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Chapter 3

Internal Anatomy of the Decapoda: An Overview

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INTRODUCTION

This chapter presents an overview of the gross and fine morphological features of the internal anatomy of the Decapoda. Despite the tremendous amount of information that has been reported on specific aspects of a particular organ system (e.g., hepatopancreas, see Gibson and Barker, 1979), few investigations have presented a general overview of the anatomy of this diverse order of crustaceans. Exceptions to this are the early works of Huxley (1880), a beautiful and accurate anatomical review of the common crayfish, of Herrick (1896) on the American lobster *Homarus americanus,* of Pearson (1908) on the brachyuran crab genus *Cancer,* and Calman's (1909) excellent comparative study of all known crustaceans, wherein he presented a detail description of the internal as well as the external features of the Decapoda. Since these pioneering efforts many descriptive microscopic investigations at all levels (e.g., light, transmission and scanning electron microscopy have been undertaken on specific aspects of decapod anatomy, especially with the technical advances in light microscopy (LM) (e.g., differential interference contrast optics—Nomarski) and the advent of transmission (TEM) and scanning electron microscopy (SEM). A complete accounting of these investigations is beyond the scope of this chapter, but several major works must be mentioned.

Young (1959) provided a survey of the external and internal anatomy of the white shrimp *Penaeus setiferus*. This careful study is an extensively illustrated anatomical compendium of this common dendrobranchiate shrimp and represents one of the few complete investigations of a natant (swimming) decapod. Studies on the general anatomy of reptant decapods of note are those of Warner (1977) on brachyuran crabs' anatomy and many other aspects of their biology, and Johnson's (1980) thorough histological investigation of the blue crab *Callinectes sapidus*.

In addition to these contributions, Waterman (1960), McLaughlin (1980, 1983), and Schram (1986) elaborated upon many aspects of decapod internal anatomy in their texts on general crustacean biology.

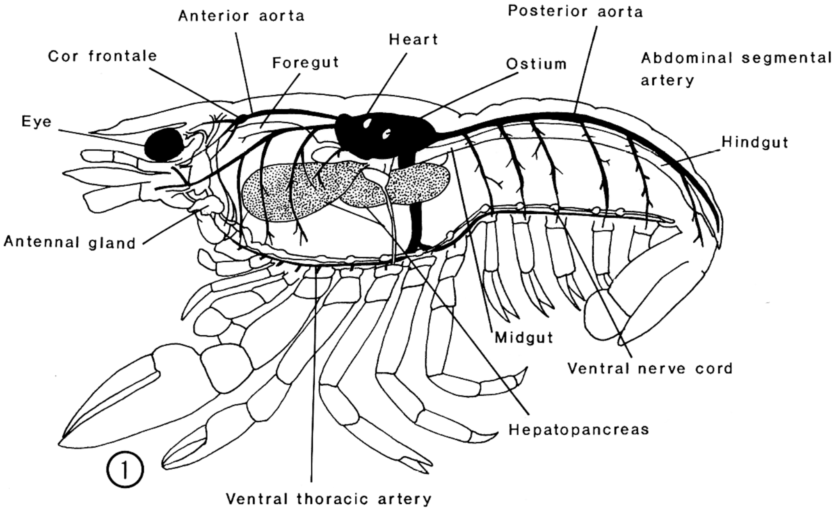


Fig. 1. Schematic drawing of internal anatomical features of a typical macruran decapod. (After McLaughlin, 1980.)

The purpose of this chapter is to illustrate at the microscopic level the general features of the major decapod organ systems. The gross morphology of most organ systems is described and augmented by brief histological and ultrastructural discussions of the fine structures of each. For more detailed presentations, the reader should refer to the chapters that follow in this volume.

Note that emphasis in this chapter is on the natant or swimming forms of decapod crustaceans. This is in part because the author is more familiar with these decapods and because the general layout of the internal anatomy is quite similar between the natant and reptant (crawling) forms. In addition, the aforementioned work, *Histology of a Blue Crab* (Johnson, 1980), elaborated in detail on the brachyurous form of decapods. However, features unique to the reptant decapods are included for comparative purposes.

ORGANIZATION OF DECAPOD ORGAN SYSTEMS

Figures 1 and 2 illustrate the general layout of the internal organs of both the macrurous and brachyurous forms of decapods. The reader should refer to these figures for gross orientation of organ systems within each body type as the features of each organ system are described below.

THE ALIMENTARY SYSTEM

The alimentary system of decapods is composed of three basic regions: the esophagus and foregut, the midgut, and the hindgut (Fig. 3). The esophagus, foregut, and hindgut are ectodermally derived with chitinous linings, whereas the midgut is endodermally derived and lined with a nonchitinous, columnar epithelium. The foregut is located dorsally in the cephalothorax and is surrounded by a large, lobed digestive gland or hepatopancreas (Fig. 3) that may almost fill the dorsal region of the thorax in some species. The midgut and hindgut may also bear various blindly ending tubules or ceca (e.g., Fig. 4) at several locations along their length within the abdominal somites. The major features of the three regions of the alimentary canal are discussed below.

