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, espe-

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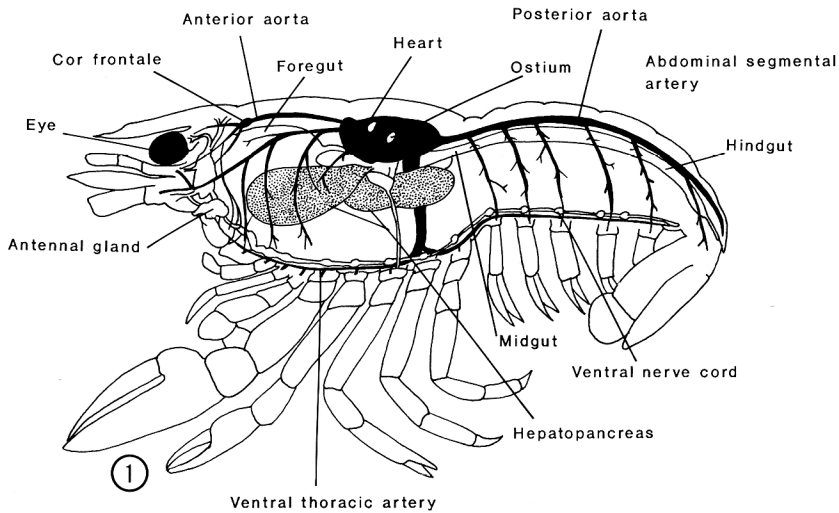
Fig. 1.   Schematic drawing of internal anatomical features of a typical macruran decapod. (After McLaughlin, 1980.)

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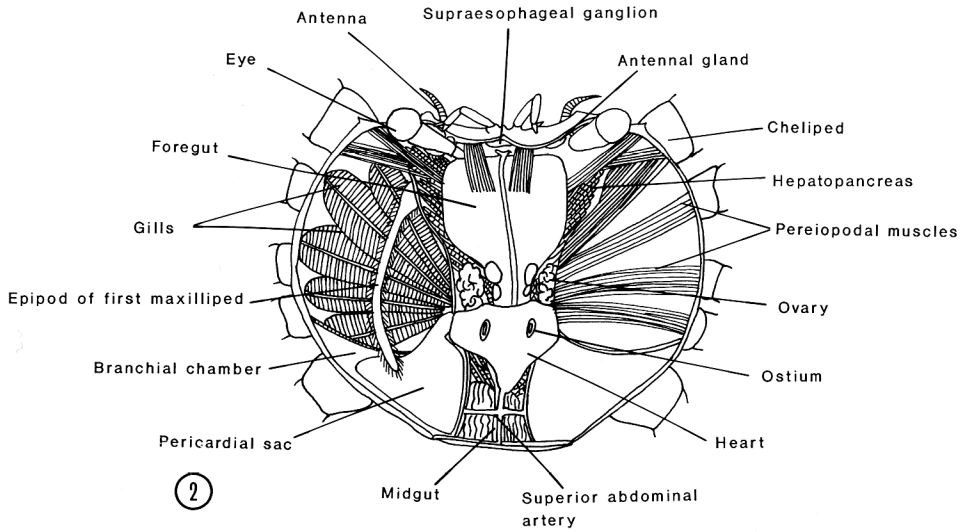
Fig. 2.   Schematic drawing of internal anatomical features of a typical brachyuran crab. (After McLaugh-lin, 1980.)
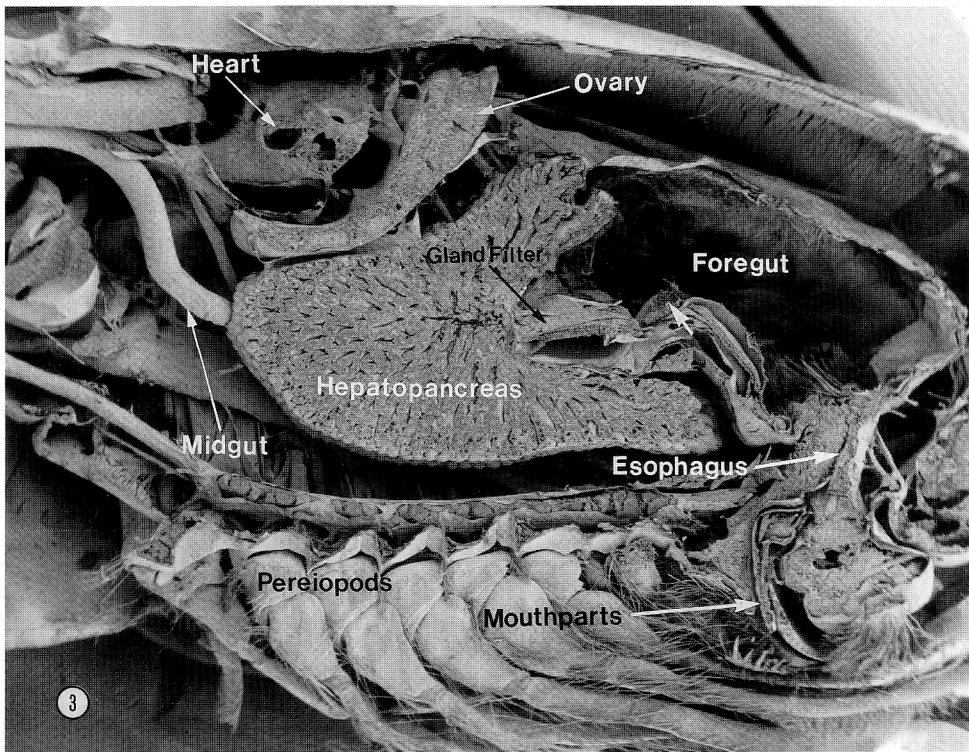

Fig. 3.   Internal anatomy of the cephalothorax region (sagittal paraffin-carved section) of a typical female natant decapod (caridean shrimp). The major organs and associated structures are labeled in the figure. SEM. (See Oshel, 1985, and Felgenhauer, 1987, for paraffin-carving procedure.)
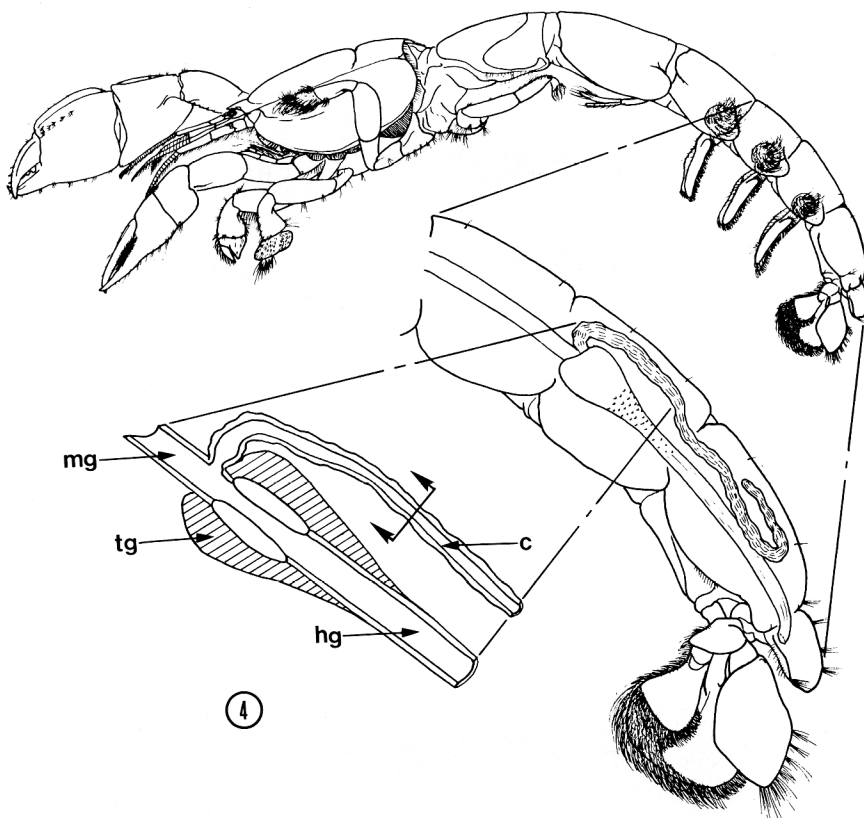
Fig. 4.   Schematic drawing of the gross anatomical features of the posterior midgut cecum (PMGC) of the thalassinoid mudshrimp *Lepidophthalmus louisianensis*. c, cecum; hg, hindgut; mg, midgut; tg, tegumental glands. (From Felgenhauer and Felder, in preparation.)

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 per-

mits 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.)
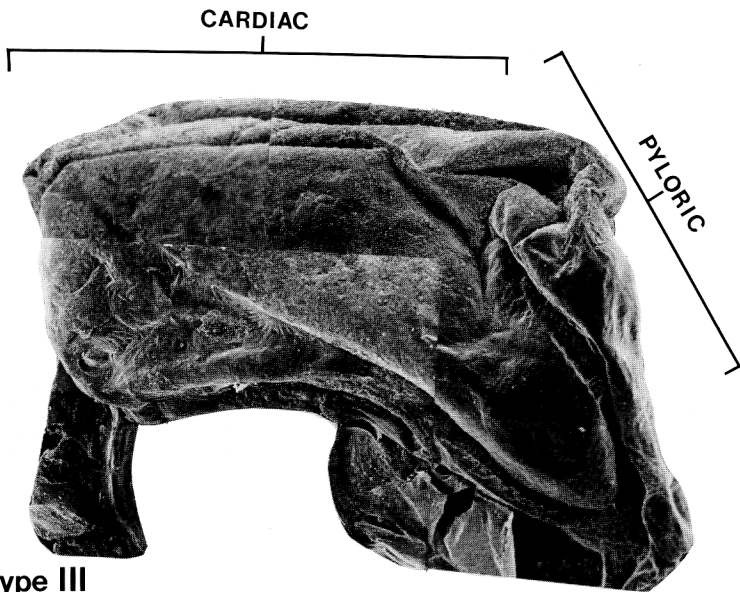
CARDIAC

