anus. Similar movements can be caused as a result of mechanical or electrical stimulation. These pronounced peristaltic movements are obviously caused by the contraction of the inner longitudinal muscles of the hind-gut, which extend in the longitudinal ridges from the anterior end of the hind-gut to the chitin lining the anal aperture. This will account for their independence of the movements of the mid-gut. Alexandrowicz has noted the independent contraction of the separate longitudinal ridges in Astacus and Palinurus, and also the fact that the presence of a large bolus of faeces stimulates the circular muscles which contract suddenly and drive the mass towards the anus.

The hind-gut is innervated from the last abdominal ganglion (fig. 17) by means of the nervus intestinalis posterior. This divides up into branches to the middle (P.B.) and anterior (A.B.) regions of the hind-gut. There are also a pair of anal nerves (A.N.). These nerves end in the muscle fibres, though neither Miller nor Alexandrowicz were able to determine the exact type of nerve ending. The latter author has described the nerve plexus with great care, and has also recorded the presence of receptor organs consisting of bipolar cells with
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one process passing into the epithelium of the hind-gut and the other coming into connection with the effector nerve plexus. Electrical stimulation of the last abdominal ganglion causes the usual contraction of the hind-gut; but as these movements occur spontaneously long after the nerve has been cut, it may be supposed that the peristaltic movement is partially regulated by, but is not dependent upon, the central nervous system. The movements speedily dispose of the faeces which are passed out through the anus.

6. The Digestive Enzymes.

The ferment cells of the hepatopancreas furnish the digestive enzymes of the Crustacea. Although it is often possible to reduce starch, coagulate calcified milk, and split butyrin by means of extracts from all parts of the alimentary canal in Nephrops, thus revealing the presence, intracellularly, of amylolytic, proteolytic, and lipolytic enzymes, yet there is no evidence that any extracellular enzyme is produced in any part but the hepatopancreas. The secretion makes its way into the cardiac fore-gut and consists of a thick brown fluid containing many fine orange coloured globules, which can be identified in all parts of the gut and are, presumably, droplets of secretion which have not lost the investing membrane within which they were elaborated. The secretion is faintly acid to litmus paper but gives no trace of free acids when tested with Gunzberg's reagent.

Jordan obtained the secretion from living specimens of

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*Astacus* by pushing a glass tube up the oesophagus and drawing off the fluid contained in the cardiac fore-gut. He was thus able to employ the same animals many times. This would be quite possible in the case of *Nephrops* if it could be kept alive as easily as *Astacus*. Unfortunately this is not the case; hence water or glycerine extracts of the hepatopancreas have been employed in order to determine the nature and properties of the enzymes, but the presence of these enzymes in the cardiac fluid has in all cases been confirmed. Hoppe-Seyler was the first to demonstrate the fact that the hepatopancreas of the Crustacea was a digestive organ, and since that time abundant evidence has been brought forward to prove the presence of carbohydrate-, protein-, and fat-splitting enzymes in that organ. Biedermann and Jordan have each given an exhaustive summary of the previous work on this subject, and reference should be made to them for the complete literature; the present account is confined to a description of the enzymes found in *Nephrops*. The glands were ground up with sand and extracts of an average strength of 20 per cent. prepared for experimental purposes. Rigorous controls consisting of boiled extracts were set up. Toluene was employed as an antiseptic and, unless otherwise stated, all digests were incubated at a temperature of 38° C.