The Esophagus and Foregut

Food passes from the mouthparts to the J-shaped esophagus and moves directly into the foregut. The esophagus may be thrown into longitudinal ridges or chitinous folds (= valves of some authors) that may limit the

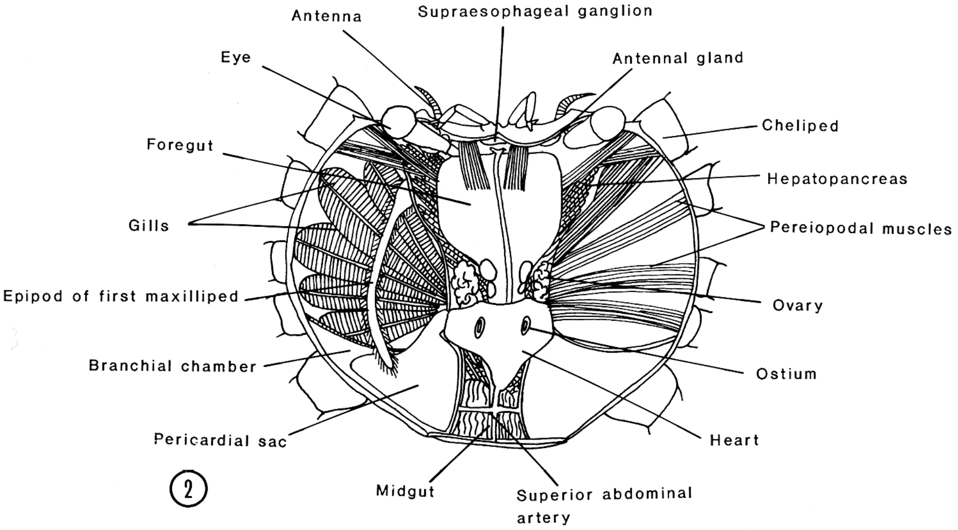


Fig. 2. Schematic drawing of internal anatomical features of a typical brachyuran crab. (After McLaughlin, 1980.)

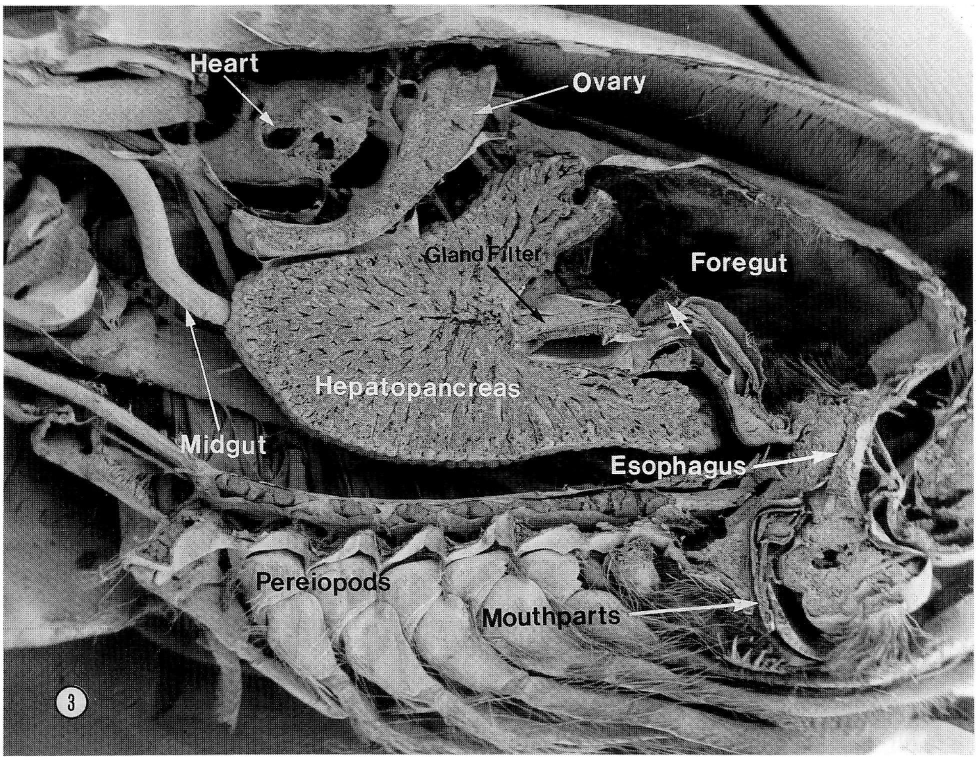


Fig. 3. Internal anatomy of the cephalothorax region (sagittal paraffin-carved section) of a typical female natant decapod (caridean shrimp). The major organs and associated structures are labeled in the figure. SEM. (See Oshel, 1985, and Felgenhauer, 1987, for paraffin-carving procedure.)