PYLORIC

Type I

REDUCTION

CARDIAC   PYLORIC

Type II

CARDIAC

PYLORIC

Type III

⑤
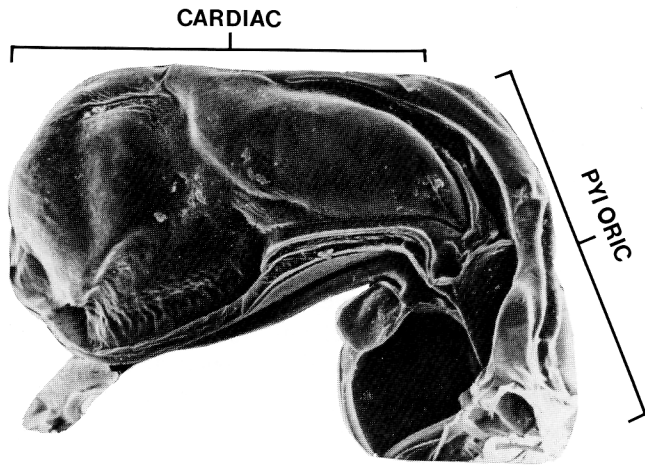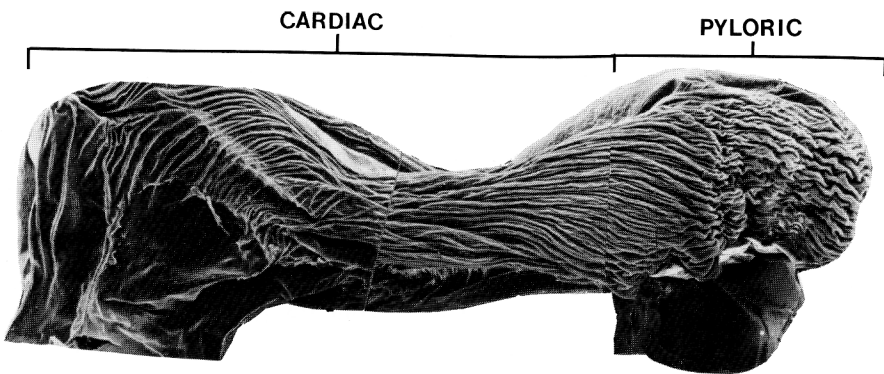
lature that controls the action on the foregut. The basic arrangement of ossicles is consistent throughout the Decapoda (see Mocquard, 1883; Maynard and Dando, 1974; Felgenhauer and Abele, 1989, for discussions). Despite the consistency of ossicle arrangement, much fusion has occurred across the various 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
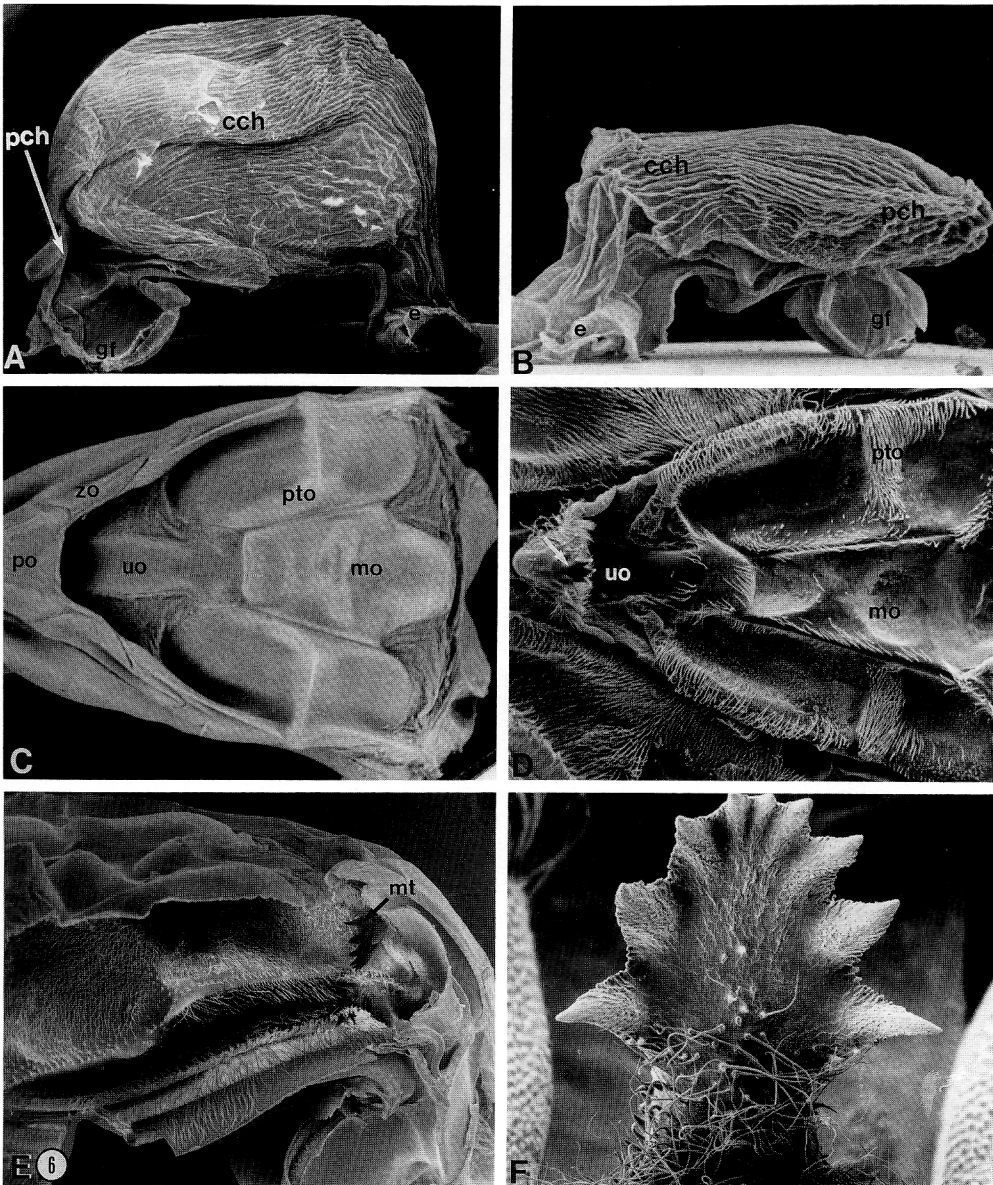
Fig. 6. Examples of foreguts type I and II among the Decapoda. SEM. **A:** External features of type II foregut of *Saron marmoratus;* note extremely small pyloric chamber. ×20. **B:** Type II foregut of *Thalassocaris obscura*. ×45. **C:** Dorsal view of type I foregut of *Rhynchocinetes hiattia*. Note 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.
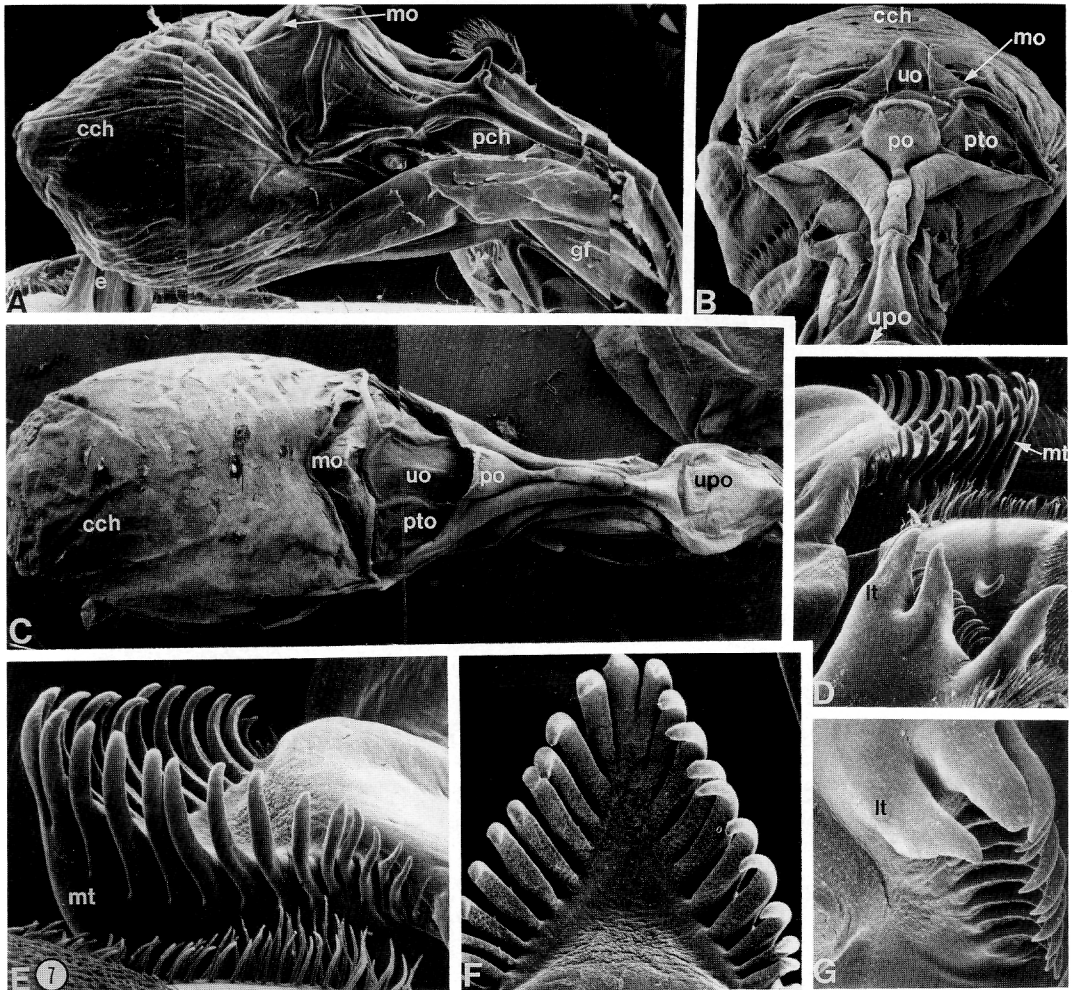
Fig. 7. Examples of type I foreguts from dendrobranchiate shrimp. SEM. **A:** External lateral view of *Sicyonia brevirostris* with ossicles indicated. ×16. **B:** Posterior view of pyloric and cardiac chambers of *Sicyonia brevirostris* with ossicle indicated. ×32. **C:** Dorsal view of foregut of *Sicyonia 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
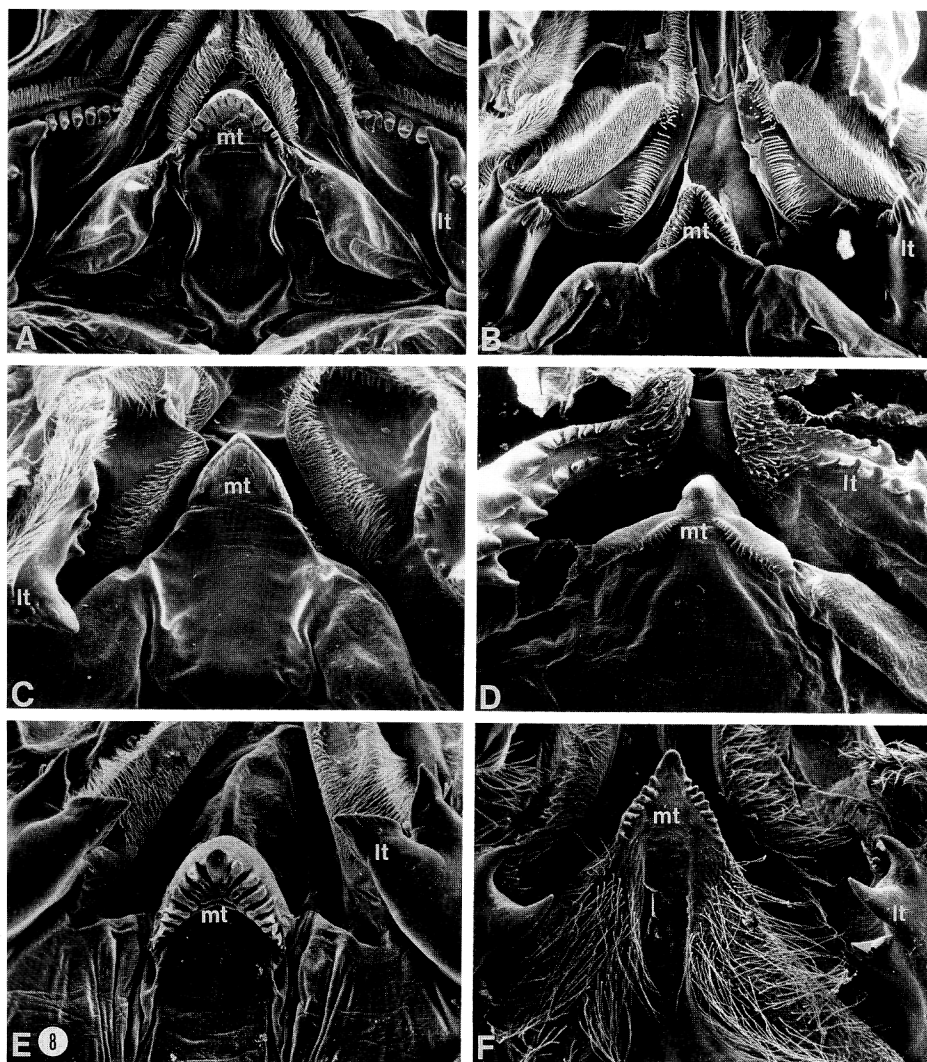
Fig. 8. Internal aspects of type I foreguts of natant decapods. SEM. On each, note the prominent median tooth flanked by strong lateral teeth. **A:** *Penaeus setiferus.* ×18. **B:** *Solenocera vioscai.* ×18. **C:** *Aristaeomorpha foliacea.* ×22. **D:** *Sergestes similis.* ×33. **E:** *Sicyonia brevirostris.* ×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).

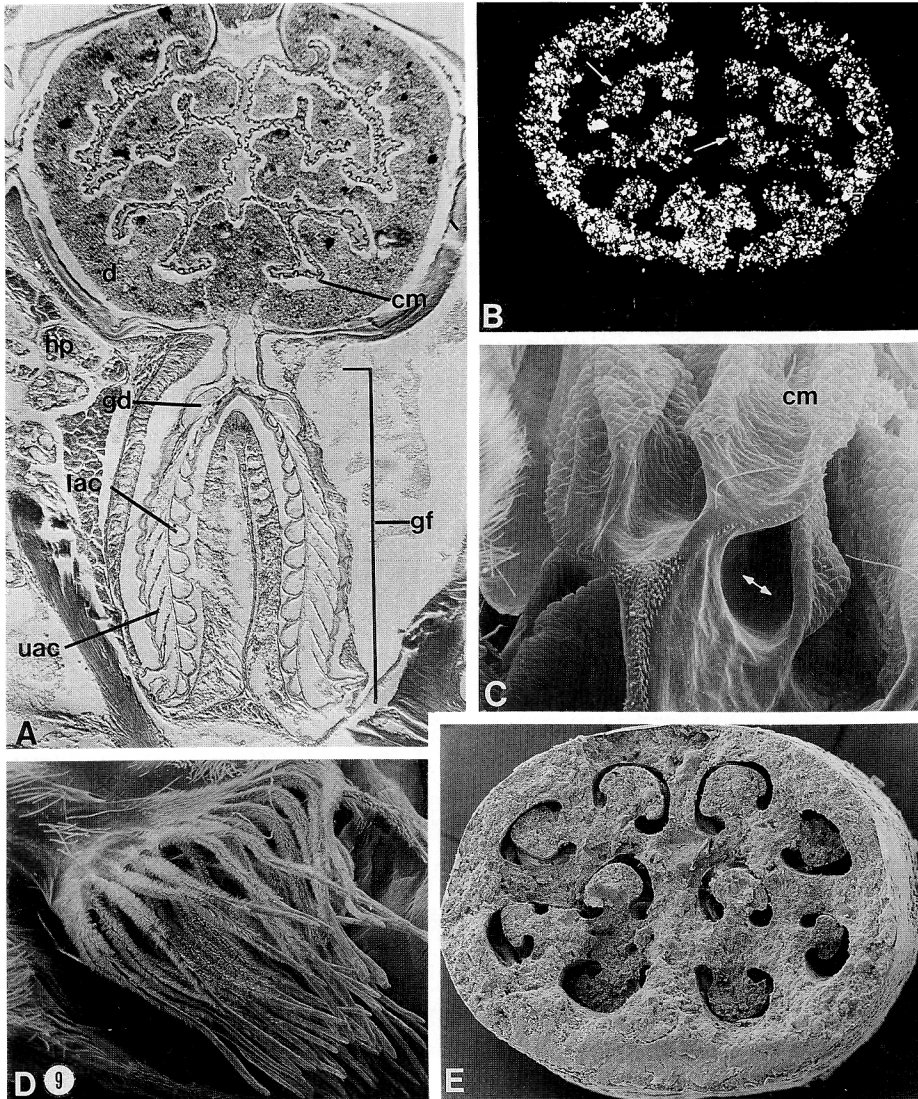B-cells, or "blister cells" (Fig. 10E), are