*a. The Digestion of Carbohydrates.* — Table I. shows the principal results of a series of experiments on the specificity of the carbohydrate-splitting ferments. Owing to the presence of traces of reducing sugar in the extracts, the results had to be determined quantitatively by means of Benedict’s solution, the reduction of disaccharides being determined by means of Barfoed’s solution. It will be seen that the enzymes digest starch, glycogen, sucrose, maltose, and lactose, but not inulin or raffinose. Starch was digested much better in neutral, than in acid or alkaline, media. There is no trace of a cytase such as Biedermann and Moritz found in *Astacus*; there being not only no sign of any action on pure cellulose (which is never attacked by any cytase), but also no sign of any action on the hemicelluloses which are contained in wood.
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<table>
<thead>
<tr>
<th>Experiment</th>
<th>Time</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. A. 10 c.c. + 10 c.c. 1 per cent. starch medium, neutral</td>
<td>3 hours</td>
<td>Titrated into 10 c.c. Benedict's solution.</td>
</tr>
<tr>
<td>B. ditto, medium, 0.2 N HCl</td>
<td></td>
<td>A. 15.2 c.c.</td>
</tr>
<tr>
<td>C. ditto, medium, 0.2 N Na₂CO₃</td>
<td></td>
<td>B. 33 c.c.</td>
</tr>
<tr>
<td>2. A. 10 c.c. + 10 c.c. 0.5 per cent. glycogen</td>
<td>3 days</td>
<td>C. 40 c.c.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. A. 10 c.c. + 10 c.c. 2 per cent. sucrose</td>
<td>3 days</td>
<td>Titrated into 4 c.c. Benedict.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td>A. 7.1 c.c.</td>
</tr>
<tr>
<td>4. A. 10 c.c. + 10 c.c. 1 per cent. inulin</td>
<td>3 days</td>
<td>B. 15.6 c.c.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. A. 10 c.c. + 10 c.c. 1 per cent. raffinose</td>
<td>3 days</td>
<td>Titrated into 4 c.c. Benedict.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td>A. 5 c.c.</td>
</tr>
<tr>
<td>6. A. 10 c.c. + 10 c.c. 2 per cent. maltose</td>
<td>2 days</td>
<td>B. 16 c.c.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. A. 10 c.c. + 10 c.c. 2 per cent. lactose</td>
<td>4 days</td>
<td>Titrated into 4 c.c. Benedict.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td>A. 16 c.c.</td>
</tr>
<tr>
<td>8. A. 15 c.c. + 1 gm. sawdust</td>
<td>8 days</td>
<td>B. 16 c.c.</td>
</tr>
<tr>
<td>B. ditto, boiled</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Further experiments were carried out in order to determine the optimum temperature and temperature of destruction of the amylolytic enzyme. Preliminary experiments revealed the interesting fact that the optimum temperature was high—at or above 50°C. The following experiment was then set up:

A. 10 c.c. extract + 10 c.c. 2 per cent. starch at 38°C. for 4 hours
B. " " + " " " 42°C. "
C. " " + " " " 46°C. "
D. " " + " " " 50°C. "
E. " " + " " " 54°C. "
F. " " + " " " 58°C. "
G. " " + " " " 62°C. "

At the end of the four hours each digest was boiled, filtered, made up to exactly 20 c.c. again, and titrated.
into 20 c.c. of Benedict's solution, with the following results:

A. needed 7.2 c.c.  E. needed 6.4 c.c.
B. " 7.0 c.c.  F. " 6.4 c.c.
C. " 6.8 c.c.  G. " 7.0 c.c.
D. " 6.6 c.c.

This result is expressed in the form of a graph in fig. 18, and the optimum temperature is seen to lie at about 57° C.

![Fig. 18.—Temperature curve of the amylolytic enzyme.](image)

Preliminary experiments revealed the fact that the temperature of destruction was also high, and the following final experiment was then carried out:

A. 10 c.c. extract at 68° C. for 15 mins.
B. " 70° C. "
C. " 72.5° C. "
D. " 75° C. "
E. " 78° C. "
F. " 81° C. "
G. " 84° C. "
H. " 100° C. "

Ten c.c. of a 1 per cent. starch solution was then added to each and all incubated at 38° C. for two days. They were then boiled, filtered, made up to 20 c.c. each, and

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titrated into 10 c.c. of Benedict's solution, with the following results:

A. needed 5.2 c.c. C. needed 7.6 c.c.
B. " 5.2 c.c. D. " 9.3 c.c.
E, F, G, H, needed about 21 c.c. each.

i.e. the enzyme is destroyed at a temperature of between 76° and 78° C.