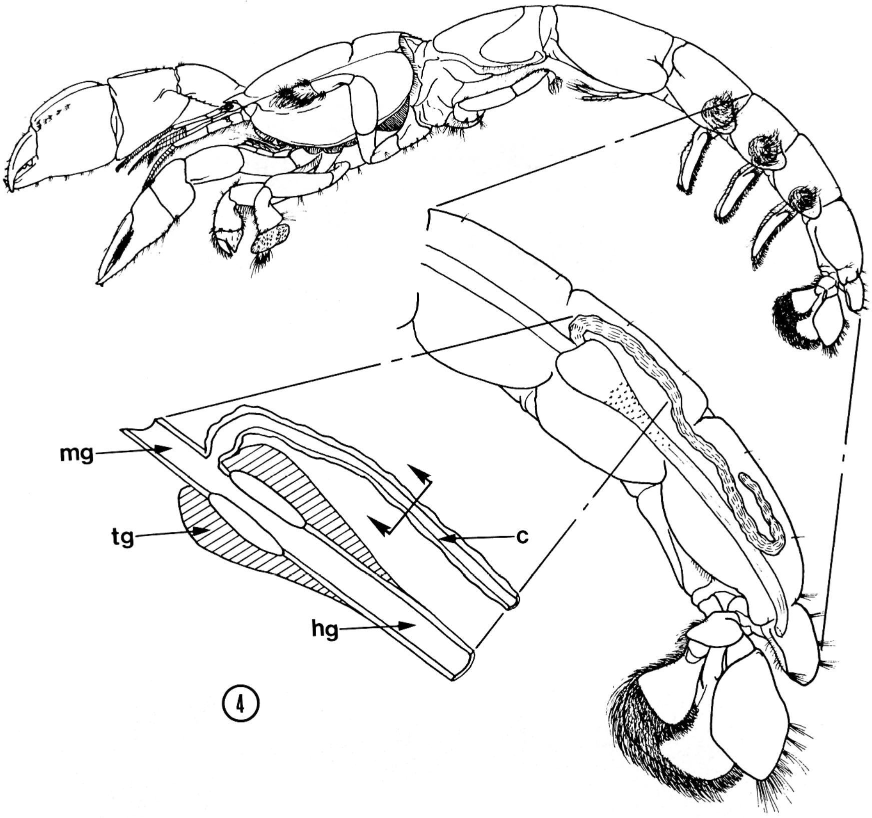
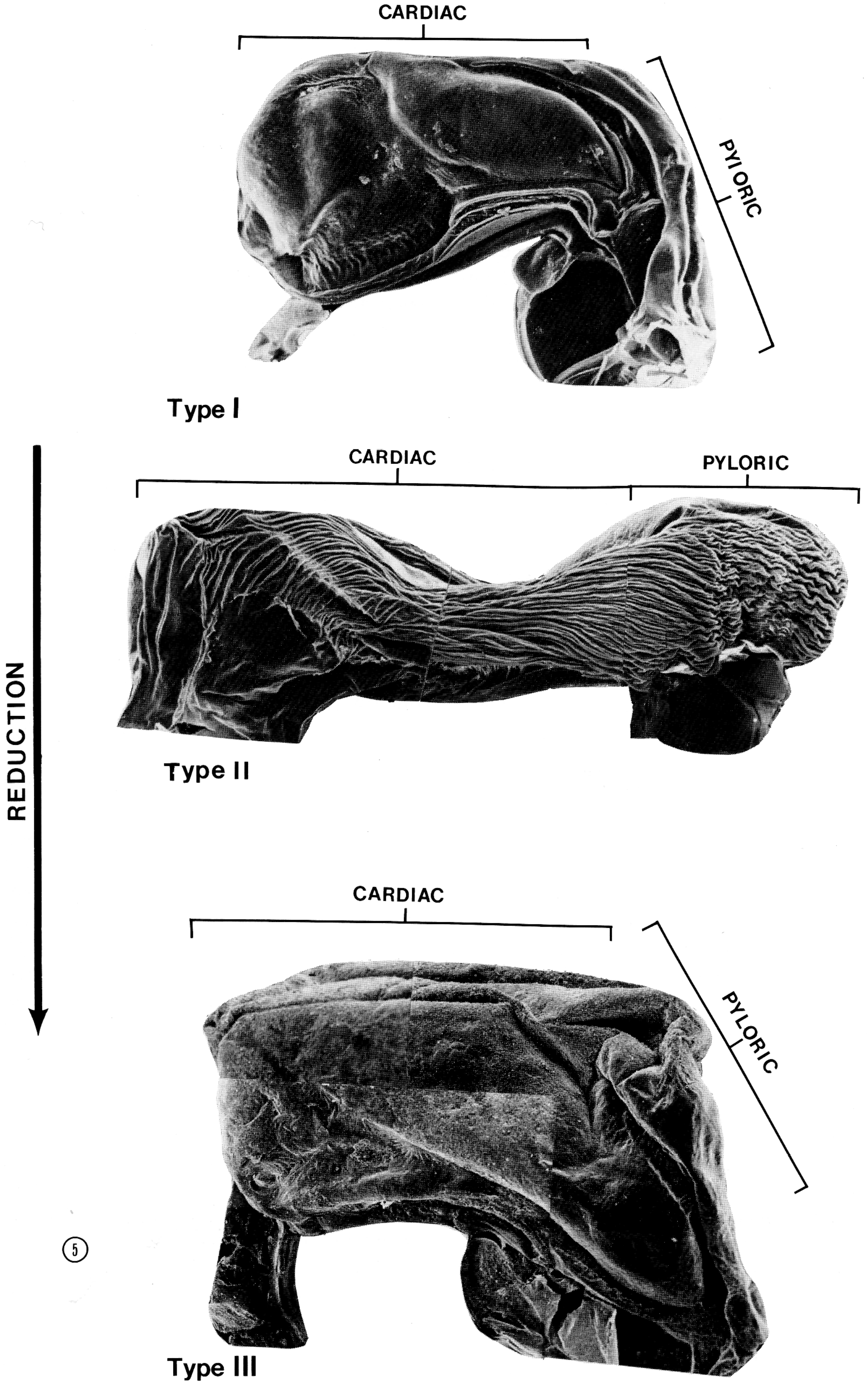


Fig. 4. Schematic drawing of the gross anatomical features of the posterior midgut cecum (PMGC) of the thalassinoid mudshrimp *Lepidophthalmus louisianensis*. c, cecum; hg, hindgut; mg, midgut; tg, tegumental glands. (From Felgenhauer and Felder, in preparation.)

size of the lumen (in conjunction with the extrinsic musculature), presumably preventing the regurgitation of ingested material. The foregut is a dual-chambered, chitinous sac that varies greatly among decapods (Fig. 5; for review, see Felgenhauer and Abele, 1989). The anteriormost region, the cardiac chamber (Fig. 5), is a spacious sac in most decapods with a variety of internal structures that apparently facilitate sorting and mastication of ingested food. The cardiopyloric valve separates the cardiac chamber from the posterior pyloric chamber. The pyloric chamber is divided into an upper portion that leads directly to the midgut and a ventral region that leads to a straining device called the gland filter or ampulla (Figs. 3, 5, 9A) which permits only the finest particles to enter the digestive gland or hepatopancreas (Figs. 3, 9A). Both the cardiac and pyloric chambers are composed of a varying number of chitinous plates or ossicles that differ in their size and morphology. The ossicles are connected to one another by membranous ligaments permitting movement by the extrinsic muscu-

Fig. 5. Morphological trends in the evolution of the lower decapod foregut. Foregut type I *(Rhynchocinetes)* is characterized by the presence of distinct ossicles and well-developed internal gastric armature (gastric mill). Foregut type II *(Barbouria)* is defined by an overall rugose external appearance corresponding internally to longitudinal folds extending the length of cardiac and pyloric chambers, with a marked reduction of internal gastric armature. Type III *(Systellaspis)* foreguts exhibit complete fusion of the ossicles; internal gastric armature is absent. Figure 5 is not meant to imply linear evolutionary trend within any taxonomic unit. (From Felgenhauer and Abele, 1989.)