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),
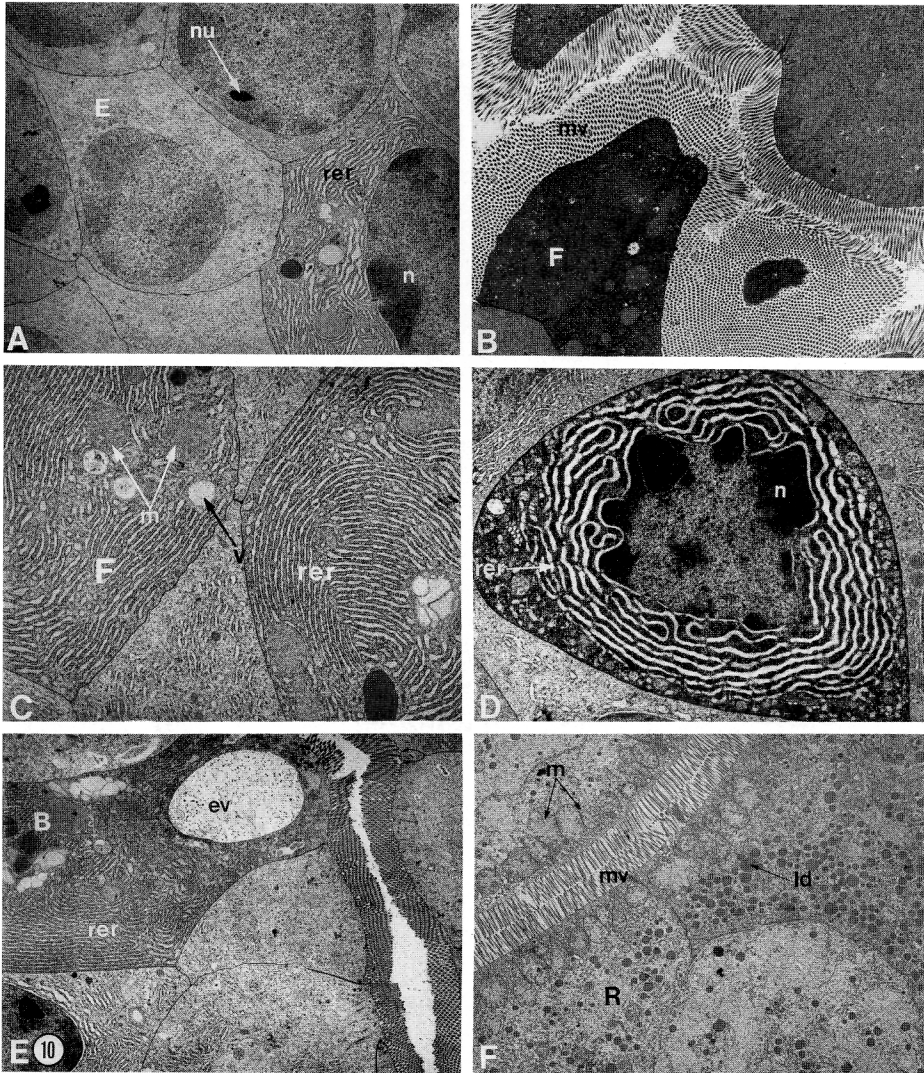
Fig. 10. Ultrastructure of hepatopancreas cells. (A–F from caridean shrimp *Procaris ascensionis*.) TEM. **A:** E-cells (embryonic cells); note undifferentiated nature and prominent nucleolus. ×3,000. **B:** Low-magnification view of F-cell; note distinct brush border. ×3,650. **C:** Close-up of details 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).
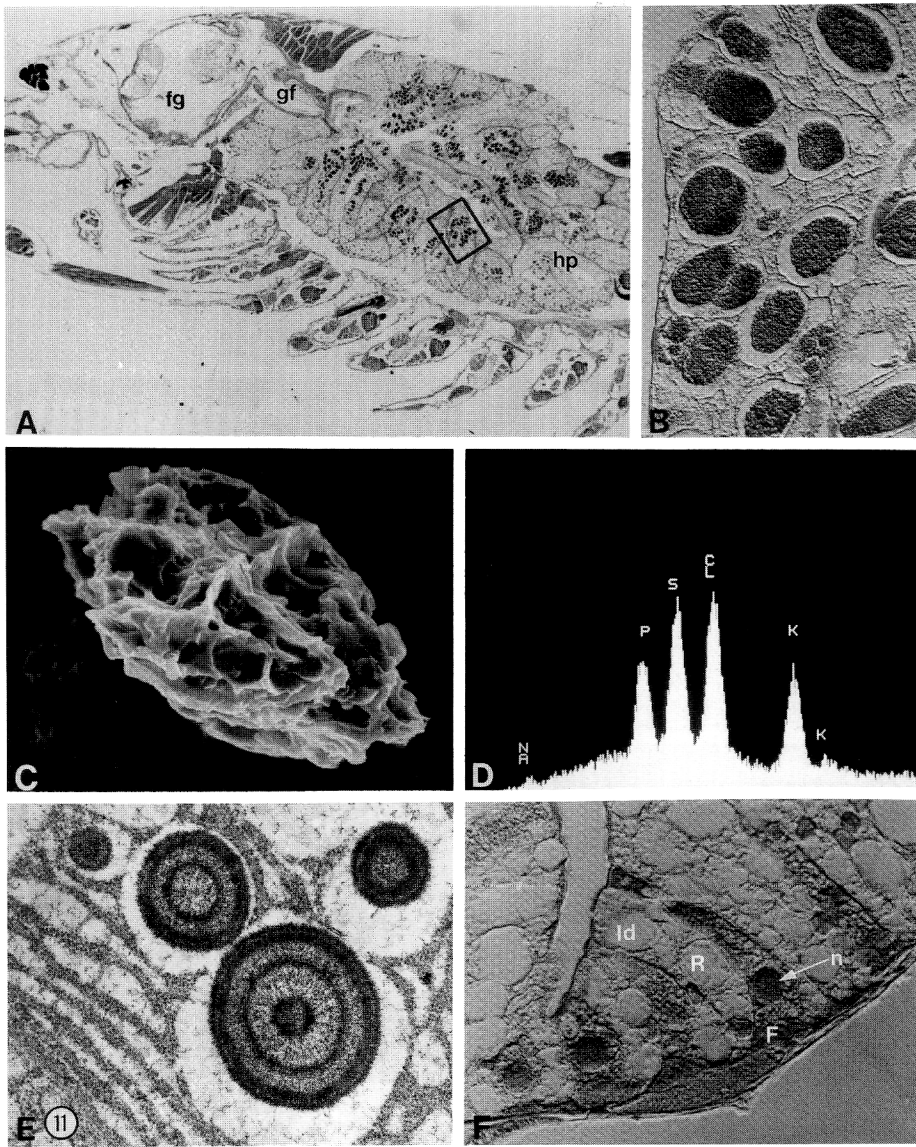
Fig. 11. Mineral inclusions of the decapod hepatopancreas. **A:** Sagittal histological section through the cephalothorax of *Procaris ascensionis;* black box indicates region of gland that harbors mineral inclusions. ×50. **B:** Close-up histological section of mineral inclusions within the R-cells (Nomarski image). ×500. **C:** Individual inclusion from R-cell; note rugous morphology. SEM. ×1,600. **D:** X-ray elemental analysis of inclusion shown in C. **E:** Calcium concretions from hepatopancreas of *Procambarus leonensis*. ×16,000. **F:** Histological section of hepatopancreas of *Procaris ascensionis;* note R- and F-cells. ×700. F, fibrillar cell; fg, foregut; gf, gland filter; hp, hepatopancreas; ld, lipid droplet; n, nucleus; R, reserve cell.

Al-Mohanna et al. (1985) described M-cells, or midget cells, from the dendrobranchiate shrimp *Penaeus semisulcatus,* adding a new cell type for the decapod hepatopancreas. M-cells are round in section and always are in direct contact with the basement membrane. These cells may produce cytoplasmic extensions which ramify among
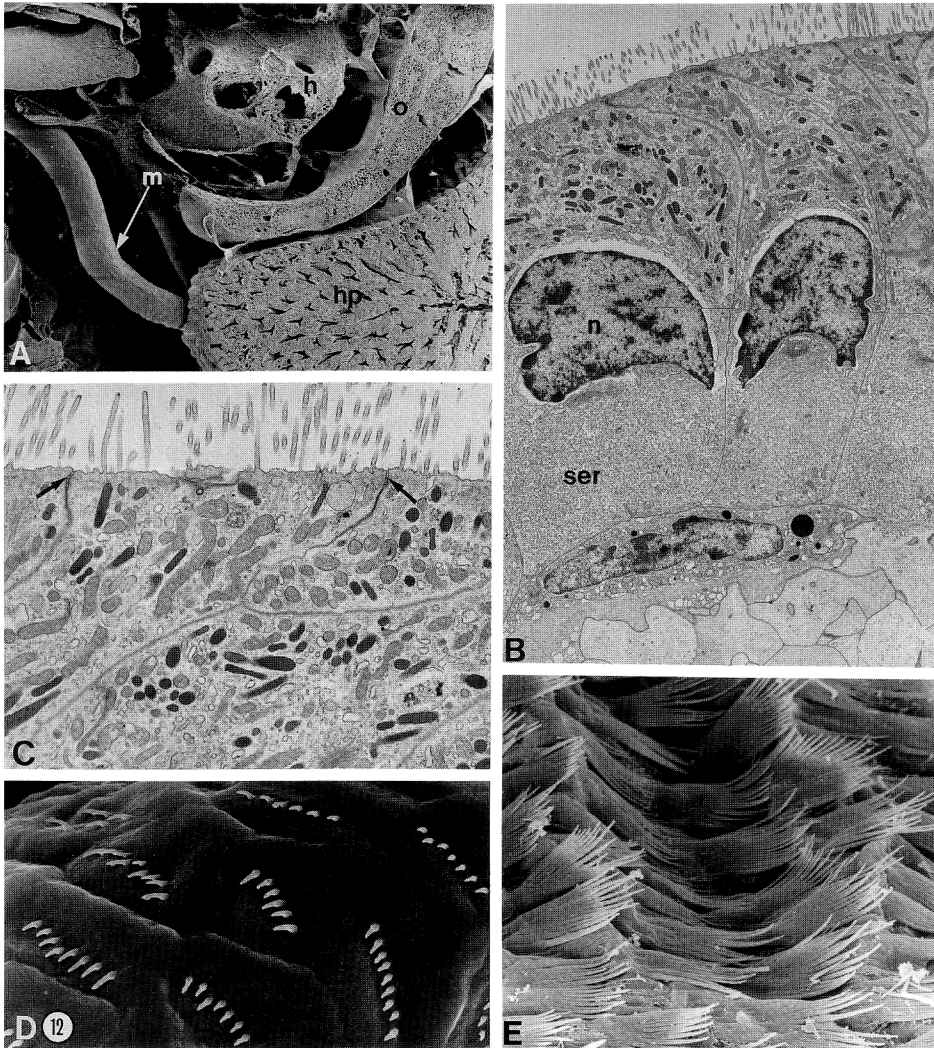
Fig. 12. Ultrastructural features of the midgut and hindgut. **A:** Close-up in region where the midgut exits the posterior portion of the hepatopancreas of *Systellaspis* (by paraffin-carving, SEM). ×650. **B:** Longitudinal section of columnar midgut cells of *Procaris ascensionis;* note prominent fields of SER located below the level of the nucleus. TEM. ×2,800. **C:** Close-up of apical portion of midgut cells shown in B; arrows indicate cell junctions; note cellular inclusions and numerous mitochondria. TEM. ×5,000. **D:** Hindgut of *Procambarus leonensis;* note posteriorly directed clusters of spines. SEM. ×1,500. **E:** Armature of the hindgut of *Lepidophthalmus louisianensis*. SEM. ×2,000. h, heart; hp, hepatopancreas; m, midgut; n, nucleus; o, ovary; ser, smooth endoplasmic reticulum.

neighboring cells (see Icely and Nott, chapter 6, this volume). One of the more distinctive features of this cell is the presence of spheres, rods, and other membrane-bound cytoplasmic inclusions that may occupy the entire cell volume. The function of M-cells is probably storage of some organic reserve (Al-Mohanna et al., 1985).

The Midgut

The endodermally derived midgut may vary greatly in its length from quite short, as in many reptant decapods (e.g., *Galathea,* Pike [1947]; *Astacus,* Huxley [1877]; brachyuran crabs; Smith [1978]), to elongate, as in many caridean shrimps (e.g., *Systellaspis,* Figs. 3, 12A). The length of the midgut is not

uniform within taxonomic divisions (Smith, 1978). The midgut extends from the foregut, through the posterior portion of the hepatopancreas, into the abdominal somites (Figs. 3, 12A) before joining the hindgut. The low to tall columnar cells of the midgut sit on a variously developed basement membrane (Factor, 1981) and usually exhibit a prominent microvillous border (Fig. 12B,C) that in many species exhibits a glycocalyx (e.g., *Penaeus;* Talbot et al., 1972; Lovett and Felder, 1990). The apical cell surfaces are connected by prominent junctional complexes (Fig. 12C; see also Talbot et al., 1972). The nucleus may be basally or centrally located. Rough and smooth endoplasmic reticulum are present (Fig. 12B,C). The RER is usually found in the apical portion of the cell, whereas the smooth endoplasmic reticulum (SER) is basal and rarely occurs above the level of the nucleus (Fig. 12B). Mitochondria, Golgi complexes, and large numbers of round to rod-shaped inclusions and secretory granules are also found in the apical cytoplasm of the cell (Fig. 12C). The function(s) of the midgut are not entirely clear, but osmoregulation, nutrient absorption, and the production of the peritrophic membrane that wraps the fecal material of most decapods have been attributed to this region of the gut (Forster, 1953; Vonk, 1960; Talbot et al., 1972; Gibson and Barker, 1979; Felder, 1979; Hopkin and Nott, 1980, and many others).

The Midgut Ceca. In many decapod crustaceans, the midgut gives rise to blindly ended ceca in a variety of locations and patterns (see Mykles, 1977; Smith, 1978, for review). Anterior (at the foregut juncture) and posterior midgut ceca (PMGC, arising from the midgut–hindgut juncture) have been described from many decapods (Smith, 1978). As an example of this common but little known gut appendage, the posterior midgut cecum of the thalassinoid mudshrimp *Lepidophthalmus louisianensis* will be described.

The PMGC extends dorsally from the juncture of the midgut and hindgut (Figs. 4, 13A,B) and lies freely in the hemocoel. A large acinar tegumental gland complex surrounds the gut at the midgut–hindgut junction at the level where the PMGC arises from the gut proper (Figs. 4, 13A,B; Felgenhauer, chapter 2, External Anatomy and Integumentary Structures, this volume). The gland cells empty their contents via ducts that exit at the anterior region of the hindgut. The PMGC is composed of tall columnar cells exhibiting a microvillous border lacking a glycocalyx (Fig. 13C). The nuclei are basally located, with most of the common cell organelles such as Golgi complexes, mitochondria, RER, and extensive fields of basally located SER (Fig. 13C). Electrondense cellular inclusions are also commonly found throughout the cytoplasm (Fig. 13C). A presumably unique feature of the PMGC is the presence of cells within the connective tissue on the hemocoel side of the PMGC. These cells contain large numbers of myelinlike figures or multilamellar bodies similar to those found within the surfactant-producing type II alveolar cells of vertebrate lung (Fig. 13D–F; see Williams, 1977).

The Hindgut

The hindgut of decapods is, like the foregut, ectodermally derived and lined with chitin (Figs. 4, 12D,E). As is seen in the midgut, the length of the hindgut is variable throughout the Decapoda (see Smith, 1978, for discussion). The most striking feature of the decapod hindgut is the presence of cuticular scales (Fig. 12E) or groups of spines (Fig. 12D). These cuticular modifications always direct their spines in the direction of the anus and presumably aid in movement of the fecal mass toward the anus.