These results are remarkable. Nephrops is a cold-blooded animal living in comparatively deep water, where the temperature is never very high, and yet the optimum temperature for the action of the amylolytic enzyme is considerably higher than that of the hot-blooded mammals which live in a much warmer environment. The optimum temperature of the amylolytic enzyme present in the crystalline style of Mya arenaria was shown in a previous paper (Yonge 1) to lie at 32° C. and the temperature of destruction at 51° C., and yet Mya is a shore dwelling animal living under distinctly warmer conditions than Nephrops.

b. The Digestion of Fat.—The presence of a fat-splitting enzyme has been demonstrated in a variety of ways. An emulsion of olive oil is split up, the presence of oleic acid being detected by titrating in N/10 NaOH, phenolphthalein being used as indicator. Boiled milk, to which phenol red has been added, and which has been rendered alkaline with 4 c.c. of N/10 Na₂CO₃, is turned yellow within eighteen hours through the enzyme converting the butyrin into butyric acid. The following esters have also been split up by the hepatopancreatic secretion: methyl acetate, amyl acetate, butyl acetate, and ethyl acetate. The range of action of this enzyme is apparently very wide.

c. The Digestion of Protein.—A powerful proteolytic enzyme is present in the secretion. This works best in alkaline media, slightly in neutral, and is practically inhibited in acid media. Krukenberg (quoted by Biedermann 4) maintained that there are two proteolytic enzymes, a "tryp tic" one and a "peptic" one, but there is no evidence for the presence of the latter. Fibrin is readily dissolved by the extract after it has been made alkaline with Na₂CO₃. After four days' incubation
at 38°C, the digest was acidified with acetic acid which gave a slight precipitation of undigested globulin matter. The precipitate was then filtered off and the following tests applied to the filtrate: biuret reaction, almost negative; Millon's reagent, deep red coloration; bromine water, deep pink coloration—i.e. albuminoses are almost absent but the amino-acids tryptophane and tyrosin are present in large quantities. After the remaining filtrate had been evaporated almost to dryness leucin crystallised out in the form of round masses.

The extract also digested casein and peptone with the same production of amino-acids, and coagulated calcified milk.

In order to determine the optimum degree of alkalinity, digests were set up in media possessing varying degrees of alkalinity, each containing 0.5 gm. of fibrin. A control was set up in each medium. After two days' incubation at 38°C, the digests were boiled, filtered, and all made up to the same volume. The amino-acids which had been formed were then estimated by Sörensen's method, 20 c.c. of 10 per cent. neutral formaldehyde being added to each, and the acidity estimated by titrating in N/10 Na₂CO₃, phenolphthalein being employed as the indicator. The figures obtained from the control experiments were deducted from the figures obtained from the corresponding experiments, in order to obtain the quantities of amino-acids formed. The results were as follows: neutral, 4.7 c.c.; N/80 Na₂CO₃, 6.1 c.c.; N/40 Na₂CO₃, 5.8 c.c.; N/25 Na₂CO₃, 6.1 c.c.; N/20 Na₂CO₃, 7.5 c.c.; N/10 Na₂CO₃, 7.5 c.c. These results agree with those of Roaf, who found that in Carcinus the optimum lay in a medium of N/20 Na₂CO₃.

d. Other Enzymes.—Giaja has demonstrated the presence of enzymes hydrolysing glucosides among the Decapod Crustacea. He worked on Astacus, Portunus, Maja, Platy-carcinus, Homarus, Palinurus, and Carcinus, and found that the hepatopancreatic secretion from these animals digested amygdalin, salicin, arbutin, coniferin, and phloridzin, with the exceptions that the secretion of Palinurus did not digest salicin, and that of Portunus, Maja, and Platy-carcinus did not digest phloridzin. Extracts from the hepatopancreas of Nephrops were incubated with 2 per cent. solutions of salicin.
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and amygdalin for ten days. It was found that salicin was not digested, but that amygdalin was split up with a formation of glucose and hydrocyanic acid. It seems highly improbable that this digestive power can be of any use to the animal.