CARDIAC
PYLORIC
Type I
REDUCTION
CARDIAC
PYLORIC
Type II
CARDIAC
PYLORIC
Type III

⑤

lature that controls the action on the foregut. The basic arrangement of ossicles is consistent throughout the Decapoda (see Mocquard, 1883; Maynard and Dando, 1974; Felgenhauer and Abele, 1989, for discussions). Despite the consistency of ossicle arrangement, much fusion has occurred across the various groups of decapods. An extensive survey of the foreguts of the lower Decapoda by Felgenhauer and Abele (1989) discovered three distinctive foregut types (types I, II, III; Figs. 5, 6A–D, 7A–F). These authors considered the foregut type I as the most primitive, exhibiting the highest degree of ossicle number and complexity (Fig. 5). Types II and III show a reduction in ossicle number and complexity along with a loss of internal gastric armature (gastric mill) as well (Fig. 5). Foregut type I is used here to describe the basic internal armature of the decapod foregut and the major ossicles that contribute to the so-called gastric mill (term coined by Huxley, 1880) located in the posterior region of the cardiac chamber. In addition, the ossicles associated with the roof of the pyloric chamber are described here. The lateral and ventral ossicles contribute little to the internal armament of the foregut other than accessory spines and are not discussed.

The Cardiac Chamber. The roof of the cardiac chamber is composed of the anterior, unpaired mesocardiac ossicle, paired pterocardiac ossicles, paired, lateral zygocardiac ossicles, and the unpaired centrally placed urocardiac ossicle (Figs. 6C,D, 7A–D). The urocardiac ossicle extends internally to form the median tooth (Figs. 6C,D [arrow], E,F, 7D–G, 8A–F). The lateral teeth arise from the zygocardiac ossicles (Figs. 6C, 7A–D). Presumably the action of the lateral teeth grinding against the central median tooth (Figs. 6E,F, 7E,F) masticates food by forming a "gastric mill."

Pyloric Chamber. The pyloric chamber is usually smaller and narrower than the cardiac chamber (Figs. 5, 6A,B) and is composed of the unpaired pyloric ossicle, which butts against the urocardiac ossicle (Figs. 6C, 7B,C). Directly posterior, and connected to the pyloric ossicle, is the uropyloric ossicle (Fig. 7B,C). A pair of exopyloric ossicles may (uncommonly) flank the usually broadly rounded pyloric ossicle.

The roof of the pyloric chamber may be variously modified depending on the diet of the species. In those decapods that filter feed, such as species within the caridean shrimp genus *Atya,* a dorsal median projection, borne on the uropyloric ossicle, projects into the chamber (Fig. 9A–C). The median projection is continuous with a complex series of thin chitinous folds, the convoluted membrane, which fills the posterior two-thirds of the pyloric chamber (Fig. 9A–C). The thalassinoid mudshrimp *Upogebia pugettensis,* another filter-feeding decapod, has a pair of pyloric fingerlets that extend into the lumen of the pyloric chamber (Fig. 9D). Both the convoluted membrane and pyloric fingerlets of these shrimp break the food bolus into small parcels, presumably allowing digestive enzymes from the hepatopancreas to penetrate (Fig. 9A,B,E). The floor of the pyloric chamber leads to the filter press or gland filter (Fig. 9A).

The Gland Filter (Ampulla). The external morphology of the gland filter in decapods is quite variable, with the internal arrangement being very uniform. The gland filter is most commonly elliptically shaped and is composed of upper and lower ampullary chambers that are armed with setae that form a "screen" that strains (via the extrinsic foregut musculature) the smallest particles into the ampullary channels of the lower ampullary chamber (Fig. 9A). These particles pass through these channels into the hepatopancreas; those that are too large to enter the channels move directly into the midgut.

The Hepatopancreas (Digestive Gland). The hepatopancreas or digestive gland is a large, bilobed organ composed of many blindly ending tubules (Fig. 3). This important organ functions in food absorption, transport, secretion of digestive enzymes, and storage of lipids, glycogen, and a number of minerals (for