RESPIRATORY SYSTEM
Branchiae (Gills)

All decapod crustaceans possess branchiae (gills), with the exception of the aberrant dendrobranchiate shrimp *Lucifer* (Sergestoidea). The number and arrangement of gills varies depending on the species, but typically four gills are attached to some or all of the thoracic somites. One gill blanket, the pleurobranch
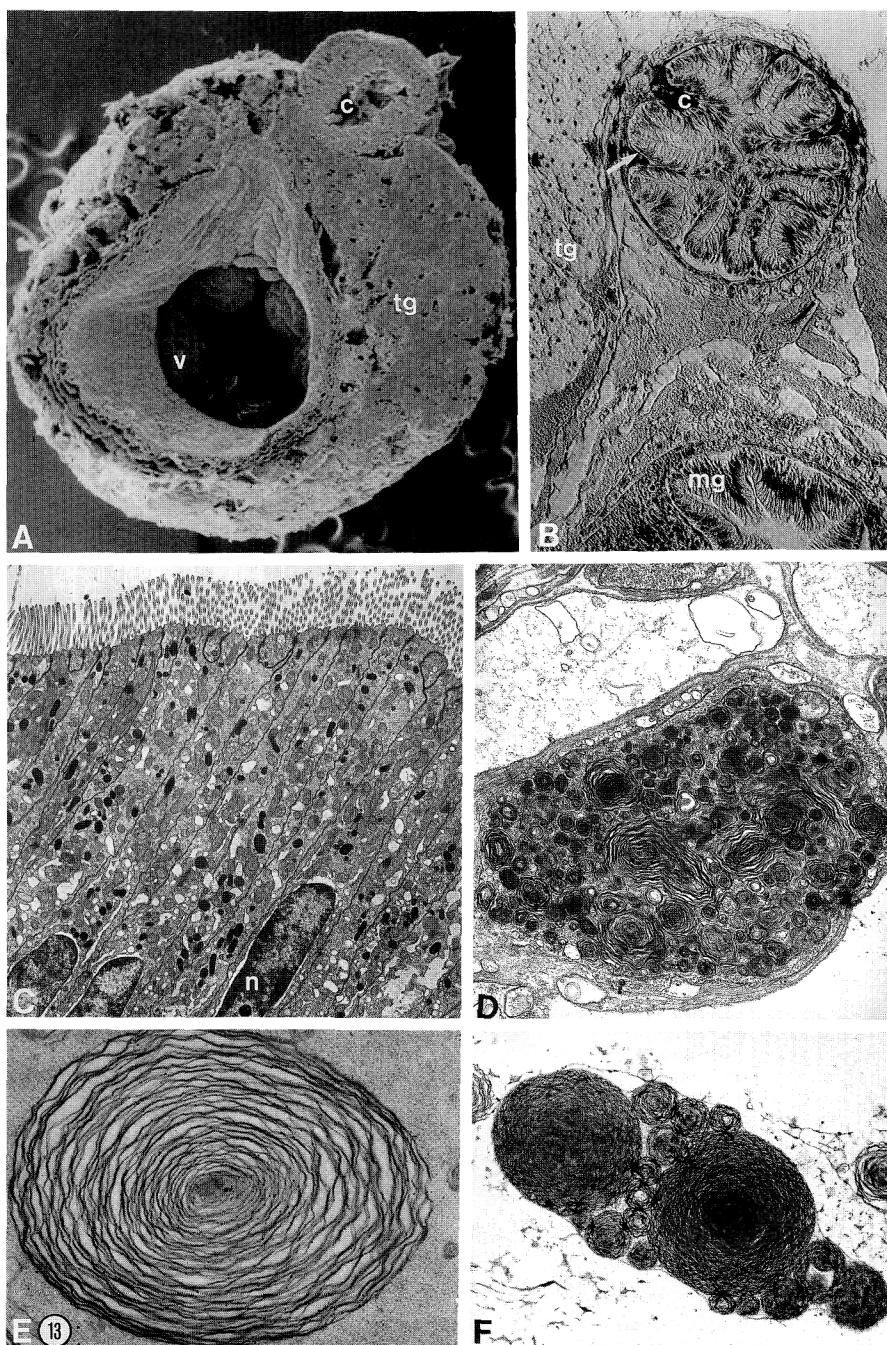
Fig. 13. Posterior midgut cecum (PMGC) of *Lepidophthalmus louisianensis*. **A:** Paraffin-carved cross section through the midgut–hindgut juncture; note the dorsal cecum (c), tegumental gland mass (tg) surrounding the juncture, and the internal valves (v). SEM. ×150. **B:** Histological cross section through the anterior midgut and PMGC; arrow indicates basement membrane of the PMGC. ×600. **C:** Ultrastructure of columnar cells making up the PMGC. TEM. ×2,900. **D:** Surfactant cell of PMGC; note fields of myelin-like multilamellar bodies. TEM. ×8,500. **E:** Close-up of multilamellar body. TEM. ×25,000. **F:** Freeze-substitution of multilamellar bodies. TEM. ×12,000.
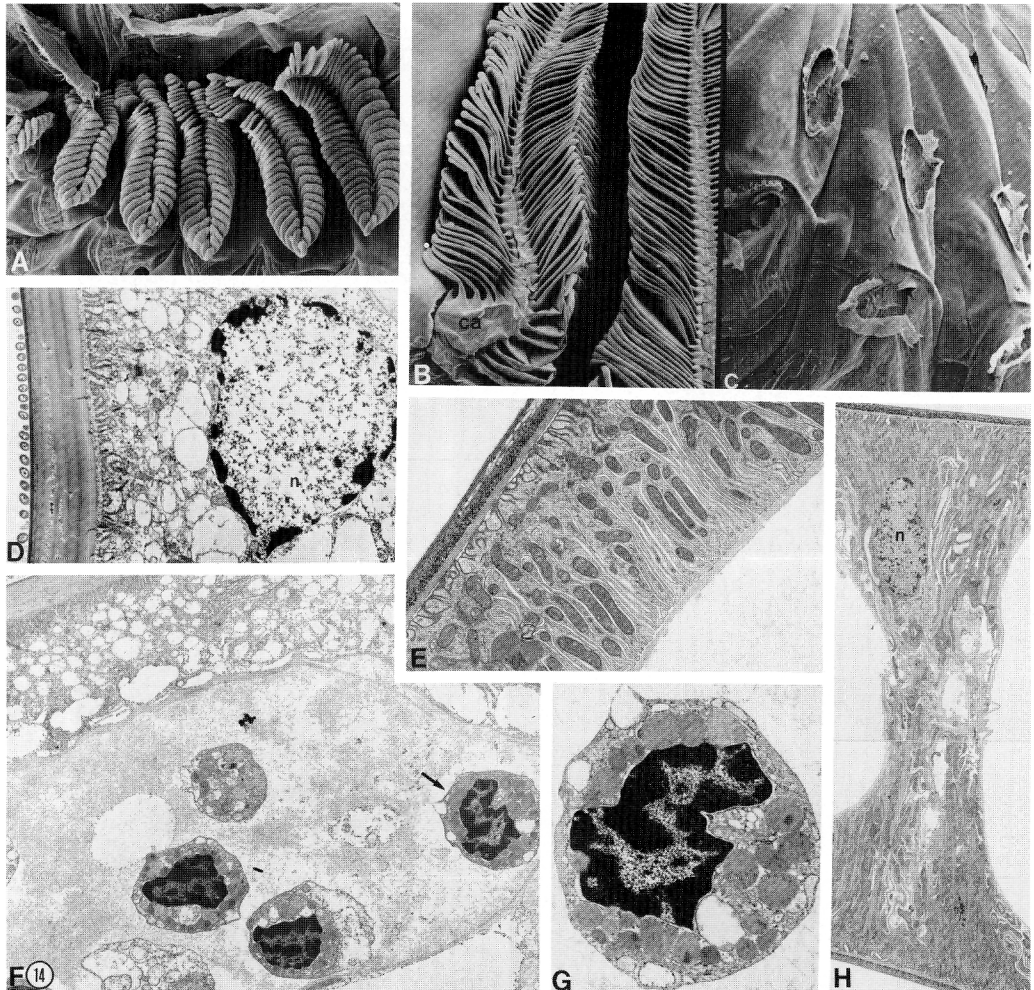
Fig. 14. Ultrastructure of decapod gills. **A:** Lateral view of phyllobranch gills of *Palaemonetes kadiakensis*. SEM. ×30. **B:** Phyllobranch gill of *Ranilia* sp.; note central axis (ca). **C:** Attachment sites of phyllobranch gills of *Systellaspis* (gills removed by sonication). SEM. ×100. **D:** Ultrastructure of phyllobranch gill cuticle from *Sesarma reticulatum;* note row of bacteria on outer surface. TEM. ×10,000. **E:** Ion regulatory region of the phyllobranch gill of *Callinectes sapidus* sp.; note mitochondria in elaborate basal infoldings. TEM. ×18,000. **F:** Low-magnification view of the hemocoel below the gill cuticle of *Sesarma reticulatum;* note circulating hemocytes (arrow) within hemocoel. TEM. ×10,000. **G:** Close-up of hemocyte pictured in f. TEM. ×20,000. **H:** Pillar cell of *Callinectes sapidus*. TEM. ×18,000. n, nucleus.

(Fig. 14C), is usually attached to the lateral wall of the somite dorsal to the articulation of the walking leg. Two gills, the arthrobranchs (Fig. 14C), are usually attached to the arthrodial membrane between the coxa and the body wall. The remaining gill, the podobranch, is attached to the coxa of the walking leg (pereiopod) (Calman, 1909).

The arrangement of the gills on the thoracic somites, walking legs, and mouthparts is termed the branchial formula (Fig. 14A) and is commonly used in most modern species descriptions of decapods.

Gill Types. Three distinct gill morphologies, dendrobranchiate, trichobranchiate, and phyllobranchiate (Fig. 15A–F), are found among the members of the Decapoda. The dendrobranchiate gill (Fig. 15A,B) is unique
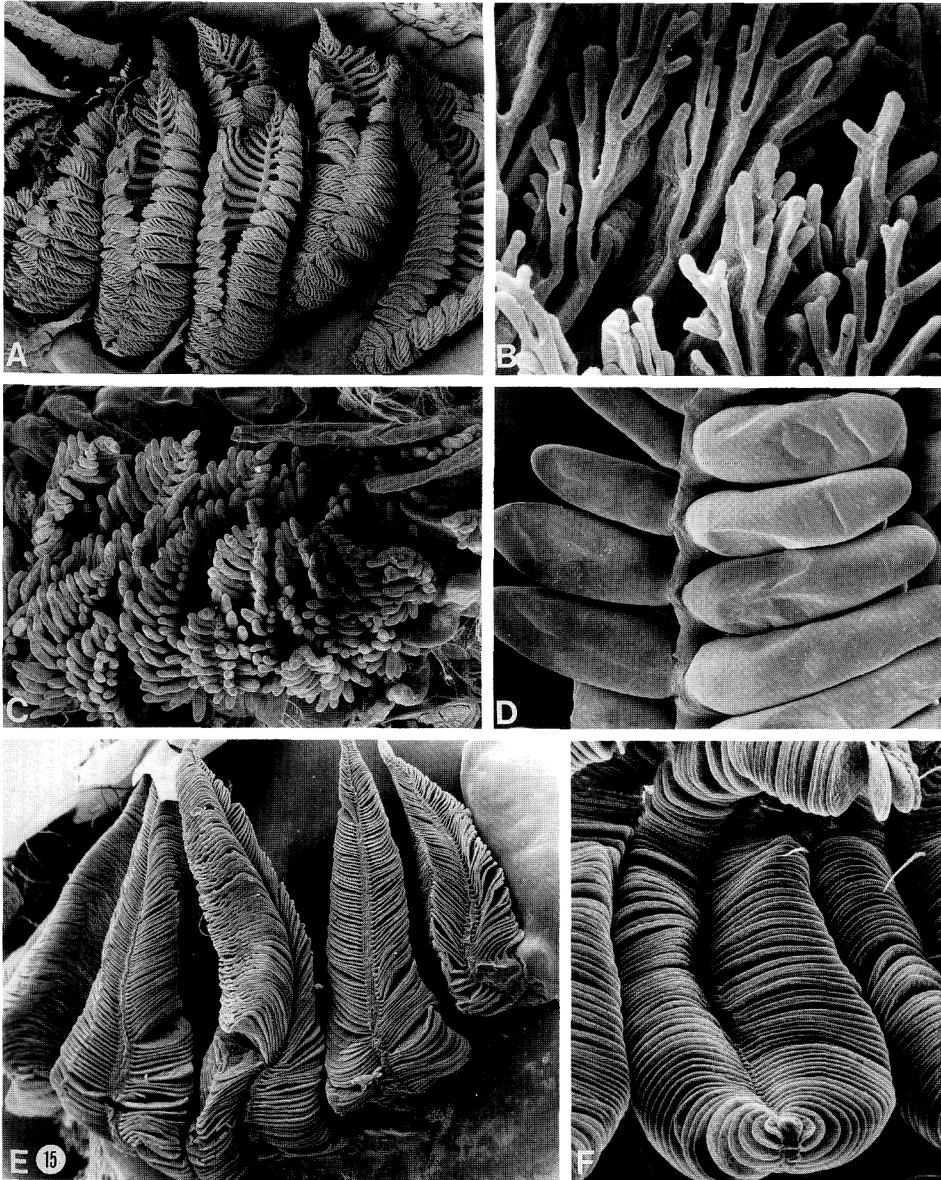
Fig. 15. Gill types of the Decapoda. SEM. **A:** Dendrobranchiate gills of *Penaeus setiferus*. ×50. **B:** Close-up of dendrobranchiate gill lamellae of *Penaeus setiferus*. ×125. **C:** Trichobranchiate gills of *Stenopus hispidus*. ×50. **D:** Close-up of trichobranchiate gill lamellae of *Nephrops* sp. ×220. **E:** Phyllobranchiate gills of *Ranilia* sp. ×15. **F:** Close-up of phyllobranchiate gills of *Lysmata wurdemanni*. ×200.

to the suborder Dendrobranchiata (penaeoid and sergestoid shrimps). The trichobranchiate (Fig. 15B,C) and phyllobranchiate gills (Figs. 14A,B, 15E,F) are widely distributed in apparently unrelated taxa throughout the suborder Pleocyemata (Felgenhauer and Abele, 1983). It must be noted, however, that intermediate forms of the above types are not uncommon throughout the Decapoda (Calman, 1909; Felgenhauer and Abele, 1983).
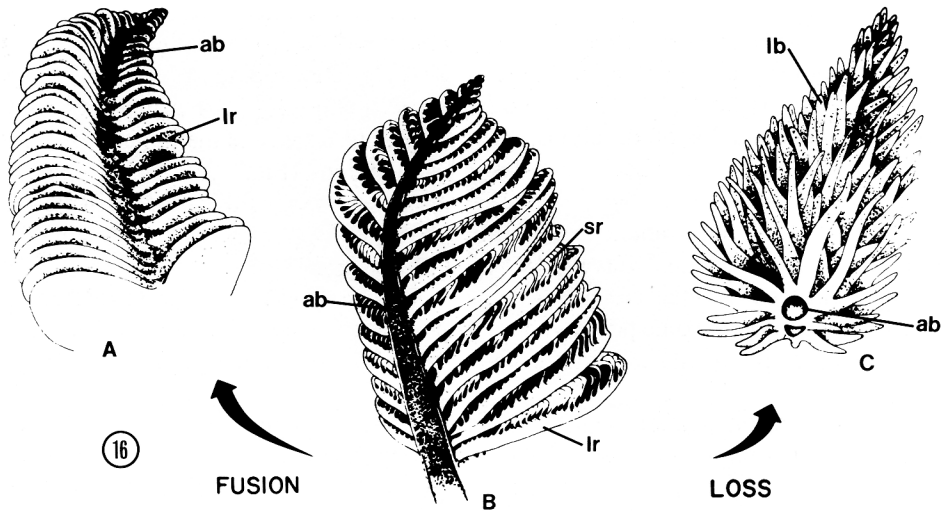
Fig. 16. Hypothesis suggested by Boas (1880) and Burken-road (1981) for the evolution of gill types among the Decapoda. **B:** Typical dendrobranchiate gill, consisting of lateral branches (lb,lr) extending from the main branchial axis (ab) with a series of subdivided secondary rami (sr) from each lateral branch. Expansion of the lateral branches of the dendrobranchiate type would result in **A,** phyllobranchiate gill. Loss of secondary rami (sr) and/or reduction of the lateral branches would give rise to **C,** trichobranchiate gill. (From Felgenhauer and Abele, 1983.)

The dendrobranchiate gill (Fig. 15A,B) has paired lateral branches arising from the central branchial axis, with a series of subdivided secondary rami coming off each lateral branch (Fig. 15B). Variation does occur and the secondary rami may be rather complex, as in some species of sergestid shrimp. The trichobranch gill is characterized by serial, tubular rami arising from the central branchial axis (Fig. 15C,D). No secondary rami are ever present as in dendrobranch gills. The phyllobranch gill exhibits flat paired lamellar branches extending from the branchial axis (Fig. 15E,F). The lamellar branches are much more flattened and leaflike than those of the trichobranch gill (Fig. 14B).