e. Other Functions of the Hepatopancreas.—Assimilation and storage in the hepatopancreas will be considered in later sections; but other functions have been ascribed to this organ, and a short reference to these will not be out of place. Weber considered that the hepatopancreas secreted bile, but Hoppe-Seyler has shown that there is no trace of bile constituents throughout the Invertebrates. The usual tests for bile salts and pigments all give negative results when applied to the hepatopancreas of Nephrops. The brown pigment which is present can be extracted with absolute alcohol or ether, and Newbigin, who worked on Nephrops, amongst other Crustacea, found that this pigment gave none of the reactions of a lipochrome. This has been confirmed and the pigment is apparently a lutein with no trace of the red lipochrome, tetronerythrin, found in the shell, although this is probably formed from it.*

Cuénot considered that the gland possessed the three additional functions of excretion, elimination, and regulation. That foreign matter injected into the abdomen of a Decapod is passed into the gut by way of the ferment cells of the hepatopancreas has been known for a considerable time. This can most easily be demonstrated by injecting methylene blue into the abdomen and examining the animal after a day. The fore-gut and mid-gut are found full of the pigment and the hepatopancreas stained a deep blue. Fragments of the gland examined in glycerine show that the pigment has been taken up in discrete round globules, which correspond in number and size to the ferment cells, which cells can easily be distinguished as deeply staining masses after whole tubules have been stained with Delafield's hematoxylin. Moreover, after injecting iron lactate and proceeding as described in a previous section, iron was detected in the ferment cells as well.

* For a full account of these pigments, see J. R. Fulton (1922), "Animal Chlorophyll . . ." Q.J.M.S., 66.
as in the blood sinuses. Jordan, who has investigated this matter very carefully, has shown that the presence of iron in these cells can be demonstrated up to thirty-six days after injection. He points out, however, that, since the taking up of foreign matter is performed by glandular secreting cells, this cannot be considered a primary function of the gland. Moreover, he considers the amount which is "excreted" too small to be of any practical advantage, while a proportion of what is passed into the lumen of the gland is reabsorbed by the absorption cells, so that the process cannot even be considered an accessory function, but only, like the occasional presence of constituents of urine and other foreign matter in the milk of mammals, as an "accessory appearance" (Nebenerscheinung).

Cuénot and Guieysse (quoted by Jordan) thought that the hepatopancreas possessed the power of eliminating toxic products by arresting their passage and fixing them in the gland cells where they were inoffensive. The former found that out of a series of pigments on which they had been fed, only Bismark brown in the case of *Astacus*, and methyl green in the case of *Carcinus* were ever found in the blood-stream, the remainder being "arrested" by the hepatopancreas. Although a large number of pigments were injected into the fore-gut of *Nephrops* none were ever identified in the blood, though all were found in the lumen of the hepatopancreas. Jordan considers that the rejection or taking up of various substances depends rather on the nature of the substances. Thus, the same cells which take up iron readily will absorb no copper, although the latter has been shown to be the more abundant in the blood and is far from toxic. Assimilated material is held back by the hepatopancreas but only because it serves as a store of reserve food material.

Cuénot also considered that the hepatopancreas regulated the composition of the blood. He states that small quantities of injected colouring matter were excreted by the antennary gland, but that if the same amount was diluted to three times its bulk a certain amount was abstracted by the hepatopancreas, passing through by osmosis without staining the cells. Similar experiments were performed on *Nephrops* but
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the results were negative, no sign of any coloration in the lumen of the gland being detected. In any case the experiment is hardly a satisfactory proof of what may quite possibly form one of the functions of the gland.

7. Assimilation.

a. Absorption.—Two methods of experimental feeding have been employed in order to determine where assimilation is performed. In either case animals were starved for three or four days previously in order to empty the gut, and then either olive oil or a 2 per cent. solution of ferrous lactate or ferrum oxydatum saccharatum was injected into the cardiac fore-gut by means of a pipette. The animals were left for from one to three days and then removed from water and the tissues fixed; those fed with olive oil with Flemming's solution, and those fed with the iron solutions with 95 per cent. alcohol containing 5 per cent. ammonium sulphide. It is useless employing the former method to test for assimilation in the hepatopancreas owing to the great amount of fat already present, an amount which in Jordan's experiments it took three weeks of starvation to remove from the hepatopancreas of Astacus. On the other hand, Flemming's solution gives the better fixation, so the oil method was employed to determine absorption in the gut and the iron method in the hepatopancreas.