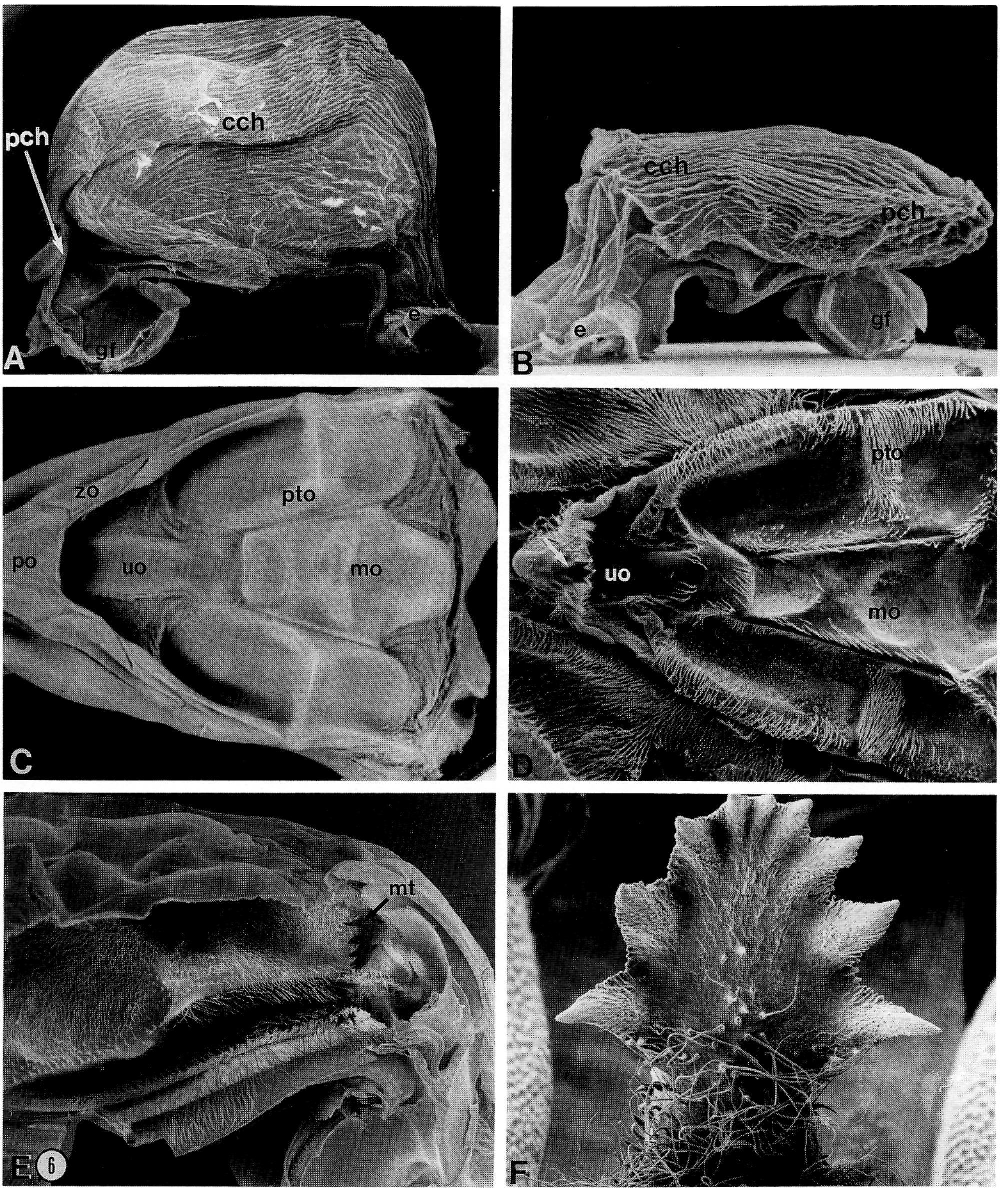


Fig. 6. Examples of foreguts type I and II among the Decapoda. SEM. **A:** External features of type II foregut of *Saron marmoratus;* note extremely small pyloric chamber. ×20. **B:** Type II foregut of *Thalassocaris obscura*. ×45. **C:** Dorsal view of type I foregut of *Rhynchocinetes hiattia*. Note the major ossicles that compose this foregut type. ×28. **D:** Internal view of foregut presented in the same orientation as in C. Note the internal features that extend from the dorsal ossicles (e.g., arrow indicates the median tooth that extends from a continuation of the urocardiac ossicle). ×30. **E:** Sagittal internal view of the type I foregut pictured in C and D. Note the median tooth that projects from the urocardiac ossicle into the lumen of the posterior cardiac chamber. ×40. **F:** Frontal view of the median tooth shown in E. ×225. cch, cardiac chamber; e, esophagus; gf, gland filter; mo, mesocardiac ossicle; mt, median tooth; pch, pyloric chamber; po, pyloric ossicle; pto, pterocardiac ossicle; uo, urocardiac ossicle; zo, zygocardiac ossicle.