Huxley (1878) and Bate (1888) suggested that the trichobranchiate gill type gave rise to the dendrobranchiate and phyllobranchiate types. Boas (1880) and Burkenroad (1981) both suggested that the dendrobranchiate gill could have given rise to the trichobranchiate and phyllobranchiate gills. Whichever suggestion is correct, there is little doubt that the phyllobranchiate condition represents the de-

rived state (Fig. 16; Felgenhauer and Abele, 1983).

Branchial Ultrastructure. The branchiae are the primary sites of respiration in decapods. Additionally, these structures have been found to play a role in ion regulation and excretion (Gilles and Pequeux, 1985, and references therein). The branchial cuticle may vary greatly in its thickness, depending on whether the gills are anterior or posterior in the branchial chamber. Morphological differences may be seen in anterior gills, which may have a respiratory function versus the posterior lamellae that serve as ion regulators (Copeland, 1968; Barra et al., 1983; Towle and Kays, 1986; Goodman and Cavey, 1990). Thicker epithelial conditions are seen in areas involved with ion regulation (Fig. 14E) versus those that have a purely respiratory function (Fig. 14D). Those areas of the gill that function in ion regulation characteristically show extensive infoldings of the basal–lateral membranes and abundant mitochondria (Fig. 14E). Other regions of decapods (e.g., branchiostegites; see Talbot et al., 1972; Felder

et al., 1986; Taylor and Taylor, chapter 7, this volume) have also been determined to have ion regulatory and respiratory abilities.

At least six cell types have been reported within branchial epithelia of decapods: the chief cells, pillar cells (= trabecular or pilaster cells), striated cells, glycocytes, nephrocytes (= podocytes), and granular cells (see Johnson, 1980; Goodman and Cavey, 1990, for review). Chief cells, pillar cells, and striated cells make contact at some point with the endocuticle of the gill lamella, whereas nephrocytes, glycocytes, and granular cells are not associated with the endocuticle (Foster and Howse, 1978; Goodman and Cavey, 1990). Chief cells make up the majority of the branchial epithelia (Goodman and Cavey, 1990). Pillar cells (Fig. 14H) are supportive cells that are thought to provide the structural framework facilitating efficient blood flow (Johnson, 1980; Ciofi, 1984, and others). Striated cells are usually restricted to areas near the excurrent hemolymph channel and presumably function in ion regulation (Goodman and Cavey, 1990). Nephrocytes are usually fixed phagocytic cells exhibiting interdigitating foot processes that attach by desmosomes to branchial membranes. Nephrocytes filter hemolymph via pedicel pore diaphragms and the basal lamina. Sequestered substances are enclosed within vacuoles in these cells (Fontaine and Lightner, 1974; Foster and Howse, 1978; Johnson, 1980; Goodman and Cavey, 1990). Glycocytes and granulocytes are packed with glycogen granules and complex fibrillar aggregates (Foster and Howse, 1978; Goodman and Cavey, 1990). Little is known concerning the function of these cells other than storage.

REPRODUCTIVE SYSTEM
Male System

The Testes. In general, the testes lie dorsally in the posterior third of the thoracic cavity and may, in some groups (e.g., most reptant decapods), extend diverticula into the abdominal somites. In dendrobranchiate shrimps, the testes are lobular in form. The testes of caridean shrimps are simple tubes connected to one another anteriorly (Fig. 17A,B). Developing spermatids (= spermatocytes) (Fig. 17C) are usually round to oval within the testes and mature as they transit the vas deferens (Fig. 17F) to the gonopore. A good discussion of this process in the caridean shrimp *Crangon* is found in Arsenault et al. (1979).

The Vas Deferens. The vas deferentia are paired structures that conduct spermatozoa from the testes to the genital apertures (gonopores) at the base of the fifth walking legs (Fig. 17F). In addition to acting as a conduit for spermatozoa, the vas deferens is also responsible for "packaging" the spermatozoa into a spermatophore (Fig. 17E). Within the dendrobranchiate and caridean shrimp, the spermatophore is a simple cordlike mass. The spermatophore of most brachyuran and anomuran crabs are singular units of spermatozoa or "sperm balls" (Fig. 17G). However, in some species of the lower brachyuran crabs (e.g., *Dromidia, Ranilia*) and some anomuran crabs (e.g., *Clibanarius*), spermatophores are linked to one another in a chainlike fashion via a thin membranous sheath.

The Spermatozoa. Decapod spermatozoa are rather unusual among invertebrates in being aflagellate and nonmotile. The spermatozoa of decapods can be divided into those that exhibit a single spike, unistellate spermatozoa (Fig. 18A–E), to those with a variable number of spikes that surround the cell body, multistellate spermatozoa (Fig. 18F). Natant decapods typically exhibit the unistellate condition, whereas many reptant decapods are multistellate in form. Below I describe briefly the basic ultrastructural features of each morphological type.

Unistellate Spermatozoa. This spermatozoan type is frequently referred to as "thumbtack" or "button" type, owing to the spermatozoans' resemblance to tacks (Fig. 18A–E). Three distinct regions can be discerned at the ultrastructural level: the cell body, cap, and spike (Fig. 18A–D). The cell body contains the typically uncondensed nucleus, which is
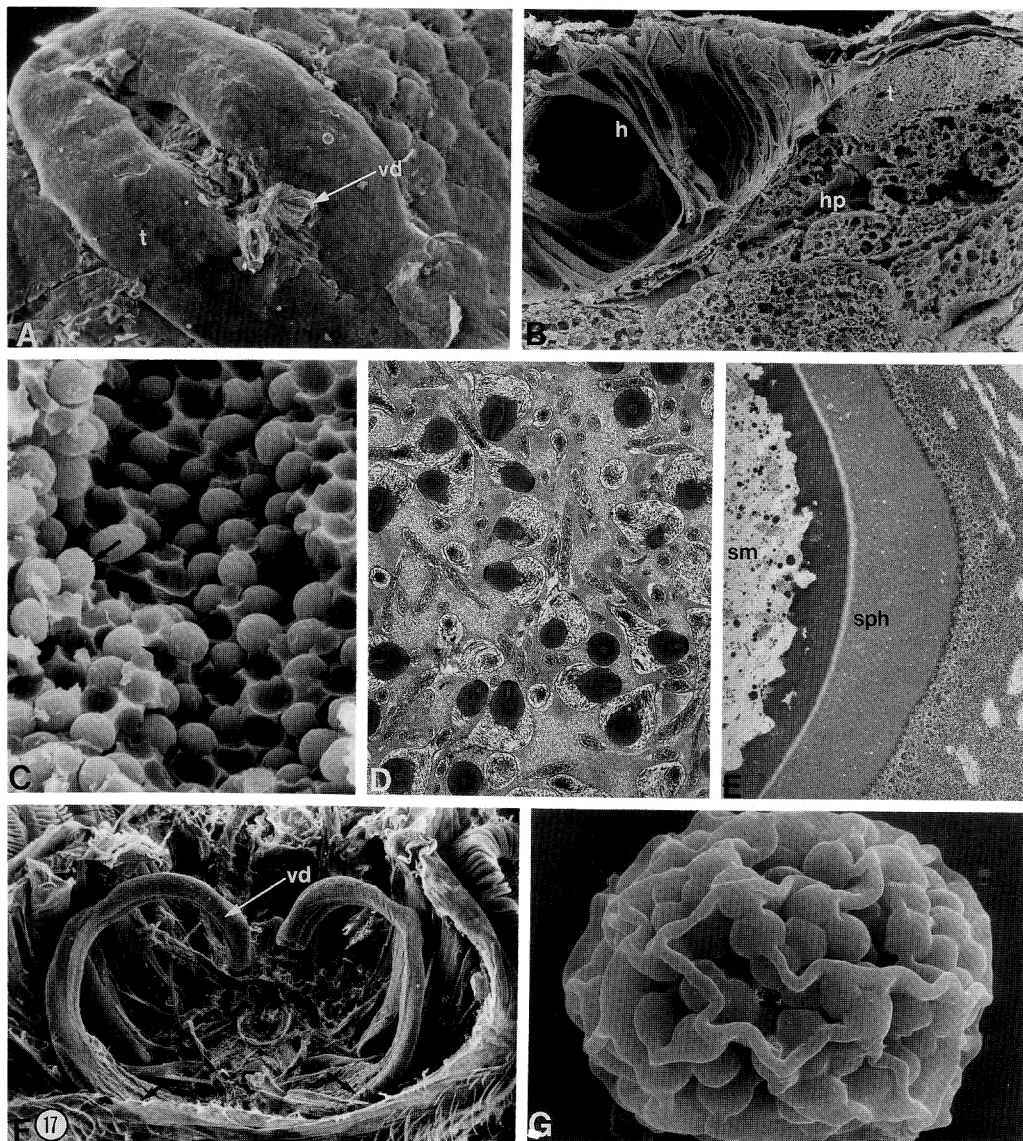
Fig. 17.   Features of the male reproductive system. **A:** Bilobed testis of *Lysmata wurdemanni;* note the vas deferentia that exit each lobe of the testis. SEM. ×125. **B:** Sagittal paraffin-carved section (SEM) through the male thorax of *Procaris ascensionis;* note the lobe of the testis lying dorsal to the hepatopancreas. ×100. **C:** Spermatids (arrows) within the testis of *Penaeus setiferus.* SEM. ×900. **D:** Multistellate spermatozoa of *Iliacan-tha* sp. within the testis. TEM. ×3,800. **E:** Spermatophore wall and internal sperm mass of *Palaemonetes kadiakensis.* TEM. ×8,000. **F:** Vas deferens of *Lysmata wurdemanni;* note they exit at the base of the fifth pereiopod (black arrows). SEM. ×45. **G:** Spermatophore (sperm ball) of *Parthenope* sp. SEM. ×200. h, heart; hp, hepatopancreas; sm, sperm mass; sph, spermatophore wall; t, testis; vd, vas deferens.

not bounded by a nuclear envelope (Fig. 18C). In addition to the nucleus, mitochondria may be present (sometimes only present in spermatids in some species; see Koehler, 1979).

The cap region contains electron-dense fibrils of varying diameters and accompanying centrioles (one or two) in the central portion just above the spike. These fibrils usually exhibit a characteristic cross-striated pattern
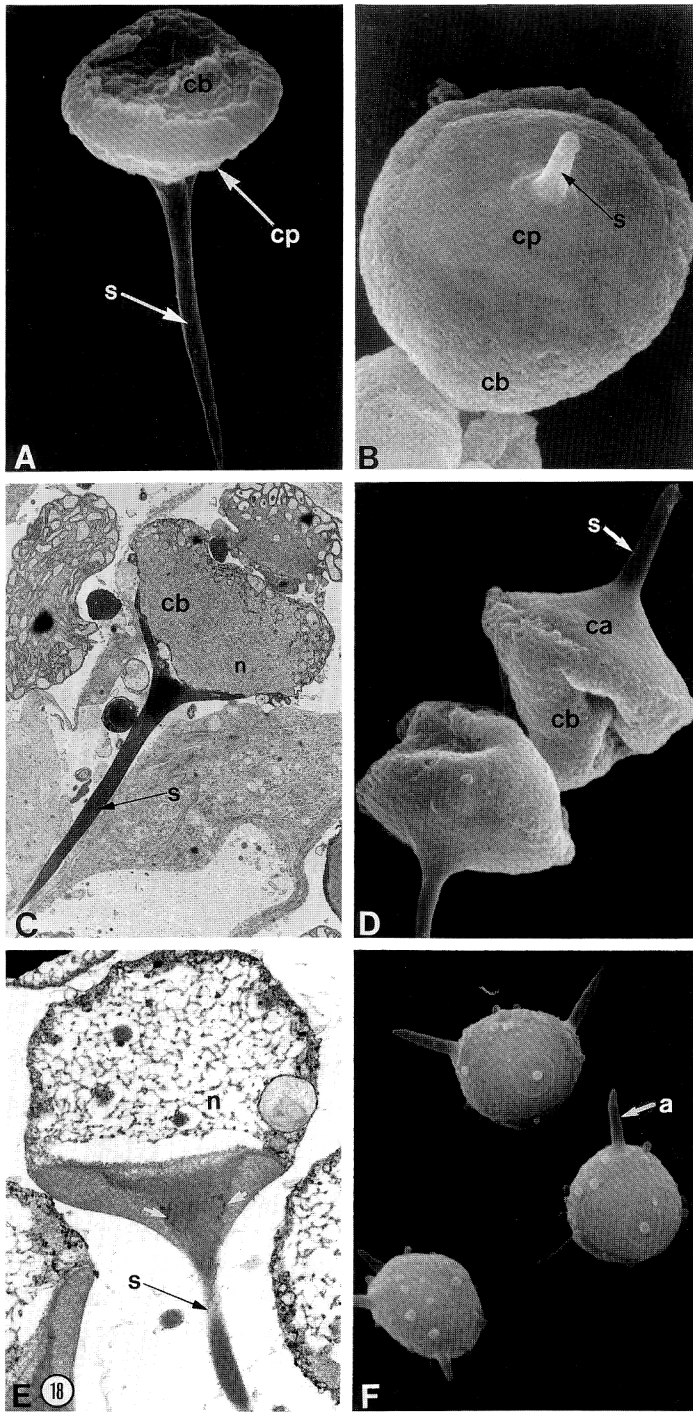
Fig. 18.   Spermatozoan types of the Decapoda. **A:** Unistellate spermatozoan of *Palaemonetes kadiakensis*. SEM. ×4,000. **B:** Ventral view of spike region of spermatozoan pictured in A; note that the three basic divisions (spike, cap, and cell body) of the spermatozoan can be easily recognized. SEM. ×10,000. **C:** Transverse section through unistellate spermatozoan shown in A. TEM. ×4,200. **D:** Unistellate spermatozoa of *Penaeus setiferus*. SEM. ×4,000. **E:** Transverse section of unistellate spermatozoan pictured in D. TEM. ×4,500. **F:** Multistellate spermatozoa of *Callinectes sapidus;* note multiple arms (a) extending from the cell body. SEM ×4,100. s, spike; cp, cap; cb, cell body; n, nucleus.

in many species (Koehler, 1979; Lynn and Clark, 1983b; Felgenhauer and Abele, 1988). The fibrils may anastomose and extend down into the spike (Fig. 18C). An organized acrosomal complex has been described for the dendrobranchiate shrimp *Sicyonia ingentis* by Kleve et al. (1980), but for most species, especially caridean shrimp, no distinct acrosome has been demonstrated. Shigekawa and Clark (1986) provide an excellent discussion of what is known concerning the acrosomal reaction.

The spike may be elongate in some species (Fig. 18A–C) to quite short in others (e.g., *Crangon;* see Arsenault et al., 1979; Boddeke et al., 1991). Two basic types of spike association with the egg surface have been described: either a spike-first contact with the egg (Kleve et al., 1980; Barros et al., 1986) or a cap-first egg interaction (Lynn and Clark, 1983a,b).