No trace of any absorption by the cells lining the fore-gut and hind-gut was found. The cells of the mid-gut (including those of the dorsal cæcum and the diverticulum) showed the presence of minute, darkly staining fat-globules, which began just beneath the striated border and were found throughout the cells. They were never found actually in the striated border. Murlin has described the process of fat ingestion in the mid-gut of the terrestrial Isopods, ideal Crustaceans for the purpose. He can find no trace of fat either in the striated border or the basement membrane, and considers that it is split up into glycerol and fatty acid in order to pass through these membranes and is not, as is often maintained, reduced to a fine emulsion and passed through in that form. Cuénot and Jordan both found that the mid-gut of the Decapods
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absorbs fat, and both considered that this region is specialised for fat absorption. There seems no reason to assume this, but what is undoubtedly true is that food which is easily soluble is passed immediately from the fore-gut into the hepatopancreas, and only less soluble substances, such as fat, which is not quickly split up, pass into the mid-gut, the contents of which usually consist of a fine amorphous powder containing little fluid.

Sections of the hepatopancreas of an animal fed for three days on an iron solution and prepared in the usual way reveal the presence of a great deal of iron in the lumen of the tubules, and also as round masses lying in small vacuoles in the absorption (never the ferment) cells. Jordan found exactly the same condition in *Astacus*.

In the majority of Decapods, such as *Astacus*, in which the mid-gut is extremely small the hepatopancreas is by far the most important organ of assimilation; while in *Nephrops*, although it does not supply so large a proportion of the assimilative surface, yet, owing to the structure and functioning of the pyloric fore-gut, the greater part of the soluble products of digestion are passed into it, and not into the mid-gut. It is certainly the most important organ of assimilation throughout the Decapods.

b. Permeability of the Gut.—The question of the permeability of the gut has been investigated, the methods of Jordan and Lam being employed. The fore-gut and mid-gut were excised from living animals and carefully washed out with sea-water introduced by means of an injection syringe. They were then ligatured with cotton thread at one end (in the case of the fore-gut round the cardio-pyloric valve) and then filled with a series of solutions, coloured red with carmine, in order to detect any escape of liquid. The other end was then ligatured (round the oesophagus in the case of the fore-gut) and the whole placed in a small glass dish containing liquid of a known composition.

Table II. shows the results of six experiments on the fore-gut. In the first two the fluid contained in the fore-gut and the surrounding liquid were isotonic, in the third and fourth the fluid in the fore-gut was hypertonic to the surrounding
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fluid, and in the last two it was hypotonic. The weights of the fore-guts (previously carefully dried on filter papers) were taken before and after immersion in the dish of fluid. The experiments were all maintained for twenty hours. Comparison between the two columns of weights shows that there was practically no difference in weight when the solutions were isotonic, an average gain of 8.2 per cent. when the contained fluid was hypertonic, and an average loss of 9.8 per cent. when it was hypotonic.

TABLE II.

<table>
<thead>
<tr>
<th>Concentration of Solution.</th>
<th>Inside Fore-gut</th>
<th>Outside Fore-gut</th>
<th>1st Weight in Grams</th>
<th>2nd Weight in Grams</th>
<th>Difference in Weights</th>
<th>Absolute</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea-water</td>
<td>Sea-water</td>
<td>5.353</td>
<td>5.355</td>
<td>+ 0.002</td>
<td>+ 0.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>3.94</td>
<td>3.900</td>
<td>+ 0.02</td>
<td>+ 0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea-water</td>
<td>60 % sea-water</td>
<td>6.272</td>
<td>6.750</td>
<td>+ 0.478</td>
<td>+ 7.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>5.632</td>
<td>6.130</td>
<td>+ 0.498</td>
<td>+ 8.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>60 % sea-water</td>
<td>Sea-water</td>
<td>4.296</td>
<td>3.820</td>
<td>- 0.476</td>
<td>- 11.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>4.725</td>
<td>4.323</td>
<td>- 0.402</td>
<td>- 8.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The results of other experiments in which solutions of glucose in various concentrations of sea-water were contained in the fore-gut which was immersed in ordinary sea-water and again under the reverse conditions, the sea-water (whether it was within or without) being tested with Fehling's solution after twenty-four hours, prove that there is no transference of glucose in either direction, even though the solution containing it is considerably hypotonic to sea-water.