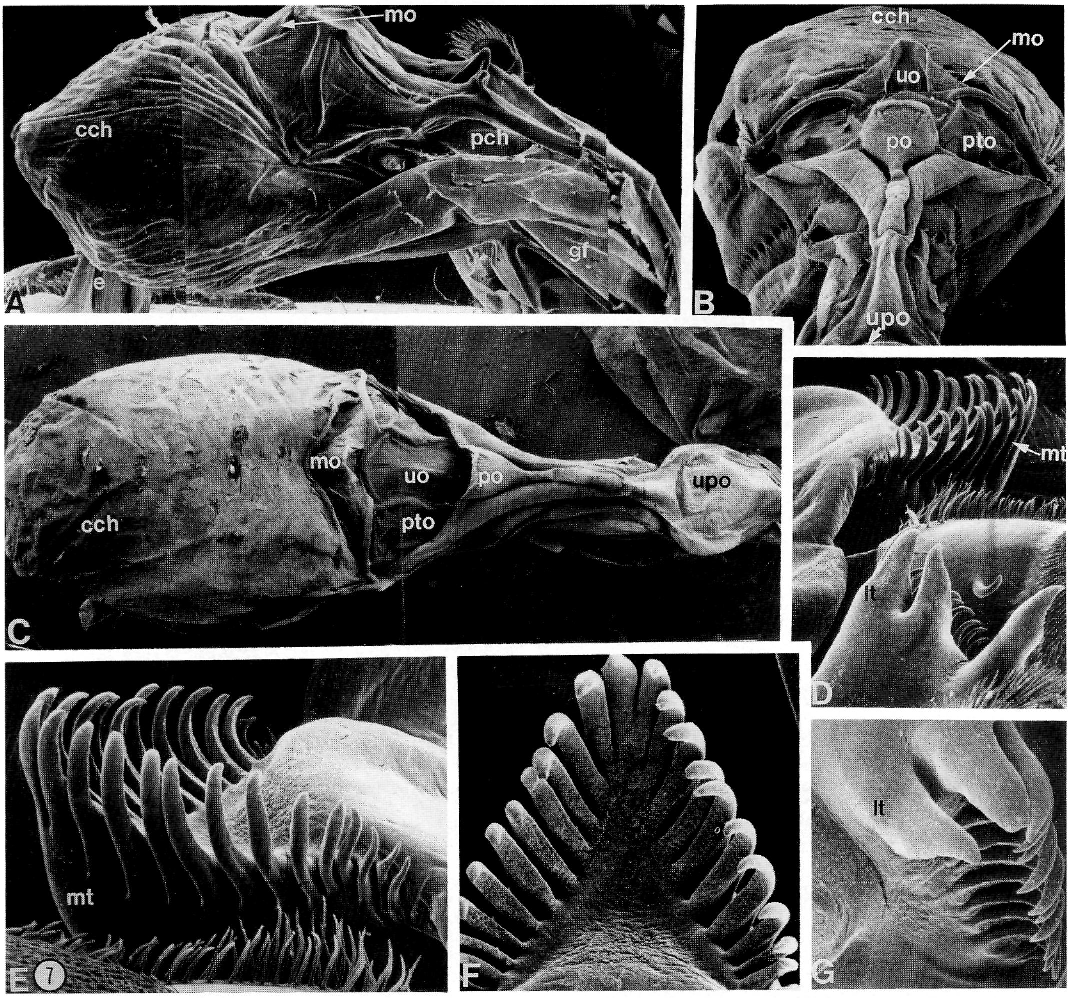


Fig. 7. Examples of type I foreguts from dendrobranchiate shrimp. SEM. **A:** External lateral view of *Sicyonia brevirostris* with ossicles indicated. ×16. **B:** Posterior view of pyloric and cardiac chambers of *Sicyonia brevirostris* with ossicle indicated. ×32. **C:** Dorsal view of foregut of *Sicyonia brevirostris* with dorsal ossicles indicated. ×20. **D:** Lateral view of gastric mill of *Solenocera vioscai* showing relationship of lateral teeth from the zygocardiac ossicle to the central median tooth arising from the urocardiac ossicle. ×29. **E:** Lateral view of median tooth shown in D. ×75. **F:** Front view of median tooth shown in E. ×80. **G:** Close-up of lateral tooth figured in D. ×72. cch, cardiac chamber; e, esophagus; gf, gland filter; lt, lateral tooth; mt, median tooth; mo, mesocardiac ossicle; pch, pyloric chamber; po, pyloric ossicle; pto, pterocardiac ossicle; uo, urocardiac ossicle; upo, uropyloric ossicle. (After Felgenhauer and Abele, 1989.)

extensive review, see Gibson and Barker, 1979). The tubules are made up of four basic cell types: E-, F-, R-, and B-cells (Fig. 10A–F). Below, I describe the basic morphology of these cell types at primarily the TEM level. Additional ultrastructural information and possible functions of these cells are presented in detail by Icely and Nott in chapter 6, this volume.

The E-cells, or "embryonic cells," are small cells found at the blind ends of the tubules and presumably give rise to the other three cell types of the gland (Jacobs, 1928; Gibson and Barker, 1979, and others). They