Multistellate Spermatozoa. This spermatozoan type is a multistellate cell with radiating arms (= spikes of some authors) extending from the cell body (Fig. 18F). These appendages are not homologous to the unistellate spike (Talbot and Summers, 1978; Hinsch, 1986). The most striking feature of this gamete is its highly structured acrosome (Fig. 19A,B). The nucleus surrounds the large electron-dense acrosomal complex that is composed of several distinct ultrastructural features. The acrosomal vesicle is bilayered in most brachyuran crabs, consisting of an inner and outer region (Fig. 19A,B,D). The acrosomal vesicle may be flanked by a prominent lamellar region (Fig. 19A,B). The acrosomal tubule is presumably supported by a battery of microfilaments or microtubules (Fig. 19A–D), depending on the species. The anterior portion of the acrosomal tubule is covered by a distinct electron-dense acrosomal cap (Fig. 19A,B). At the base of the acrosomal tubule is a thickened ring that evidently aids in the support of the tubule (Fig. 19A). The nucleus may or may not extend into the usually stellate arms. The brachyuran crab *Iliacantha* sp. exemplifies nuclear penetration into the arms (Fig. 19E,F). Other species of reptant decapods may have a microtubular component within the radiating arms, as in the crayfish *Procambarus leonensis* (Fig. 20A–C,E). The acrosomal reaction is essentially an eversion of the cell, turning the acrosome "inside out" with subsequent injection of the nucleus (Brown, 1966, Talbot and Chanmanon, 1980; Goudeau, 1982, and others; Fig. 19G).

The spermatozoan of astacoid reptant decapods (e.g., crayfish) is different in its organization from that described above. The prominent acrosomal vesicle is horseshoe-shaped and is not bilayered, but is crystalline in nature (Fig. 20A,D). The acrosomal tubule is much reduced and distinct microtubules are not easily discerned (Fig. 20D,F). The radiating arms are greater in number (up to 20 or more in some species) and are supported by microtubular arrays (Fig. 20A,B,E). The cell membrane of this gamete is much thicker than that of most decapod spermatozoa and has been termed the cell capsule (Fig. 20A,E). Mechanics of the acrosomal "reaction" and egg interactions have not been described.

Female System

The ovary is located in the dorsal portion of the cephalothorax in the same relative position as the male testis (Fig. 3), e.g., lying dorsal to the hepatopancreas (Fig. 12A). As in the testis, the ovary is paired and its size depends on the age and reproductive condition of the individual. Unlike the testis, the ovary commonly extends into the abdominal somites, and in some groups, such as many of the anomuran crabs, the ovary is restricted to this position (Kaestner, 1970; McLaughlin, 1983). Details concerning the maturation process and ultrastructural features of the ovary and follicles can be found in Johnson (1980) and Talbot (1981a,b). In macrurous forms, the ova pass from the ovary down the oviducts and exit via the gonopore on the third walking legs (pereiopods). In brachyurous forms, the short oviducts lead to a saclike spermatheca within the musculature of the second walking
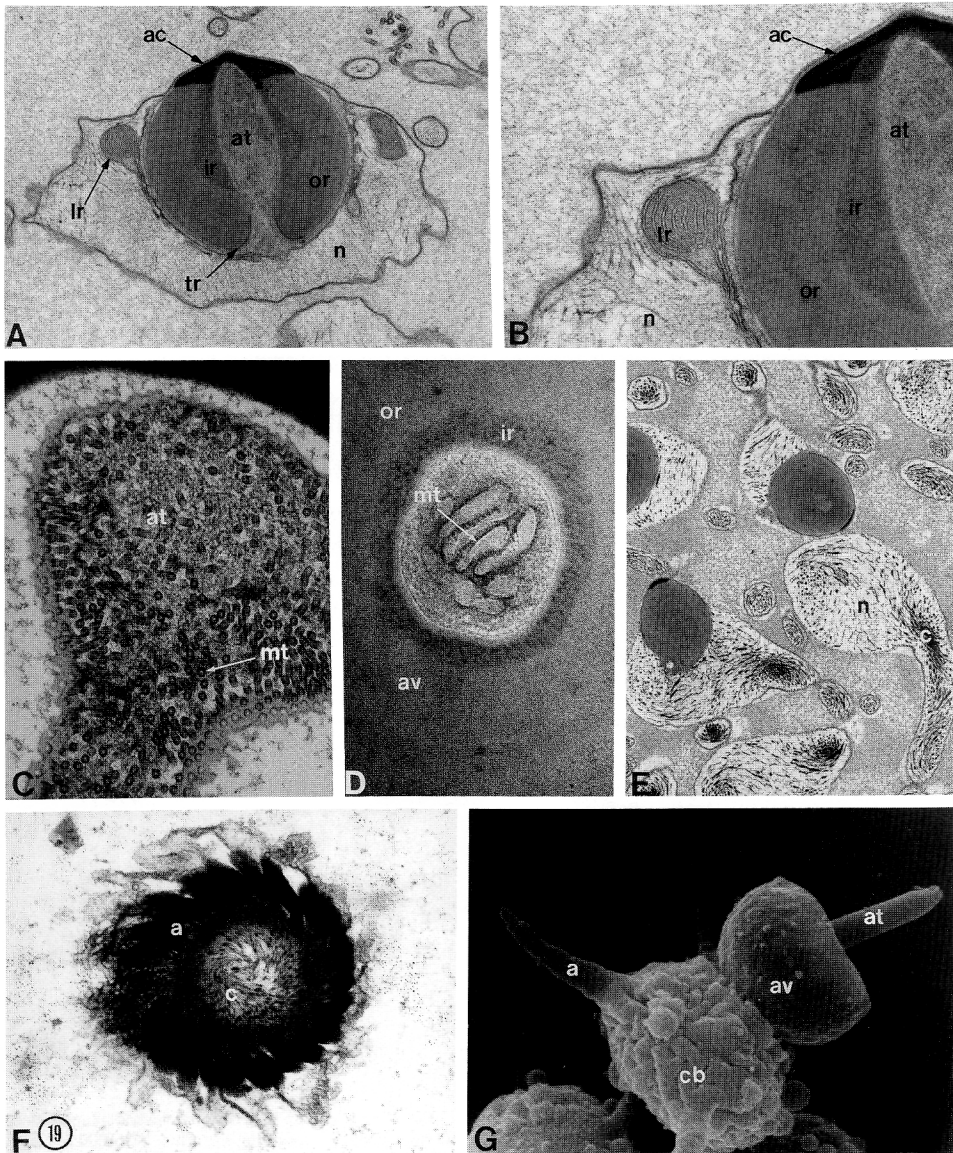
Fig. 19. Ultrastructural details of decapod multistellate spermatozoa. A–F by TEM. **A:** Multistellate spermatozoan of *Callinectes sapidus*. ×3,000. **B:** Close-up of acrosomal region of *Callinectes sapidus*. ×10,000. **C:** Oblique section through acrosomal tubule from the spermatozoan of *Parthenope* sp.; note numerous microtubules (arrow). ×22,000. **D:** Cross section through the acrosomal tubule of *Iliacantha* sp. Note the microtubules within the tubule and the bilayered condition of the acrosomal vesicle. ×80,000. **E:** Multistellate spermatozoan of *Iliacantha* sp. ×9,000. **F:** Cross-section through the arms of the spermatozoan pictured in E; note chromatin extending into the arms from the nucleus. ×35,000. **G:** Artificially induced acrosomal reaction of the multistellate spermatozoan of *Eurydium* sp. SEM. ×8,500. a, arm; ac, acrosomal cap; at, acrosomal tubule; av, acrosomal vesicle; cb, cell body; ir, inner region; lr, lamellar region; mt, microtubules; n, nucleus; or, outer region; tr, thickened ring.
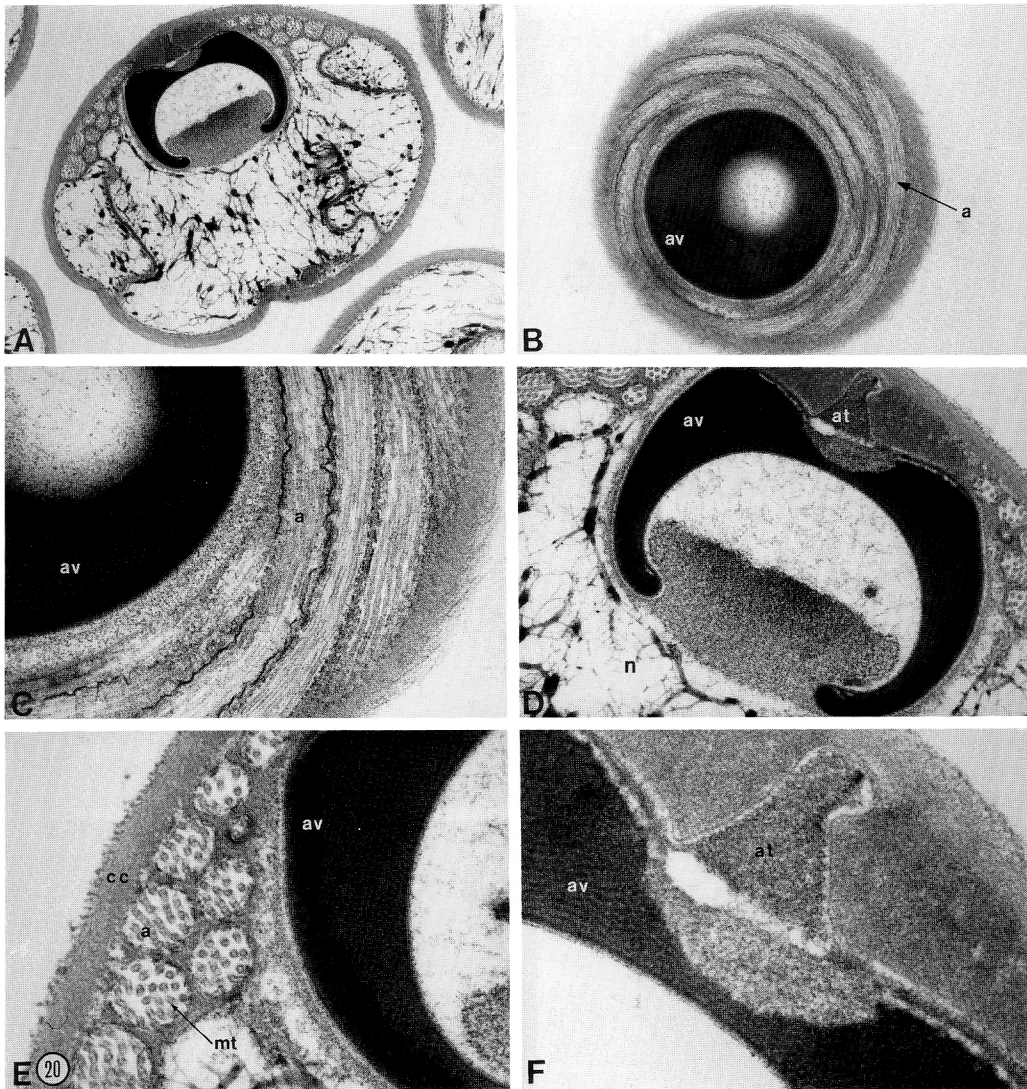
Fig. 20. Ultrastructural features of crayfish spermatozoa. TEM. **A:** Ultrastructural aspects of the spermatozoan of *Procambarus leonensis*. ×3,000. **B:** Oblique section through anterior region showing arms supported by microtubules. ×22,000. **C:** Close-up of acrosomal vesicle and microtubules within the arms. ×40,000. **D:** Ultrastructural details of acrosome. ×36,000. **E:** Close-up of acrosomal vesicle; note thick cell coat and microtubules supporting the arms. ×36,000. **F:** High magnification of acrosome and presumed acrosomal tubule. ×50,000. a, arm; av, acrosomal vesicle; at, acrosomal tubule; cc, cell coat; mt, microtubules; n, nucleus.

legs (pereiopods). Unlike most macrurous decapods, internal fertilization is practiced by this large group of crabs and spermatozoa are stored within the spermatheca following copulation. The eggs are fertilized as they pass onto the abdominal pleopods for brooding (Warner, 1977). The method by which decapods incubate their eggs varies depending upon the group. Dendrobranchiate decapods release eggs into the water (although *Lucifer* carries them briefly on the pereiopods; Burkenroad, 1981), while all other decapods

for which data are available carry the eggs on the pleopodal setae (Felgenhauer and Abele, 1983).

THE EXCRETORY–OSMOREGULATORY SYSTEMS

The antennal, urinary or green glands are paired excretory organs located at the base of the second antennae. The excretory pore exits on the coxa of the antenna (Fig. 21A, arrow) and its location is a constant feature among decapods. Antennal glands are generally composed of four components: the coelomosac (= end sac), labyrinth, proximal and distal tubules (= nephridial canal), and bladder (Fig. 22). The description below is of the green gland of the crayfish *Procambarus leonensis*.

The mesodermally derived coelomosac is composed of podocytes that perform an ultrafiltration function similar to that of the vertebrate glomerular nephron (Kummel, 1964; Schmidt-Nielsen et al., 1968; Tyson, 1968; Peterson and Loizzi, 1974; Johnson, 1980). The labyrinth is composed of an extensive network of coiled cuboidal cells in the inactive state and columnar cells in the active secretory condition. The labyrinth cells typically have a centrally located nucleus (Fig. 21E) with numerous mitochondria packed within the extensive infoldings of the basal lamina (Fig. 21F,G) characteristic of transport tissue (e.g., gills, branchiostegite; Mantel and Farmer, 1983). The apical portion of these cells has an extensive brush border (Fig. 21E,F). The labyrinth is a transport system involved in the movement of ions and reabsorption of proteins (Peterson and Loizzi, 1974). The nephridial canal (= proximal–distal tubules) acts as the conduit between the labyrinth and bladder. The length of the nephridial canal varies greatly depending upon species. The bladder is usually a large reservoir for urine storage and may play a role in final urine modification (Riegel, 1972).

CIRCULATORY SYSTEM

The circulatory system of decapods is centered around a bulbous, dorsal heart, located in the posterior region of the cephalothorax. The heart receives blood through a series of ostia (Figs. 3, 23). It is surrounded by a pericardial sac that is penetrated by passageways where venous blood returns to the pericardial chamber. The number of ostia of the heart may vary depending on the species, but three pairs is the most commonly reported number (McLaughlin, 1983; Schram, 1986). The location of the ostia varies also from paired arrangements in the dorsal, lateral, and ventral positions around the heart (Figs. 12A, 23).

Figure 23 illustrates the general layout of the major arteries comprising the circulatory pattern of most decapods (Burnett, 1984). Several major arteries exit the anterior aorta (Fig. 23) servicing the rest of the body. The anterior aorta (= dorsal artery) may be equipped with an enlargement termed the cor frontale, first described by Baumann (1917). The basic anatomy of this modification is remarkably similar among the decapods studied by Steinacker (1978), who considered the cor frontale to function as an "auxiliary heart" (= accessory heart of Maynard, 1960).