The fore-gut is semi-permeable. It allows water to pass in or out according to the laws of osmosis until an isotonic condition has been established between the contained and surrounding fluids, but it will not allow dissolved substances to pass through it. The same results are recorded by Jordan and Lam for both the fore-gut and hind-gut of Astacus. The hind-gut of Nephrops is too small for satisfactory experiments to be performed upon it, but there is no reason to doubt that it would behave in the same way as the fore-gut, or as the hind-gut of Astacus.

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A different state of affairs is found in the mid-gut. Table III. shows the results of a similar series of experiments to those performed on the fore-gut, the duration being the same. The mid-gut does not behave as a semi-permeable membrane. There was an average loss in weight of 10 per cent. when the two fluids were isotonic, one of 6.5 per cent.

![Table III.](image)

when the contained fluid was hypertonic, and one of 30.7 per cent. when it was hypotonic. In one experiment (No. 4) when the contained fluid was hypertonic there was a gain in weight of 4 per cent. A series of confirmatory experiments were carried out in which the contained fluid was again hypertonic, and in these the weight was taken after four hours and again after twenty-one hours. Table IV. shows the results of these experiments. After four hours two of the three showed an increase in weight, but after twenty-one hours only one of them, and that much reduced.

![Table IV.](image)
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Jordan and Lam found that the mid-gut of *Helix*, a non-absorbing organ, behaved as a semi-permeable membrane under these conditions, and Bottazzi and Enriques (quoted by them) found the same conditions in the mid-gut of *Aphysia*. The mid-gut of *Nephrops*, however, is an absorbing organ and this accounts for its behaviour. Where the two fluids are isotonic the physiological action of the absorbing cells which line the gut causes fluid to pass out of the gut, and where the contained fluid is hypotonic the action of the cells is helped by osmosis, the fall in weight being very pronounced. Where the contained fluid is hypertonic, however, the physiological action of the absorbing epithelium may be temporarily overcome by the opposing osmotic pressure; but, after some degree of osmotic equilibrium has been established, the former regains the upper hand and liquid begins to flow out of the gut. If a number of mid-guts are filled with solutions of glucose, isotonic, hypertonic, or hypotonic to the sea-water in which the guts are placed, in all cases the presence of glucose can be detected within a few hours in the surrounding sea-water, and the reverse has also been found to be the case. Jordan and Lam found that glucose diffused in either direction through the non-absorbing gut of *Helix*, but they state that an absorbing gut is always characterised by a definite polarity, dissolved substances passing outward but never inward. In spite of repeated experiments, in some of which the surrounding fluid which contained the glucose had an osmotic pressure of twice that of the contained sea-water, in all cases definite signs of the presence of glucose within the gut were detected within three hours. These results are practically the same, however, as Cohnheim obtained when working on the gut of the Holothurians. He found that dissolved salts passed in and out of the gut according to the laws of osmosis and independent of the cell activity, but that sea-water always passed through by physiological absorption, *i.e.* in the one direction only. A similar state of affairs would appear to exist in the mid-gut of *Nephrops*, since on those occasions in which the glucose appeared to pass inwards against osmotic pressure it has to be remembered that the physiological activity of the cells, assisted by osmotic pressure, would very soon reduce the
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osmotic pressure within the gut to the same or a lower level than that of the surrounding fluid. Enriques (quoted by Jordan and Lam) has criticised Cohnheim’s experiments on the ground that he used solutions of too high osmotic pressure and kept the experiments up too long (forty-eight hours); but neither of these criticisms can be applied to the present experiments on *Nephrops*.