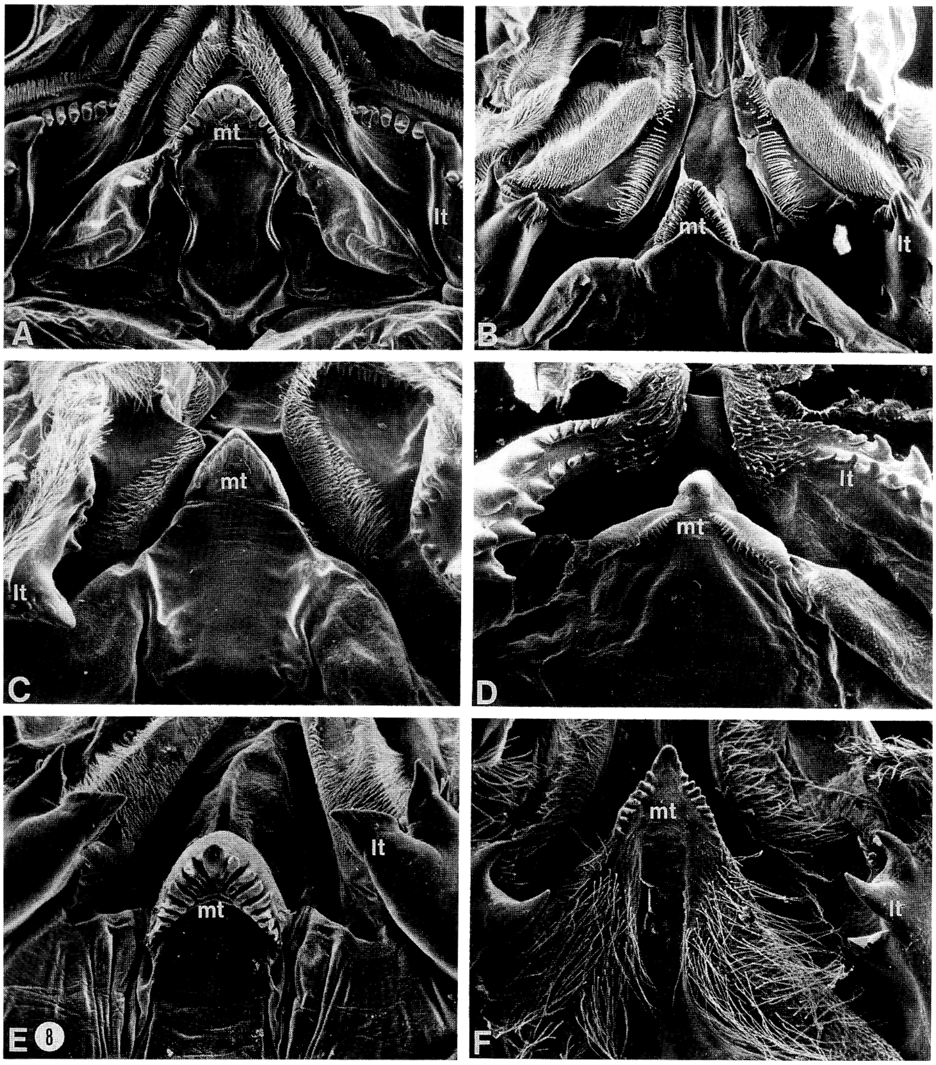


Fig. 8. Internal aspects of type I foreguts of natant decapods. SEM. On each, note the prominent median tooth flanked by strong lateral teeth. **A:** *Penaeus setiferus*. ×18. **B:** *Solenocera vioscai*. ×18. **C:** *Aristaeomorpha foliacea*. ×22. **D:** *Sergestes similis*. ×33. **E:** *Sicyonia brevirostris*. ×33. **F:** *Procaris ascensionis*. ×36. lt, lateral tooth (zygocardiac ossicle); mt, median tooth (urocardiac ossicle).

are characterized by a large nucleus with a prominent nucleolus, abundant developing rough and smooth endoplasmic reticulum, few Golgi profiles, and usually lack a brush border (Fig. 10A).

The F-cells, or "fibrillar cells," have a basally located nucleus, and an extensively developed rough endoplasmic reticulum (RER), giving them a fibrillar appearance (Figs. 10B–D, 11F). Mitochondria and Golgi profiles are also abundant, as are small vesicles throughout the cytoplasm (Fig. 10C). A prominent brush border is present (Fig. 10B). A wide variety of functions has been attributed to this cell type, such as protein synthesis (Davis and Burnett, 1964) and storage of minerals (Miyawaki and Sasaki, 1961).

B-cells, or "blister cells" (Fig. 10E), are

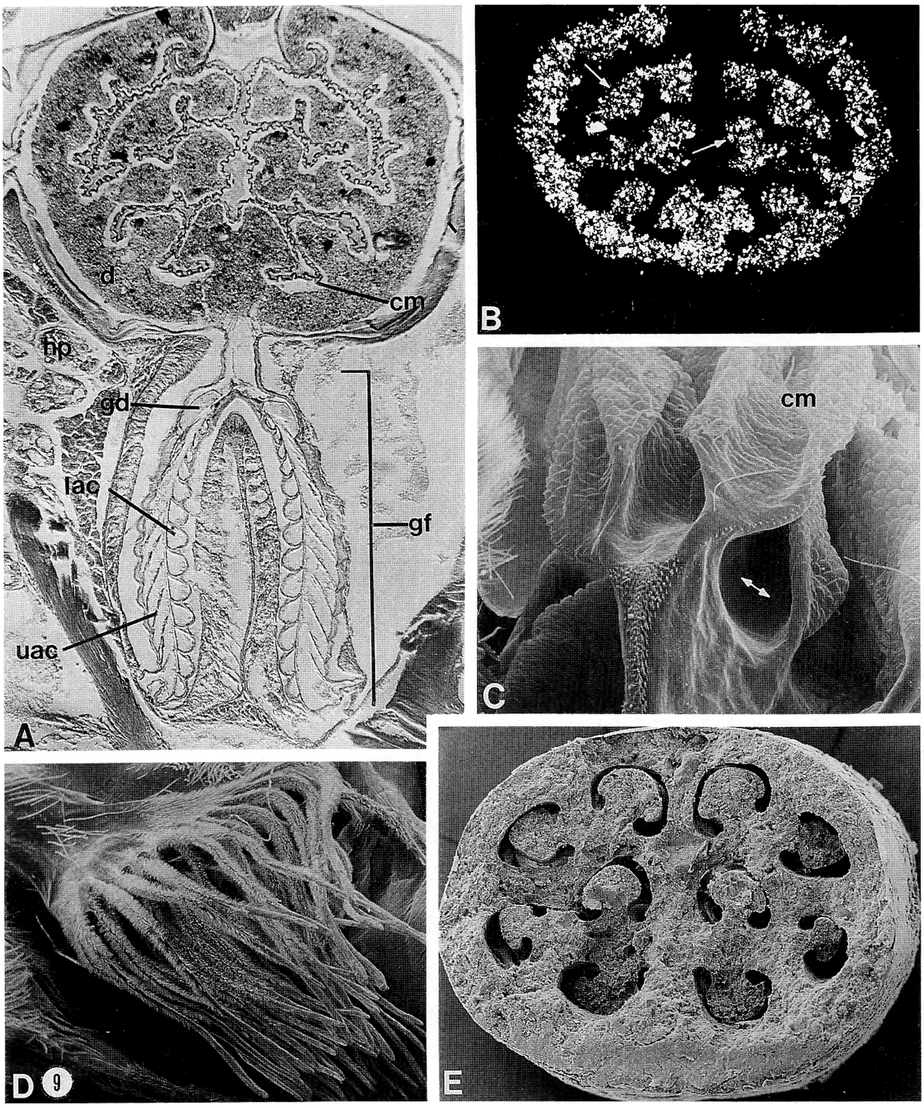


Fig. 9. Structural adaptations of the pyloric chamber. **A:** Histological cross section through the pyloric chamber and gland filter of *Atya innocous*. Note the convoluted membrane (cm) that breaks up the food bolus within the pyloric chamber. ×450. **B:** Polarized light micrograph of pyloric chamber shown in A. Birefringent structures are particulate food that is divided by the convoluted membrane (arrows) shown in A and C. ×450. **C:** Close-up view of external features of convoluted membrane shown in A. SEM. ×1,200. **D:** External view of pyloric fingerlets of *Upogebia pugettensis*. SEM. ×30. **E:** Cross section of fecal pellet from *Lepidophthalmus louisianensis*. Note characteristic pattern produced by the pyloric fingerlets in the pyloric chamber of the foregut. SEM. ×300. cm, convoluted membrane; d, diatoms (food bolus); gd, guarding denticles; gf, gland filter; hp, hepatopancreas; lac; lower ampullary channel; uac, upper ampullary channel.