The hemocytes of decapod crustaceans are circulating cells (Fig. 14F,G) of the hemolymph that perform a diversity of physiological and pathological functions (see Ravindranath, 1980; Bauchau, 1981; Hose et al., 1987), from wound repair (Fontaine and Lightner, 1973), to clotting of the hemolymph (Stutman and Dolliver, 1968), to hardening of the cuticle (Vacca and Fingerman, 1983), to name but a few. Classification of these cells has been attempted for many years, but owing to the different criteria used to determine types by many investigators, much confusion still remains and has prevented comparative inferences to be made on form and function (Martin and Graves, 1985); however, see Vascular Elements and Blood (Hemolymph) chapter 5, by Martin and Hose, this volume. Most of the investigations on these cells have been cytochemical in nature and were focused on devising a means of classifying these difficult cell lines (for discussion see Martin et al., 1987).
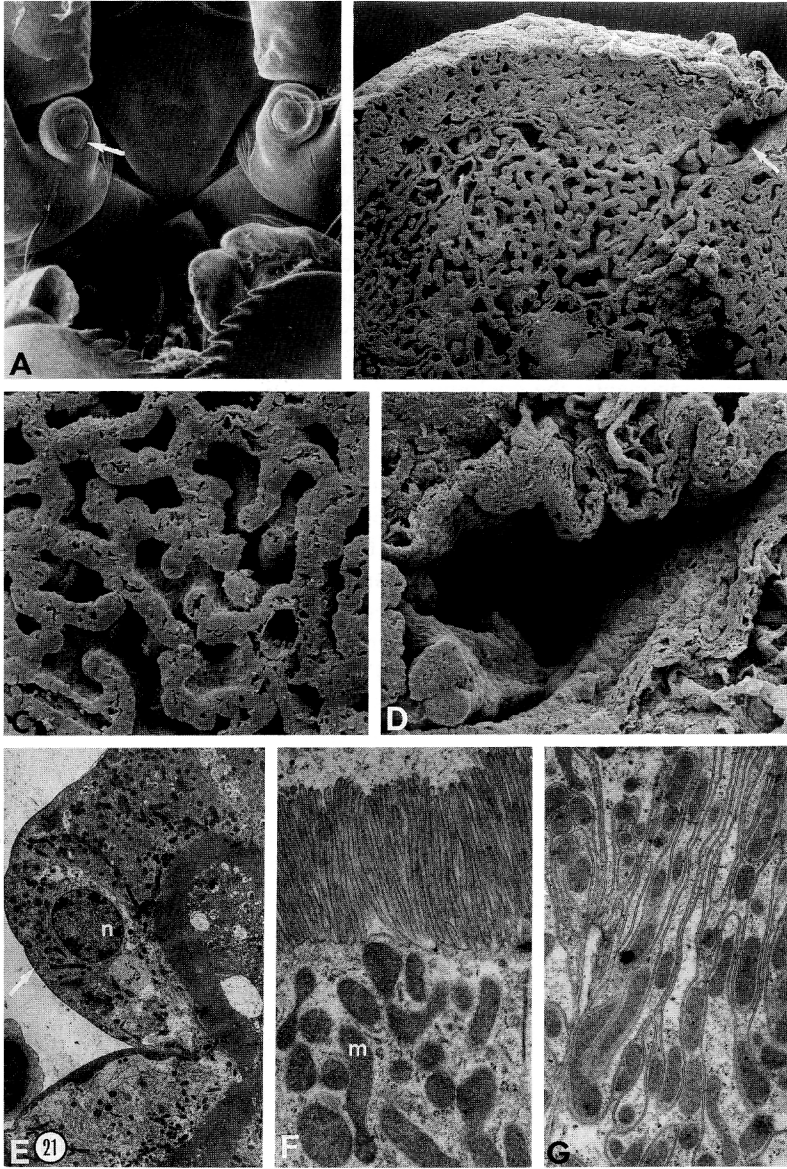
Fig. 21. Ultrastructural features of the decapod urinary and osmoregulatory systems. (A, from *Systellaspis* sp.; B–G are from *Procambarus leonensis*). **A:** Urinary pore (arrow) at base of antennal peduncle. SEM. ×50. **B:** Paraffin-carved section through the labyrinth region of the green gland; arrow indicates region that exits to the proximal tubule. SEM. ×50. **C:** Close-up of the convoluted cell layers of the labyrinth shown in B. SEM. ×450. **D:** Region of labyrinth that leads to the proximal tubule. SEM. ×200. **E:** Ultrastructure of the labyrinth cells; note centrally located nucleus (n). TEM. ×3,000. **F:** Close-up of brush border of labyrinth cells; note mitochondria (m) and long microvilli. TEM. ×18,000. **G:** Close-up of mitochondria packed within the basal lamina indicated by arrow in E. TEM. ×20,000.
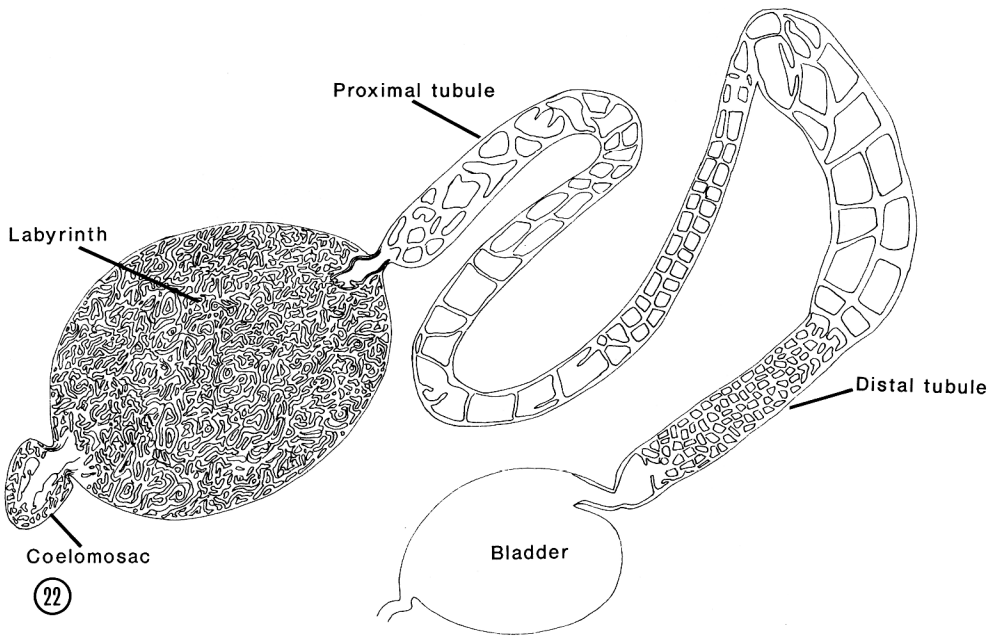
Fig. 22. Schematic drawing of the antennal green gland of the crayfish indicating the major regions of the gland. (After Riegel, 1972.)
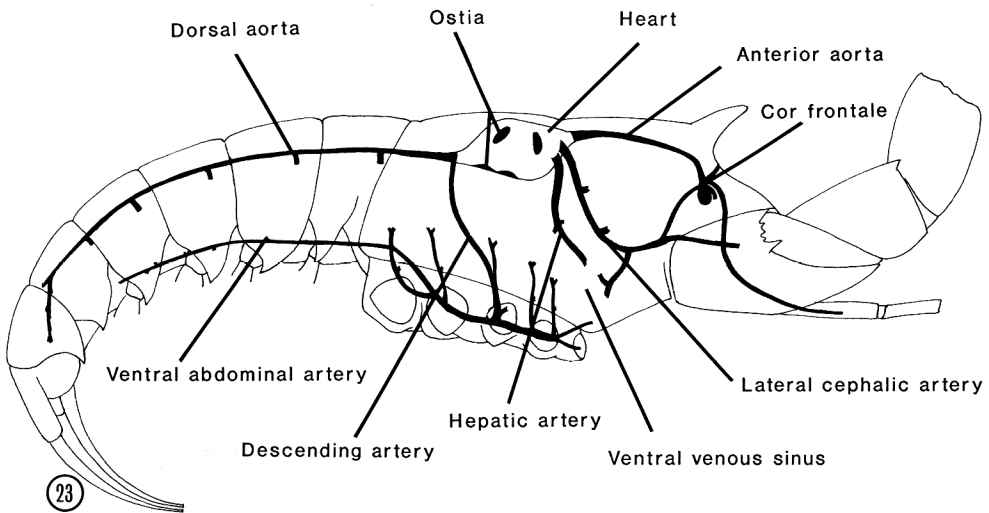

Fig. 23. Schematic drawing of the circulatory system of a typical decapod. (After Burnett, 1984.)
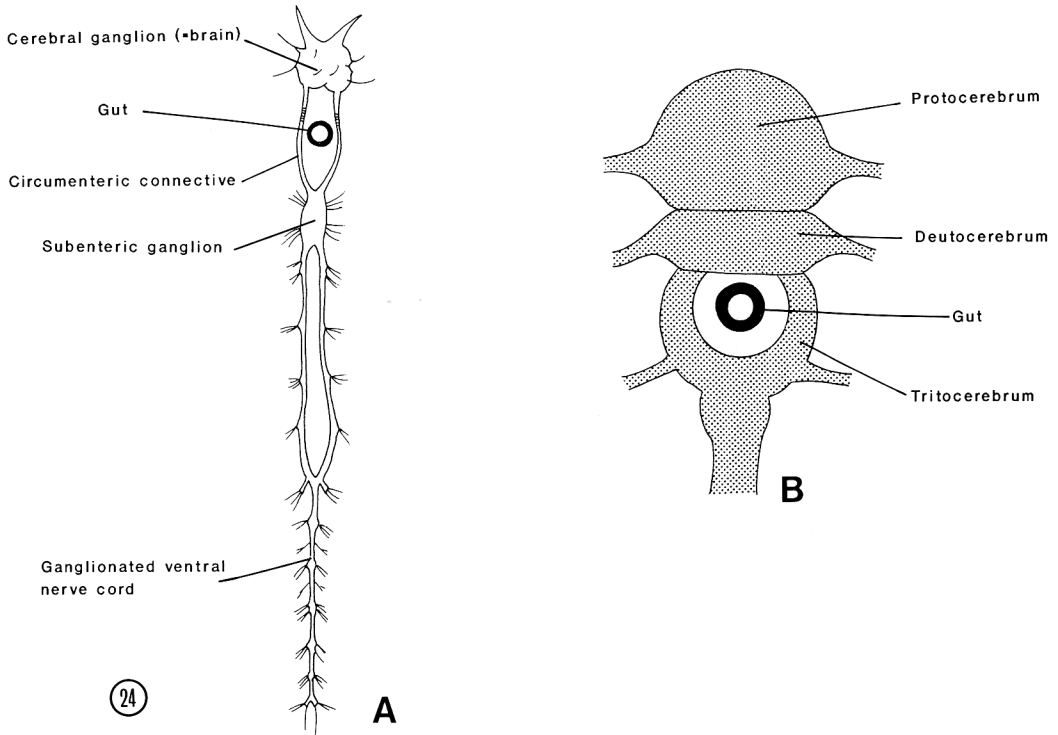
Cerebral ganglion (=brain)

Gut

Circumenteric connective

Subenteric ganglion

Ganglionated ventral
nerve cord

Protocerebrum

Deutocerebrum

Gut

Tritocerebrum

B

24

A

Fig. 24. **A:** The central nervous system of the crayfish, showing the basic ladderlike arrangement oi tne ventral nerve cord. **B:** Schematic drawing of the regions of the brain. (After Brusca and Brusca, 1990.)

optic nerve

tegumentary nerve

nerve to lst antenna

cerebral ganglion

stomatogastric ganglion

stomatogastric nerve

nerve to 2nd antenna

paraoesophageal ganglion

postoesophageal connective

circumoesophageal commissure

nerve to mandible
and lst and 2nd maxillae

nerves to maxillipeds

thoracic ganglion

foramen for the
descending artery

nerve to cheliped

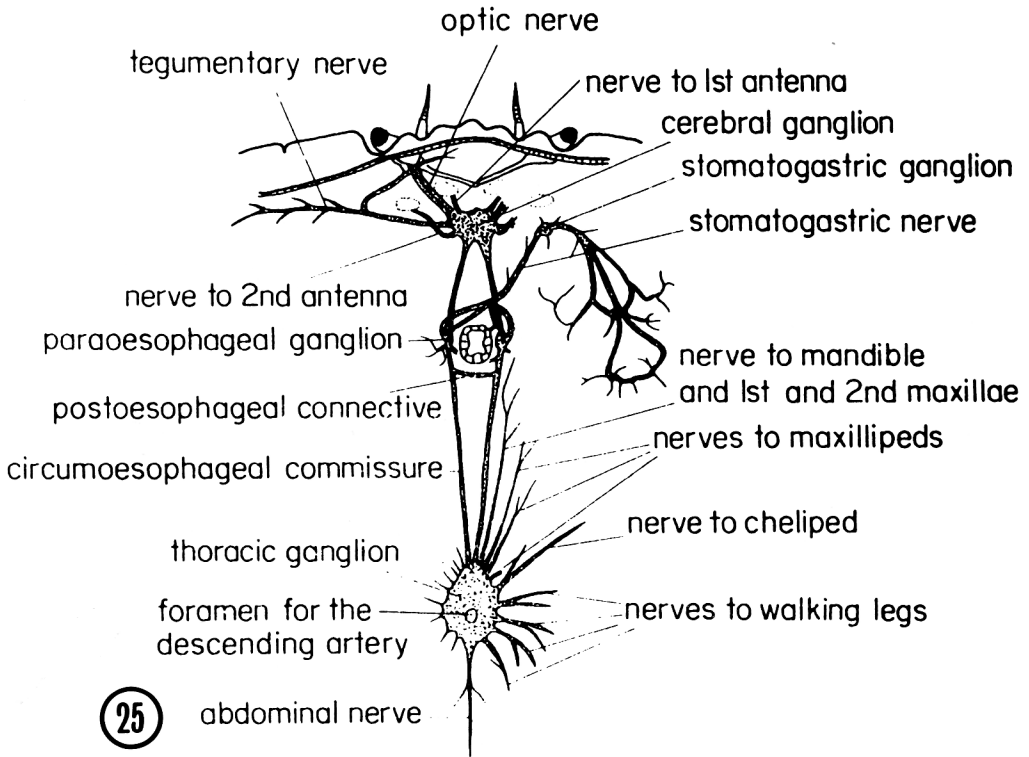nerves to walking legs

25

abdominal nerve

Fig. 25. The nervous system of a typical brachyuran crab. Note fusion of abdominal ganglia. (After Pearson, 1908.)

NERVOUS SYSTEM

The central nervous system is composed of a dorsal brain connected to a ventral longitudinal nerve cord located below the alimentary canal (Fig. 24). The brain is composed of three regions: the protocerebrum, deuterocerebrum, and tritocerebrum. The ventral nerve cord is typically a "ladderlike" system wherein fused paired ganglia occur in each of the abdominal somites of macruous forms and are reduced to a single postesophageal ganglion in brachyurous forms (Fig. 25).

ACKNOWLEDGMENTS

LITERATURE CITED

Al-Mohanna, S.Y., J.A. Nott, and D.J.W. Lane (1985) M-'Midget' cells in the hepatopancreas of the shrimp, *Penaeus semisulcatus* De Haan, 1844 (Decapoda, Natantia). Crustaceana *48:*260–268.

Arsenault, A.L., R.E. Clattenburg, and P.H. Odense (1979) Spermiogenesis in the shrimp, *Crangon septemspinosa* Say. Can. J. Zool. *57:*486–498.