The conclusions which may be drawn from the above experiments are that the fore-gut (and probably the hind-gut) are semi-permeable membranes, but that the mid-gut is an absorbing membrane and contained fluid is passed out even against the action of osmosis, although osmotic pressure beyond a certain strength will temporarily overcome it. Dissolved substances can diffuse freely in and out of the gut, but normally they will be carried through in the fluid which is passed out by the absorbing epithelium, and so pass into the blood-stream and get carried away from the gut.


The hepatopancreas is the principal storage organ for reserve food but the quantities present are intimately bound up with ecdysis, so that if quantitative estimations are to be of any value they must be made at all stages of growth, before, during, and after moulting, and the results compared. Though it has not been possible to keep *Nephrops* and make these comparative estimations yet this has already been done for so many Decapods, and the whole matter so satisfactorily worked out, that no new observations are really necessary. In *Nephrops*, glycogen is present in the hepatopancreas in great quantities, in lumps beneath the epidermis, and it has also been detected in the connective tissue round the gut and in the ovaries. C. Bernard first showed the intimate relationship between the glycogenic content of the hepatopancreas and ecdysis. He found that in the crayfish glycogen begins to be accumulated in the hepatopancreas twenty to twenty-five days before moulting, and continues to increase up to the time of moulting when it rapidly declines in amount. Kirch found that in the same animal the maximum glycogenic content (0.82 per cent. of the body weight) occurs actually at the time
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of moulting, but that four months earlier the content is only 0.08 per cent., which rises to 0.4 per cent. shortly before the moult. He found the same conditions in Carcinus, Platy-
carcinus, and Maja. At the time of moulting the glycogen is
transferred by the blood-stream to the epidermis where it is
employed to build up the new carapace. Kirch found that
glycogen was most abundant near the blind end of the
hepatopancreatic tubules, and that it was present in both
absorption and ferment cells. Smith found that the presence
of Sacculina in Carcinus depressed the glycogenic function by
making no demand for glycogen, but an excessive demand for
fat, the result being that no moulting occurred; just as
prolonged starvation, by causing the transference of glycogen
from the epidermis to the hepatopancreas, inhibits ecdysis.

Ether extracts obtained by means of a Soxhlet apparatus
show the following fat content for the wet drained tissues of
Nephrops: Hepatopancreas, 6.975 per cent.; muscle, 0.36
per cent.; gonad ♀, 14.945 per cent.; gonad ♂, 0.857 per
cent. The hepatopancreas and ovary contain traces of
lecithin. Paul and Sharpe, working on Carcinus, have
shown that the total weight of fat in the hepatopancreas
increases both in total quantity and relatively to the weight of
the body and hepatopancreas as the animal approaches the
mouling period. At the same time the quantity of lecithin
is reduced in proportion, they think, as cell proliferation
advances and the nuclei, though not the cell bodies, become
larger, the probability being that some or all of the phospho-
lipins of the nucleoprotein molecule is derived from this
source. They find that immediately after moulting the fat
content of the hepatopancreas drops to 25 per cent. of what
it had been. Smith found that the presence of Sacculina
caused an increase of 35 per cent. in the fat content of the
hepatopancreas.

There may also be a reserve of calcium, in the form of
calium phosphate, in the gland. Paul and Sharpe found that
in Cancer this is present to the extent of 23 per cent. of the
dried weight of the gland at the time of moulting, but that
immediately afterwards it drops to practically nothing. They
found a small storage in Lithodes, but none in Homarus.
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Estimations of the calcium phosphate present in the hepato-pancreas of *Nephrops* reveal a similar absence of any storage. No cholesterol has been found in *Nephrops* although it has been found in many Decapods. Traces of tryptophane, leucin, and reducing sugars have been detected in the gland.


1. *Nephrops norvegicus* is a marine Decapod Crustacean living at a depth of between 10 and 60 fathoms and never coming inshore.