large, primarily secretory cells that are defined by the presence of a single enormous vesicle surrounded by a dense cytoplasm filled with RER (Loizzi, 1968; Barker and Gibson, 1977; Gibson and Barker, 1979). A brush border is present but may be reduced (Loizzi, 1971). These cells are the primary producers of digestive enzymes in the hepatopancreas.

The R-cells are the most numerous cell type. These tall, columnar cells are characterized by a prominent brush border (Fig. 10F),

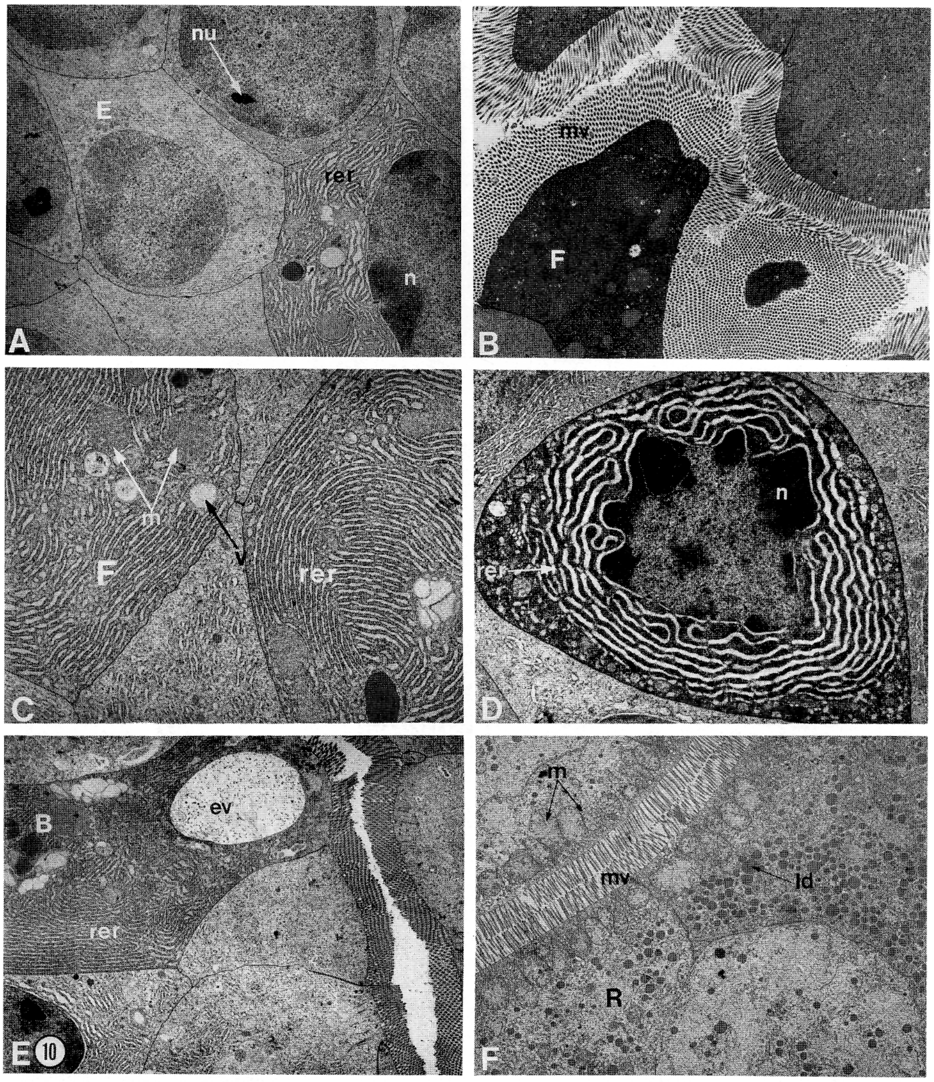


Fig. 10. Ultrastructure of hepatopancreas cells. (A–F from caridean shrimp *Procaris ascensionis*.) TEM. **A:** E-cells (embryonic cells); note undifferentiated nature and prominent nucleolus. ×3,000. **B:** Low-magnification view of F-cell; note distinct brush border. ×3,650. **C:** Close-up of details of F-cell; note prominent RER. ×7,200. **D:** Cross section of F-cell. ×5,800. **E:** Possible B-cell (blister cell); note evacuation vacuole. ×3,650. **F:** R-cells; note lipid droplets and rows of apical mitochondria. ×2,950. B, possible blister cell; E, embryonic cell; ev, evacuation vacuole; F, fibrillar cell; ld, lipid droplet; m, mitochondria; mv, microvilli; n, nucleus; nu, nucleolus; R, reserve cell; rer, rough endoplasmic reticulum.

centrally located nucleus, and large numbers of storage vesicles (primarily lipid) in their cytoplasm (Figs. 10F, 11F). These cells function in food absorption. Additionally, they commonly sequester mineral deposits such as calcium (Fig. 11E), magnesium, phosphorus, sulfur, and others (Hopkin and Nott, 1980). For example, the hepatopancreas of the primitive caridean shrimp *Procaris ascensionis* sequesters extremely large (up to 80 μm) mineral inclusions in their R-cells of the hepatopancreas (Fig. 11A–C). These irregular inclusions (Fig. 11C) are composed of a number of elements (Fig. 11D).