Barker, P.L., and R. Gibson (1977) Observations on the feeding mechanism, structure of the gut and digestive physiology of the European lobster *Homarus gammarus* (L.) (Decapoda: Nephropidae). J. Exp. Mar. Biol. Ecol. *26:*297–394.

Barra, J.A., A. Pequeux, and W. Humbert (1983) A morphological study on gills of a crab acclimated to fresh water. Tissue Cell *15:*583–596.

Barros, C., E. Dupré, and L. Viveros (1986) Sperm–egg interactions in the shrimp *Rhynchocinetes typus*. Gamete Res. *14:*171–180.

Bate, C.S. (1888) Report on the Crustacea Macrura collected by HMS Challenger during the years 1873–1876. Challenger Rept. Zool. *24:*1–942.

Bauchau, A.G. (1981) Crustaceans. In N.A. Ratcliffe and A.F. Rowley (eds.): Invertebrate Blood Cells, vol. 2. New York: Academic Press, pp. 386–420.

Baumann, H. von (1917) Das Cor fontrale bei decapoden Krebsen. Zool. Anz. *49:*137–144.

Boas, J.E.V. (1880) Studier over Decapodernes Slaegtskabsforhold, Vidensk. Selsk. Kristiania, Skrifter. *6:*25–210.

Boddeke, J.R., J.R. Bosschieter, and P.C. Goudswaard (1991) Sex change, mating, and sperm transfer in *Crangon crangon* (L.). In R.T. Bauer and J.W. Martin (eds.): Crustacean Sexual Biology. New York: Columbia University Press, pp. 164–182.

Brown, G.G. (1966) Ultrastructural studies of sperm morphology and sperm–egg interaction in the decapod *Callinectes sapidus*. J. Ultrastruct. Res. *14:*425–440.

Brusca, R.C., and G.J. Brusca (1990) Invertebrates. Sunderland: Sinauer Associates.

Burkenroad, M.D. (1981) The higher taxonomy and evolution of Decapoda (Crustacea). Trans. San Diego Nat. Hist. *19:*251–268.

Burnett, B.R. (1984) Striated muscle in the wall of the dorsal abdominal aorta of the California spiny lobster *Panuliris interruptus*. J. Crust. Biol. *4:*560–566.

Calman, W.T. (1909) Crustacea. In E.R. Lankester (ed.): A Treatise on Zoology. London: Adam and Black, p. 346.

Ciofi, M. (1984) Comparative ultrastructure of arthropod transporting epithelia. Am. Zool. *24:*139–156.

Copeland, D.E. (1968) Fine structure of salt and water uptake in the land-crab, *Gecarcinus lateralis*. Am. Zool. *8:*417–432.

Davis, L.E., and A.L. Burnett (1964) A study of the growth and cell differentiation in the hepatopancreas of the crayfish. Dev. Biol. *10:*122–153.

Factor, J.R. (1981) Unusually complex basement membranes in the midgut of two decapod crustaceans, and the stone crab *(Menippe mercenaria)* and the lobster *(Homarus americanus)*. Anat. Rec. *200:*253–258.

Felder, D.L. (1979) Respiratory adaptations of the estuarine mud shrimp, *Callianassa jamaicense* (Schmitt, 1935) (Crustacea, Decapoda, Thalassinidea). Biol. Bull. *157:*125–137.

Felder, J.M., D.L. Felder, and S.C. Hand (1986) Ontogeny of osmoregulation in the estuarine ghost shrimp *Callianassa jamaicense* var. *louisianensis* Schmitt (Decapoda, Thalassinidea). J. Exp. Mar. Biol. Ecol. *99:*91–105.

Felgenhauer, B.E. (1987) Techniques for preparing crustaceans for scanning electron microscopy. J. Crust. Biol. *7:*71–76.

Felgenhauer, B.E., and L.G. Abele (1983) Phylogenetic relationships among shrimp-like decapods. In F.R. Schram (ed.): Crustacean Phylogeny. Crustacean Issues, vol. 1. Rotterdam, Netherlands: Balkema, pp. 291–311.

Felgenhauer, B.E., and L.G. Abele (1988) Reproductive morphology of the anchialine shrimp *Procaris ascensionis* (Decapoda: Procarididae). J. Crust. Biol. *8:*333–339.

Felgenhauer, B.E., and L.G. Abele (1989) Evolution of the foregut in the lower Decapoda. In B.E. Felgenhauer, L. Watling, and A.B. Thistle (eds.): Functional Morphology of Feeding and Grooming in Crustacea. Crustacean Issues, vol. 6. Rotterdam, Netherlands: Balkema, pp. 205–219.

Fontaine, C.T., and D.V. Lightner (1973) Observations on the process of wound repair in penaeid shrimp. J. Invert. Pathol. *22:*22–33.

Fontaine, C.T., and D.V. Lightner (1974) Observations on the phagocytosis and elimination of carmine particles injected into the abdominal musculature of the white shrimp, *Penaeus setiferus*. J. Invert. Pathol. *24:*141–148.

Forster, G.R. (1953) Peritrophic membranes in the Caridea (Crustacea: Decapoda). J. Mar. Biol. Assoc. U.K. *32:*315–318.

Foster, C.A., and H.D. Howse (1978) A morphological study on gills of the brown shrimp *Penaeus aztecus*. Tissue Cell *10:*77–92.

Gibson, R., and P.L. Barker (1979) The decapod hepatopancreas. Oceanogr. Mar. Biol. *17:*285–346.

Gilles, R., and A.J.R. Pequeux (1985) Ion transport in crusta-

cean gills: Physiological and ultrastructural approaches. In R. Gilles and M. Gilles-Baillien (eds.): Transport Processes, Iono- and Osmoregulation. Berlin, Heidelberg, New York: Springer, pp. 138–158.

Goodman, S.H., and M.J. Cavey (1990) Organization of a phyllobranchiate gill from the green shore crab *Carcinus maenas* (Crustacea, Decapoda). Cell Tissue Res. *260:*495–505.

Goudeau, M. (1982) Fertilization in a crab. I. Early events in the ovary, and cytological aspects of the acrosome reaction and gamete contacts. Tissue Cell *14:*97–111.

Herrick, F.H. (1896) The American lobster: A study of its habits and development. Bull. U.S. Fish. Comm. *15:*1–251.

Hinsch, G.W. (1986) A comparison of sperm morphologies, transfer and sperm mass storage between two species of crab, *Ovalipes ocellatus* and *Libinia emarginata.* Int. J. Invert. Reprod. Dev. *10:*79–87.

Hopkin, S.P., and J.A. Nott (1979) Some observations on concentrically structured, intracellular granules in the hepatopancreas of the shore crab *Carcinus maenas* (L.). J. Mar. Biol. Assoc. U.K. *59:*867–877.

Hopkin, S.P., and J.A. Nott (1980) Studies on the digestive cycle of the shore crab *Carcinus maenas* (L.) with special reference to the B cells in the hepatopancreas. J. Mar. Biol. Assoc. U.K. *60:*891–907.

Hose, J.E., G.G. Martin, V.A. Nguyen, J. Lucas, and T. Rosenstein (1987) Cytochemical features of shrimp hemocytes. Biol. Bull. *173:*178–187.

Huxley, T.H. (1877) The Anatomy of Invertebrated Animals. London: Churchill.

Huxley, T.H. (1878) On the classification and the distribution of the crayfishes. Proc. Zool. Soc. London *1878:*752–788.

Huxley, T.H. (1880) The Crayfish, An Introduction to the Study of Zoology. London: C. Kegan Paul.

Jacobs, W. (1928) Untersuchungen über die Cytologie der Sekretbildung in der Mitteldarmdrüse von *Astacus lepodactylus.* Zellforsch. Mikrosk. Anat. *8:*1–62.

Johnson, P.T. (1980) Histology of the Blue Crab, *Callinectes sapidus:* A Model for the Decapoda. New York: Praeger.

Kaestner, A. (1970) Invertebrate Zoology. London: Wiley, pp. 266–366.

Kleve, M.G., A.I. Yudin, and W.H. Clark (1980) Fine structure of the unistellate sperm of the shrimp *Sicyonia ingentis* (Natantia). Tissue Cell *12:*29–45.

Koehler, L.D. (1979) A unique case of cytodifferentiation: Spermiogenesis of the prawn, *Palaemonetes paludosus.* J. Ultrastr. Res. *69:*109–120.

Kummel, G. (1964) Das Coelomosacken der Antennendrüse von *Cambarus affinis* Say (Decapoda, Crustacea). Zool. Beitr. *10:*227–252.

Loizzi, R.F. (1968) Fine structure of the crayfish hepatopancreas. J. Cell Biol. *198:*82a (abstr.).

Loizzi, R.F. (1971) Interpretation of crayfish hepatopancreatic function based on fine structural anatomy of epithelial cell lines and muscle networks. Z. Zellforsch. Mikrosk. Anat. *113:*420–440.

Lovett, D.L., and D.L. Felder (1990) Ontogenetic changes in enzyme distribution in the developmental stages of *Penaeus setiferus* (Crustacea, Decapoda, Penaeidae). Biol. Bull. *178:*160–174.

Lynn, J.W., and W.H. Clark (1983a) A morphological examination of sperm–egg interaction in the freshwater prawn *Macrobrachium rosenbergii.* Biol. Bull. *164:*446–458.

Lynn, J.W., and W.H. Clark (1983b) The fine structure of the mature sperm of the freshwater prawn, *Macrobrachium rosenbergii.* Biol. Bull. *164:*459–470.

Mantel, L.H., and L.L. Farmer (1983) Osmotic and ionic regulation. In D.E. Bliss and L.H. Mantel (eds.): The Biology of Crustacea. Vol. 5, pp. 53–161.

Martin, G.G., and B.L. Graves (1985) Fine structure and classification of shrimp hemocytes. J. Morphol. *185:*339–348.

Martin, G.G., J.E. Hose, and J.J. Kim (1987) Structure of hematopoietic nodules in the ridgeback prawn *Sicyonia ingentis:* Light and electron microscopic observations. J. Morphol. *192:*193–204.

Maynard, D.M. (1960) Circulation and heart function. In T.H. Waterman (ed.): The Physiology of Crustacea. New York: Academic Press, vol. 1, pp. 161–226.

Maynard, D.M., and M.R. Dando (1974) On the structure of the stomatogastric neuromuscular system in *Callinectes sapidus, Homarus americanus* and *Panulirus argus* (Decapoda Crustacea). Phil. Trans. R. Soc. Lond. *268:*161–220.

McLaughlin, P.A. (1980) Comparative Morphology of Recent Crustacea. San Francisco: Freeman.

McLaughlin, P.A. (1983) Internal anatomy. In D.L. Bliss and L. Mantel (eds.): The Biology of Crustacea. Vol. 5, pp. 1–52.

Miyawaki, M. and N. Sasaki (1961) A preliminary report on uptake by the hepatopancreas of Ca45 by the crayfish, *Procambarus clarkii.* Kumamoto J. Sci. *6:*1–11.

Mocquard, F. (1883) Estomac des crustaceans podophthalmaires. Ann. Sci. Nat. *16:*1–311.

Mykles, D.L. (1977) The ultrastructure of the posterior midgut caecum of *Pachygrapsus crassipes* (Decapoda, Brachyura) adapted to low salinity. Tissue Cell *9:*681–691.

Oshel, P.E. (1985) Paraffin carving: A preparative technique for scanning electron microscopy of crustaceans. J. Crust. Biol. *5:*327–329.

Pearson, J. (1908) Cancer. Liverpool Mar. Biol. Comm. Mem., vol. 6.

Peterson, D.R., and R.F. Loizzi (1974) Ultrastructure of the crayfish kidney—coelomosac, labyrinth, nephridial canal. J. Morphol. *141:*241–263.

Pike, R.B. (1947) Galathea. Liverpool Mar. Biol. Comm. Mem. *34:*1–138.

Ravindranath, M.H. (1980) Haemocytes in haemolymph coagulation of arthropods. Biol. Rev. *55:*139–170.

Riegel, J.A. (1972) Comparative Physiology of Renal Excretion. Edinburgh: Oliver and Boyd.

Schmidt-Nielsen, B., K.H. Gertz, and L.E. Davis (1968) Excretion and ultrastructure of the antennal gland of the fiddler crab *Uca mordax.* J. Morphol. *125:*473–496.

Schram, R.R. (1986) Crustacea. New York, Oxford: Oxford University Press.

Shigekawa, K., and W.H. Clark, Jr. (1986) Spermiogenesis in the marine shrimp, *Sicyonia ingentis.* Dev. Growth Diff. *28:*95–112.

Smith, R.I. (1978) The midgut caeca and the limits of the hindgut of Brachyura: A clarification. Crustaceana *35:*195–205.

Steinacker, A. (1978) The anatomy of the decapod crustacean auxiliary heart. Biol. Bull. *154:*497–507.

Stutman, L.J., and M. Dolliver (1968) Mechanism of coagulation in *Gecarcinus lateralis.* Am. Zool. *8:*481–489.

Talbot, P. (1981a) The ovary of the lobster, *Homarus americanus.* I. Architecture of the mature ovary. J. Ultrastr. Res. *76:*235–248.

Talbot, P. (1981b) The ovary of the lobster, *Homarus americanus.* II. Structure of the mature follicle and origin of the chorion. J. Ultrastr. Res. *76:*249–262.

Talbot, P., W.H. Clark, Jr., and A.L. Lawrence (1972) Fine structure of the midgut epithelium of the developing brown shrimp, *Penaeus aztecus.* J. Morphol. *138:*467–486.

Talbot, P., and P. Chanmanon (1980) Morphological features of the acrosome reaction of lobster *(Homarus)* sperm and the role of the reaction in generating forward sperm movement. J. Ultrastr. Res. *70:*287–297.

Talbot, P., and R.G. Summers (1978) The structure of sperm from *Panulirus,* the spiny lobster, with special regard to the acrosome. J. Ultrastr. Res. *64:*341–351.

Towle, D.W., and W.T. Kays (1986) Basolateral localization of Na^+K-ATPase in gill epithelium of two osmoregulating crabs, *Callinectes sapidus* and *Carcinus maenas.* J. Exp. Zool. *239:*311–318.

Tyson, G.E. (1968) The fine structure of the maxillary gland of the brine shrimp *Artemia salina:* The end sac. Z. Zellforsch.

Mikrosk. Anat. *86:*129–138.

Vacca, L.L., and M. Fingerman (1983) The roles of hemocytes in tanning during the molt cycle: A histochemical study of the fiddler crab, *Uca pugilator*. Biol. Bull. *165:*759–777.

Vonk, H.J. (1960) Digestion and metabolism. In T.H. Waterman (ed.): The Physiology of Crustacea, vol. 1. Metabolism and Growth. New York: Academic Press, pp. 291–316.

Warner, G.F. (1977) The Biology of Crabs. New York: Van Nostrand Reinhold.

Waterman, T.H. (1960) The Physiology of Crustacea, vols. 1, 2. New York: Academic Press.

Williams, M.C. (1977) Conversion of lamellar body membranes to tubular myelin in alveoli of fetal rat lung. J. Cell Biol. *72:*260.

Young, J.H. (1959) Morphology of the white shrimp *Penaeus setiferus* (Linnaeus 1758). Fish. Bull. *145:*1–168.