2. It lives principally upon a calcareous and carnivorous diet. Food is seized by the great chelae or second and third walking legs and passed to the third maxillipeds, which grip and tear it with their teeth and transfer it to the preceding mouth parts. It finally passes to the mandibles which grind it up still finer, and pass it into the mouth.

3. The alimentary system consists of a chitinous fore-gut, comprising an oesophagus, a cardiac fore-gut, and a pyloric fore-gut, a mid-gut which is the longest part of the gut and possesses three outpouchings—the dorsal cæcum, the posterior diverticulum, and the hepato-pancreas which opens by a pair of lateral ducts into its anterior end—and a chitinous hind-gut which opens to the exterior at the anus.

4. Tegumental glands are found in great numbers in the mouth region, the oesophagus, and the hind-gut. There is no physiological evidence to show that they possess any digestive function; they may possibly discharge a sticky secretion or be correlated with the presence of chitin in these regions.

5. The cardiac fore-gut consists of a spherical bag strengthened by calcified ossicles, a number of which form the gastric mill, a masticatory apparatus consisting of three teeth and worked by the gastric muscles.

6. The pyloric fore-gut is separated from the cardiac fore-gut by the cardio-pyloric valve. Finely divided particles pass into it by the mid-gut filter, and by the two lateral channels. Behind the valve the walls of the pyloric fore-gut are thickened to form the press and beneath this lies the gland filter, consisting of two chitinous plates, uniting in the middle line to form a ridge, and bearing transverse chitinous rods each of which is
set with a row of setæ on its inner side. Five chitinous valves pass backward into the mid-gut.

7. The hepatopancreatic secretion passes directly into the cardiac fore-gut by way of the gland filter and two ventral channels, one on either side of the cardio-pyloric valve, which open into a ventral groove in the cardiac fore-gut. Material dissolved by the secretion is passed back by the same route, being strained through the gland filter before entering the hepatopancreas.

8. The epithelium of the hepatopancreas is composed of glandular ferment cells and absorption cells which contain a mass of fat globules. The tubules are surrounded by a network of circular and longitudinal muscle fibres.

9. The mid-gut possesses a circular muscle coat and outside that a longitudinal one, but the hind-gut also possesses inner longitudinal fibres, which run within the six longitudinal ridges into which the hind-gut epithelium is raised.

10. The anus is a longitudinal slit on the under side of the telson. It possesses no sphincter but a series of radial muscles which pass to the dorsal and particularly the ventral body chitin.

11. Food is forced into the cardiac fore-gut by the action of the constrictor and dilator muscles of the oesophagus. There it is either ground up by the gastric mill and passed into the mid-gut, or dissolved by the digestive juices and passed into the hepatopancreas, the expansions and contractions of which are brought about by its muscular network. Peristaltic action forces particles backward in the mid-gut, and pronounced peristaltic contractions, due to the action of the inner longitudinal muscles, force it out of the hind-gut, the anus opening by a contraction of the radial fibres.

12. The hind-gut is innervated from the last abdominal ganglion by the nervus intestinalis posterior, which probably regulates the peristaltic movements.

13. The hepatopancreas secretes the digestive enzymes. Starch, glycogen, sucrose, maltose, and lactose are digested, the amylolytic ferment finding its optimum in a neutral medium and at a temperature of 57° C., being destroyed between 76° and 78° C. Fat and esters are split up; and protein is digested, especially in alkaline media, with the formation of amino-acids.
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14. There is no bile, but a brown lutein pigment is present in the hepatopancreas. The accessory functions of excretion, elimination, and regulation are all of doubtful occurrence.

15. Absorption is carried on by the mid-gut and its appendages, and by the absorption cells of the hepatopancreas.

16. The fore-gut (and probably the hind-gut) is a semi-permeable membrane. The mid-gut allows dissolved matter to diffuse through it in either direction, but the action of the absorbing epithelium causes contained fluid to pass outward even against strong osmotic pressure.

17. Among the Crustacea the hepatopancreas is an important storage organ for glycogen, fat (including lecithin), and calcium, which vary in amount in accordance with the particular stage of growth. *Nephrops* stores fat and glycogen but not calcium.

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